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THE GENUS *THURIDILLA* (OPISTHOBRANCHIA: ELYSIIDAE) FROM THE TROPICAL INDO-PACIFIC, WITH A REVISION OF THE PHYLOGENY AND SYSTEMATICS OF THE ELYSIIDAE

By

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ABSTRACT: This paper reviews the systematics and phylogeny of the sacoglossan genus *Thuridilla* from the Indo-Pacific tropics. The anatomy of seven previously determined species is described. Nine new species are named and described anatomically. These are: *T. carlsoni* sp. nov., *T. kathae* sp. nov., *T. flavomaculata* sp. nov., *T. hoffae* sp. nov., *T. albopustulosa* sp. nov., *T. undula* sp. nov., *T. neona* sp. nov., *T. indopacifica* sp. nov. and *T. multimarginata* sp. nov.

Phylogenetic analysis of the Elysiidae, presented here, demonstrates the monophyly of *Thuridilla* and its relationship to its sister taxon *Placobranchus*. Continued usage of the genera *Elysiella*, *Plattyclaya*, *Tridachia* and *Tridachiella* renders *Elysia* paraphyletic. For this reason the four genera are united with *Elysia* to preserve monophyly. *Bosellia* is also placed within the Elysiidae, as it possesses several synapomorphies with other members of the clade.

Anatomical data from these species, in addition to all other described members of the genus, were used to construct a phylogeny of *Thuridilla*.

Examination of biogeographical relationships of *Thuridilla* indicates that vicariance patterns of Indo-Pacific sister species have been largely masked by subsequent dispersal.

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INTRODUCTION

The genus *Thuridilla* Bergh, 1872, has recently been recognized as being distinct from *Elysia* Risso, 1818 (Jensen, 1992). The anatomy of several species was described and thirteen species were regarded as members of this genus by Jensen.

Species of *Thuridilla* are unlike most other members of the Elysiidae in that they are brightly colored and are found crawling out in the open rather than being cryptic and found in association with their specific algal food. Other derived morphological features differentiate *Thuridilla* from *Elysia*.

Of the thirteen described species now placed in *Thuridilla*, eleven are found in the Indo-Pacific tropics. Of the remaining two species, one is found in the Caribbean, East Atlantic and Mediterranean while the other is restricted to the Mediterranean. Several of the Indo-Pacific species are known only from their original description and the anatomy of only a few species has been described.

During the course of surveying the opisthobranch fauna of several Indo-Pacific localities, 16 species of *Thuridilla* were collected, including 9 undescribed species. In addition, a specimen of *Thuridilla picta* (Verrill, 1901), from the Bahamas, and two specimens of *Thuridilla hopei* (Verany, 1853), from the Strait of Gibraltar were examined. This paper further amplifies the morphology of previously named species and describes the new taxa.

Jensen (1992) described the two portions of the radular ribbon as ascending and descending. In the portion that she refers to as descending the cutting edge of the teeth is actually ascending. Owing to this ambiguity, the two portions are here referred to as dorsal and ventral. The ventral portion corresponds to Jensen's descending limb and the dorsal portion to the ascending limb. The ventral portion contains the older teeth and the dorsal portion the more newly formed ones.

A review of the known morphology of the genus permits a preliminary analysis of the phylogeny of the genus and comparison with other members of the Elysiidae.

SPECIES DESCRIPTIONS

1. **Thuridilla bayeri** (Marcus 1965)

Elysia bayeri Marcus, 1965: 270, figs. 5, 6; Carlson and Hoff, 1978:91, figs. 4, 5b, 6a, b.
Thuridilla bayeri (Marcus) Jensen, 1992: 273, figs. 14e, 15f, 16g–i, 17c, 18c.
Elysia ratna Marcus, 1965: 270, figs. 7, 8; Carlson and Hoff, 1978: 107, figs. 5e, 16d, e, 18.
Thuridilla ratna (Marcus) Jensen, 1992: 270, figs. 14b, 15d, 16a–c, 17a, 18b; Wells and Bryce, 1993: 64, fig. 66.

MATERIAL EXAMINED. — Specimens with coloration more similar to *T. bayeri*: CASIZ 065743, one specimen, dissected, harbor wharf, Madang, Papua New Guinea, 10 m depth, 15 January 1988, T. M. Gosliner. CASIZ 086385, one specimen, barrier reef wnw of Rasch Passage, 4 m depth, 14 June 1992, T. M. Gosliner. CASIZ 072919, one specimen, Daphne's Reef, between Wongat and Sinub Islands, 15 m depth, 1 October, 1986, T. M. Gosliner. CASIZ 071469, one specimen, dissected, Saint Crispin Reef, nw of Port Douglas, Queensland, Australia, 15–20 m depth, 9 December 1984, M. L. Gosliner. CASIZ 087123, one specimen, under rock, Montehage Island, Manado, Sulawesi Indonesia, 3 m depth, 17 May 1990, P. Fiene-Severns. CASIZ 099057, one specimen, radula removed, pinnacle, G. Buoy, Kwajelin Atoll, Marshall Islands, 6 m depth, 5 March 1994, S. Johnson.

Specimens with coloration resembling that described for *T. ratna*: CASIZ 078470, one specimen, dissected, Sapi Island, off Kota Kinabalu, Sabah, Borneo, Malaysia, 16 m depth, 24 July 1991, T. M. Gosliner. CASIZ 072917, one specimen, jetty, Christensen Research Institute, Madang, Papua New Guinea, 13 m depth, 3 October 1986, T. M. Gosliner. CASIZ 078471, Kapas Island, off Marang, s. of Kuala Terengganu, Malaysia, 4 m depth, 28 July 1991, T. M. Gosliner. CASIZ 083866, one specimen, Twin Rocks, sw end of Calumpan Peninsula, w. of Batangas Bay, Luzon Island, Philippines, 10 m depth, 26 February 1992, T. M. Gosliner. CASIZ 086663, two specimens, Maragajong, Flores, Indonesia, under rock, 1 m depth, 27 April, 1992, P. Fiene-Severns. CASIZ 070318, one specimen, Banne de Gorgone, Nosy Bé, Madagascar, 15 April 1989, T. M. Gosliner. CASIZ 071294, one specimen, w. point of Coror Island, wreck of fishing boat, Philippines, 10–13 m depth, 5 June 1988, R. Van Syoc. CASIZ 099058, one specimen, radula removed, reef near M. M. D. C., Palau Koror, 10 m depth, M. T. Ghiselin.

DISTRIBUTION. — Specimens with *T. bayeri* coloration are known from the Maldives (Yonow, 1994), the Marshall Islands (Marcus, 1965; Johnson and Boucher, 1983), Guam (Carlson and Hoff, 1978; Jensen, 1992), ? Fiji (Brodie and Brodie, 1990), Papua New Guinea (present study), Indonesia (present study), Australia (present study). Specimens with coloration resembling *T. ratna* are known from Palau (Marcus, 1965; present study), Guam and Ponape (Carlson and Hoff, 1978), Marshall Islands (Johnson and Boucher, 1983; Scott Johnson, pers. comm.), eastern and Western Australia (Jensen, 1992; present study), Thailand (Jensen, 1992), Philippines (present study), Indonesia (present study), Malaysia (present study), Madagascar (present study).

EXTERNAL MORPHOLOGY. — The living animals (Fig. 1A, B) are 12–20 mm in length. Specimens with coloration typical of *T. bayeri* are dark brown to black with a series of 6–10 cream to yellow longitudinal lines on the head and parapodia. The edge of the parapodia may be lined with an orange to red-orange line (a single specimen from Papua New Guinea), an absence of other pigment giving the impression of a row of black spots (specimens from Guam)

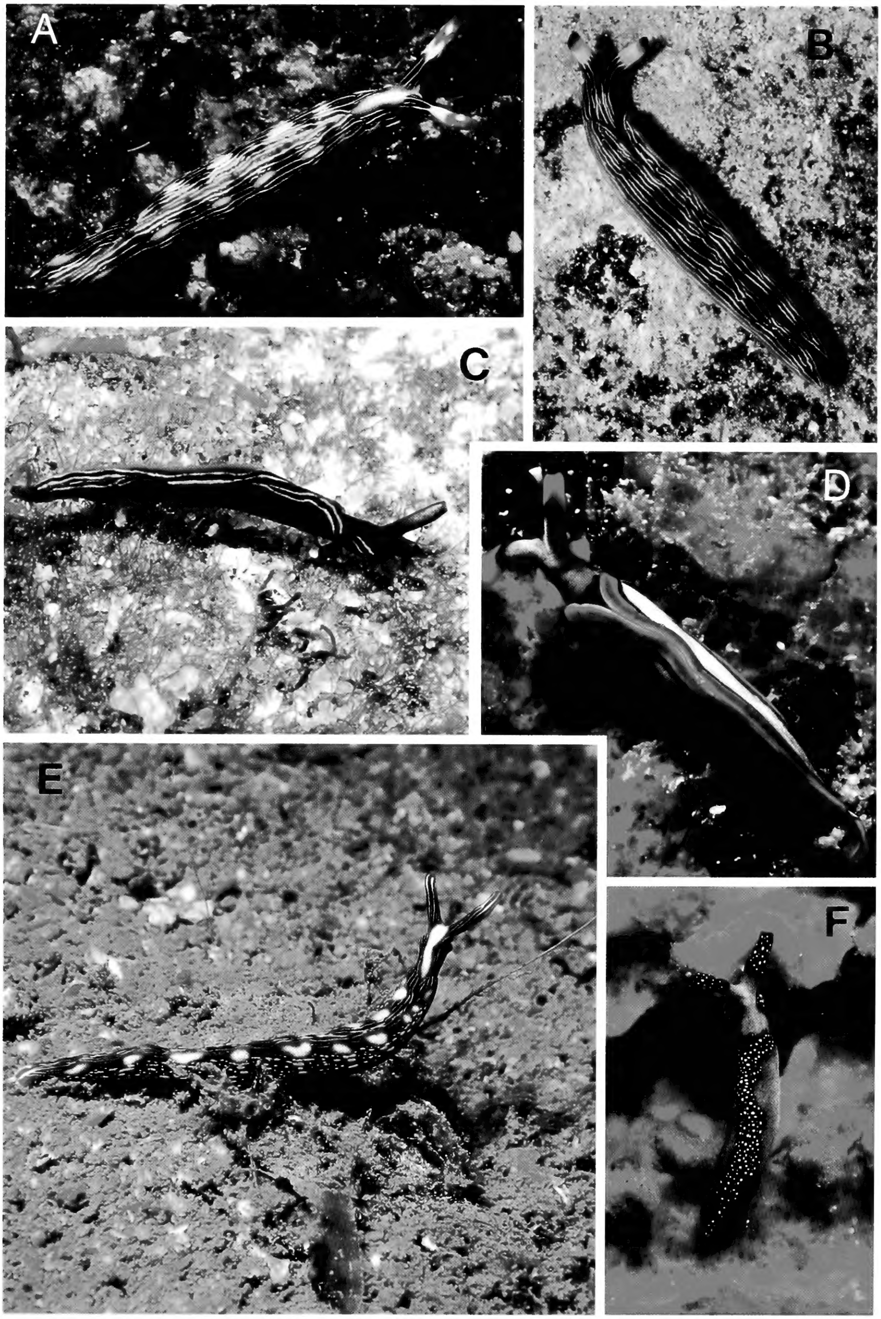

FIGURE 1. Living animals. A. *Thuridilla bayeri* (Marcus, 1965), Madang, Papua New Guinea, 20 mm in length. B. *Thuridilla bayeri* (Marcus, 1965), with coloration typical of *T. ratna* Marcus, 1965, Nosy Bé, Madagascar, 15 mm in length. C. *Thuridilla livida* (Baba, 1955), Sodwana Bay, South Africa, 17 mm in length. D. *Thuridilla lineolata* (Bergh, 1905), Manado, Indonesia, photograph by Pauline Fiene-Severns, 20 mm in length. E. *Thuridilla splendens* (Baba, 1949), Okinawa, photo by Robert F. Bolland, 25 mm in length. F. *Thuridilla moebii* (Bergh, 1888), Sodwana Bay, South Africa, 12 mm in length.

or bluish green patches (specimens from the Marshall Islands). Other specimens lack any additional pigment along the margin of the parapodia. Red-orange pigment may be present at the posterior junction of the parapodia. Six to seven bright blue, ovoid spots are found submarginally along the length of each parapodium. The head may also have a mid-dorsal blue mark or paired spots between the rhinophores. Basally, the rhinophores are the same color as the general body, with cream longitudinal lines. These lines expand and unite into a large transverse white band. This band may continue to the apex of the rhinophores or may be followed by a red band or streaks. A single specimen from the Solomon Islands (Scott Johnson, pers. comm.) has an additional apical black ring distal to the red ring. In specimens from the Marshall Islands, there is considerable variation in the presence of the white and red pigment on the rhinophores. Only white pigment may be present or there may be longitudinal red streaks that merge with the white band. The anterior margin of the foot is red, often with opaque white. Blue spots may also be present on the anterior portion of the foot. In specimens with heavy blue spotting, the inside of the parapodia has a narrow white marginal band, a broad orange band, and a broader black area. Inside the black band is an area of bright blue pigment. The coloration of the inside of the parapodia is not known from specimens with little blue pigment.

In specimens with coloration typical of *T. ratna*, the animal is dark brown with eight to ten white or cream lines along the outer side of the parapodia and on the head. The internal margin of the parapodia is usually orange. The posterior junction of the parapodia may contain some orange pigment. The head is the same color as the parapodia, without any additional pigment. Basally, the rhinophores are the same color as the remainder of the body. In some specimens, the white or cream lines widen distally and form a transverse band. In most specimens, some red or red-orange pigment may be present on the rhinophores. This may be present as a series of red longitudinal lines or a distinct transverse band. An apical transverse black band may also be present on the rhinophores. Its presence is independent of the presence of red pigment. The margin of the anterior end of the foot is red or orange. The inside of the parapodia is usually brownish with scattered turquoise blue pigment. A thin, white marginal band is present and a broader, orange submarginal band may be prominent or absent.

PERICARDIUM AND DORSAL VESSELS. — In specimens with coloration typical of *T. bayeri*, the pericardium is ovoid (Fig. 2A–C). From its sides, are two lateral vessels which bifurcate terminally or remain undivided. From the posterior end of the pericardium are two other blood vessels, that are joined basally. They are bifurcate or slightly more highly branched.

The branching of the dorsal vessels was examined in four specimens with coloration typical of *T. ratna* (Fig. 2D–G). In all cases, there are both lateral and posterior vessels. In one individual, only the left lateral branch was present, but a secondary right branch was situated off the side of the right posterior branch. The lateral branches are undivided or contain bifurcate or more highly branched tips. The posterior vessels have a common origin from the pericardium. They may entirely lack branches or have a few secondary branches.

BUCCAL MASS AND RADULA. — The buccal mass (Fig. 3A) contains a round pharyngeal pouch and relatively larger, more muscular pharyngeal portion. There is no morphological difference between specimens of different color patterns. In two specimens with coloration typical of *T. bayeri*, the radula contains 24–26 teeth. There are 7–8 teeth in the dorsal portion of the radula, 7–8 in the ventral portion and 9 arranged in a spirally coiled fashion. No loose teeth were contained in the ascus. Each tooth (Fig. 4) is elongate and arched. There are 17–18 coarse denticles on either side of the tooth. The denticles continue as faint striae on the dorsal surface of the teeth.

The radula of two specimens with coloration typical of *T. ratna* consisted of 26–27 teeth (8–9 in the ventral limb, 8–9 in the dorsal limb and 9 to more than 10 loose teeth in the ascus). The teeth (Fig. 5) are triangular with the serrated portion longer than the basal one. The cutting margin bears 16–18 coarse denticles per side of the tooth.

REPRODUCTIVE SYSTEM (Fig. 3B–D). — The reproductive morphology is complex and appears complicated, due to the diffuse distribution of the ovotestis, prostatic cells and al-

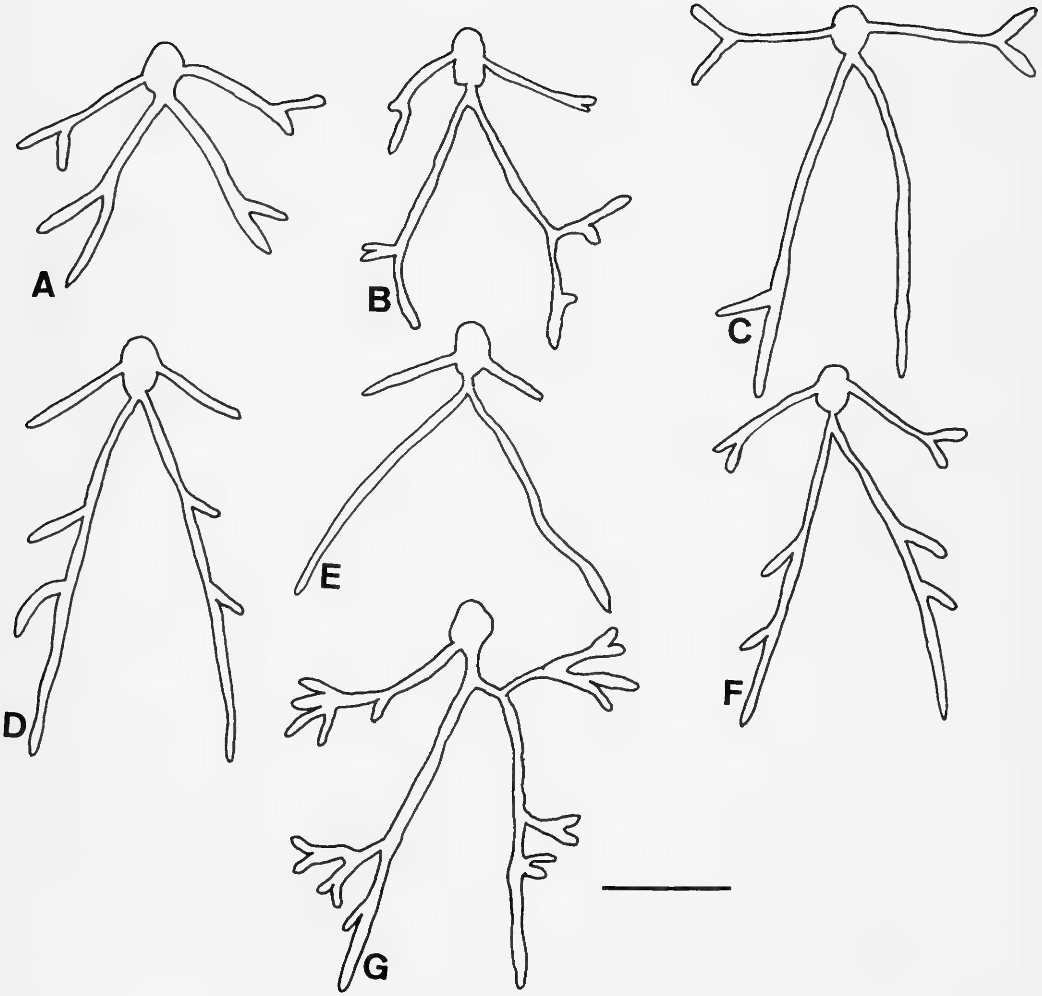

FIGURE 2. *Thuridilla bayeri* (Marcus, 1965). A–C. Variation in branching of pericardial vessels in specimens with coloration typical of *T. bayeri*. D–G. Variation in branching of pericardial vessels is specimens with coloration of *T. ratna*, *scale* = 4.0 mm.

bumen gland throughout the parapodia. The system is basically triaulic. The ovotestis contains lobate acini. They connect via a pair of elongate hermaphroditic ducts. These ducts join immediately anterior to the round, short stalked ampulla. The prostate consists of approximately six elongate finger-shaped glands. The albumen gland consists of numerous digitiform ducts with lateral glandular bodies. The prostate and albumen glands join together into a pair of ducts that join the female gland mass immediately anterior to the junction of the hermaphroditic ducts. The female gland mass consists of several distinct lobes, the largest forms the bulk of the mucous gland. Near the posterior end of the mass a spherical receptaculum seminis joins the gland mass via a thin, moderately long duct. Near the anterior end of the gland

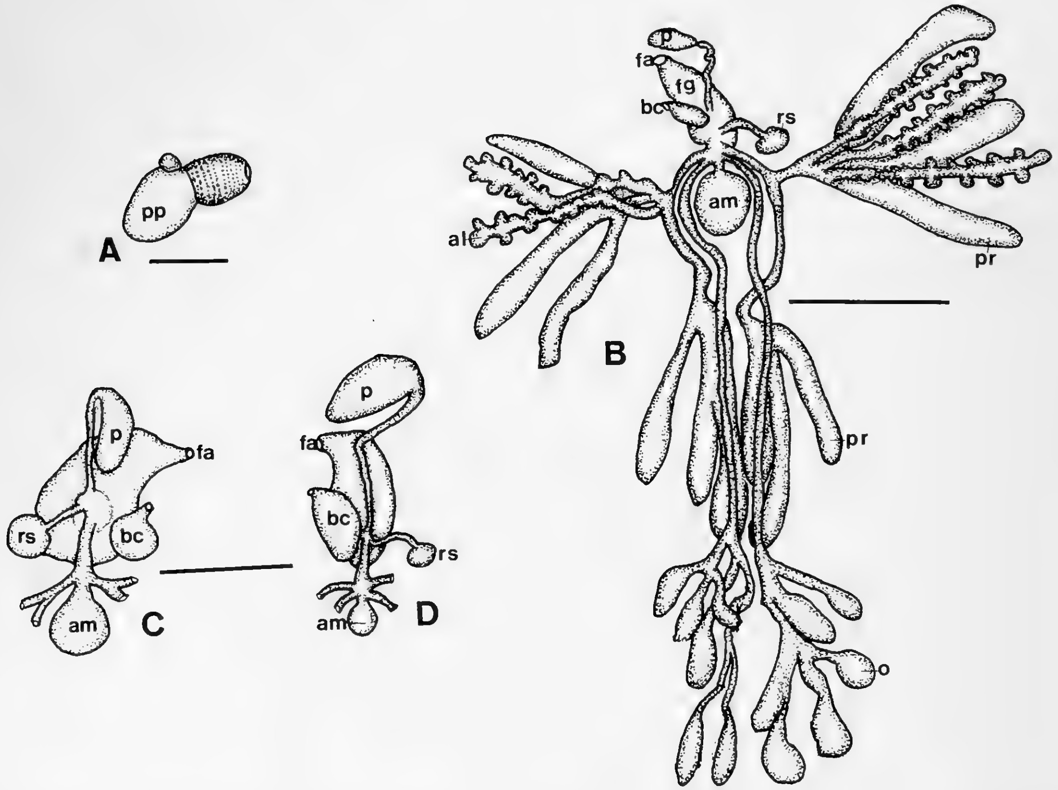

FIGURE 3. *Thuridilla bayeri* (Marcus, 1965). A. Buccal mass, pp = pharyngeal pouch, scale = 0.25 mm. B. Entire reproductive system: al = albumen gland, am = ampulla, bc = bursa copulatrix, fa =female aperture, fg = female gland mass, o = ovotestis, p = penis, pr = prostate glands, rs = receptaculum seminis, scale = 1.0 mm. C. Distal reproductive organs of specimen with color typical of *T. bayeri*, Australia. D. Distal reproductive organs of specimen with color typical of *T. ratna*. C., D., lettering same as in B., scale = 1.0 mm.

mass, the thin vas deferens emerges and joins the simple unarmed penis. A saccate bursa copulatrix emerges to the outside of the body wall near the female gonopore. The female gonopore exits into the lateral ciliated groove, adjacent to the anus. The penis exits below the right rhinophore. The reproductive morphology was examined in three specimens with coloration typical of *T. bayeri* and two with coloration characteristic of *T. ratna*.

DISCUSSION. — *Thuridilla bayeri* is similar in appearance and appears closely related to two other species, *T. ratna* and *T. splendens*. All three species are similar in having a uniformly dark blackish body with numerous longitudinal yellow or white lines. In *T. bayeri* and *T. splendens*, there are bluish markings and spots on the head and parapodia. In the latter species, there are yellow spots on the surface of the parapodia that are absent in *T. bayeri*.

Based on the similarity of color pattern, Brodie and Brodie (1990) considered *T. bayeri* and *T. ratna* as synonymous. Others (Marcus, 1965; Carlson and Hoff, 1978; Jensen, 1992) have considered them to be distinct species. Carlson and Hoff, and Jensen emphasized the distinctness of the color pattern of *T. bayeri*, blue spots along the parapodia and black spots along the parapodial margin. Carlson and Hoff (1978) also noted differences in the coloration of the inner surface of the parapodia in specimens from Guam. In *T. bayeri*, the margin of the inner portion of the parapodia is white, followed by a red-orange band, an area of black, followed by a large area of steel blue. In *T. ratna*, the submarginal red-orange band is usually absent and the inside of the parapodia is brownish, with scattered white and blue mark-

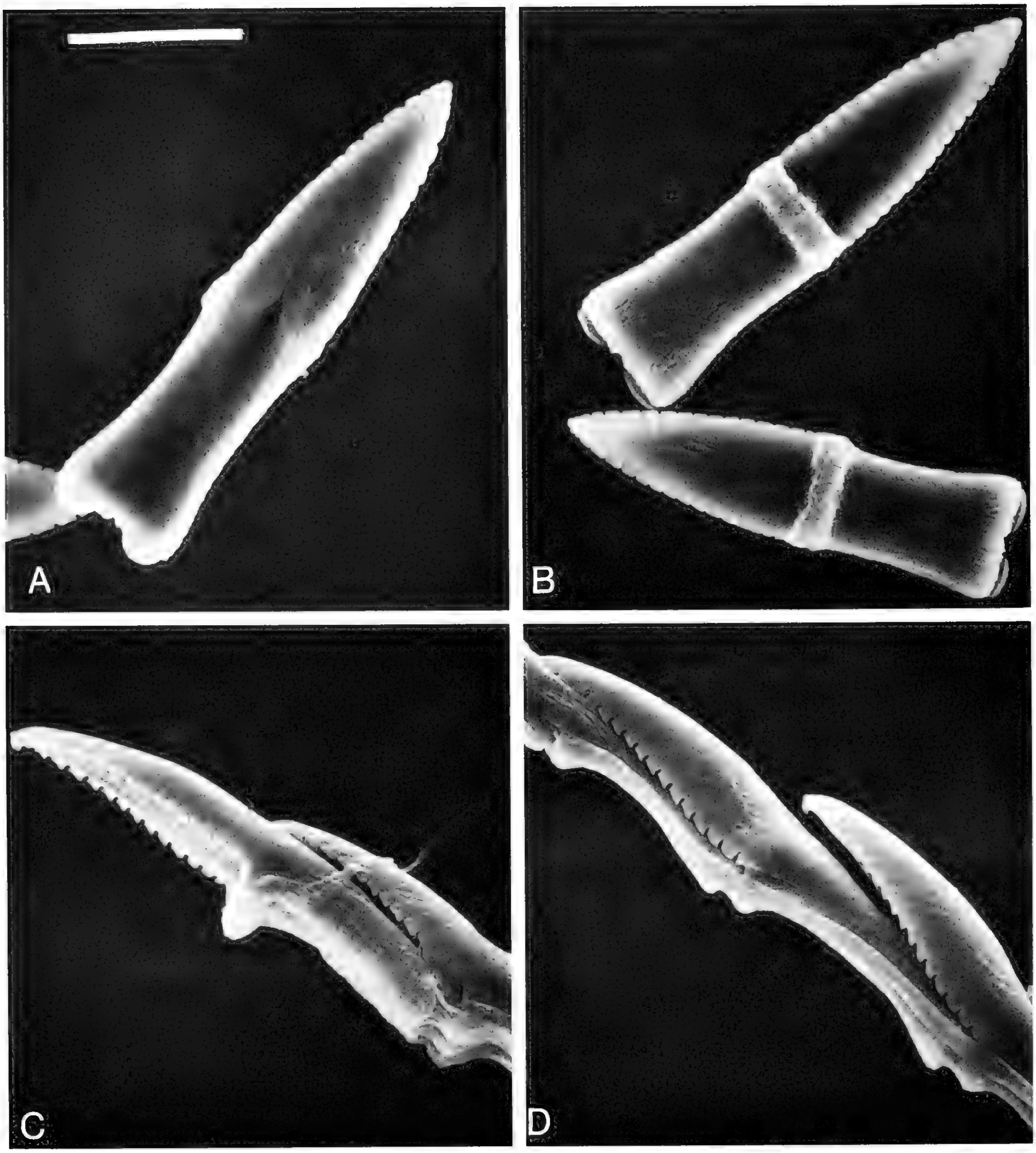

FIGURE 4. Radular teeth of specimen with color typical of *T. bayeri*. A. Dorsal view of tooth from specimen from Kwajelin, CASIZ 099057, scale = 15 μm. B. Ventral view of teeth from same radula, scale = 15 μm. C. Lateral view of tooth from specimen from Australia, CASIZ 071469, scale = 15 μm. D. Lateral view of teeth from specimen from Papua New Guinea, CASIZ 065743, scale = 15 μm.

ings. Two specimens with external coloration matching that of *T. ratna*, from Guam and Malaysia, have a prominent red submarginal band and some bluish pigment in the pericardial region. This pigment appears to be somewhat intermediate between the two species. Several specimens examined in this study further blur the distinctness of *T. bayeri*. Most specimens of *T. bayeri* have blue pigment on the dorsal surface of the head between the rhinophores and additional blue on the anterior portion of the foot. One specimen from Papua New

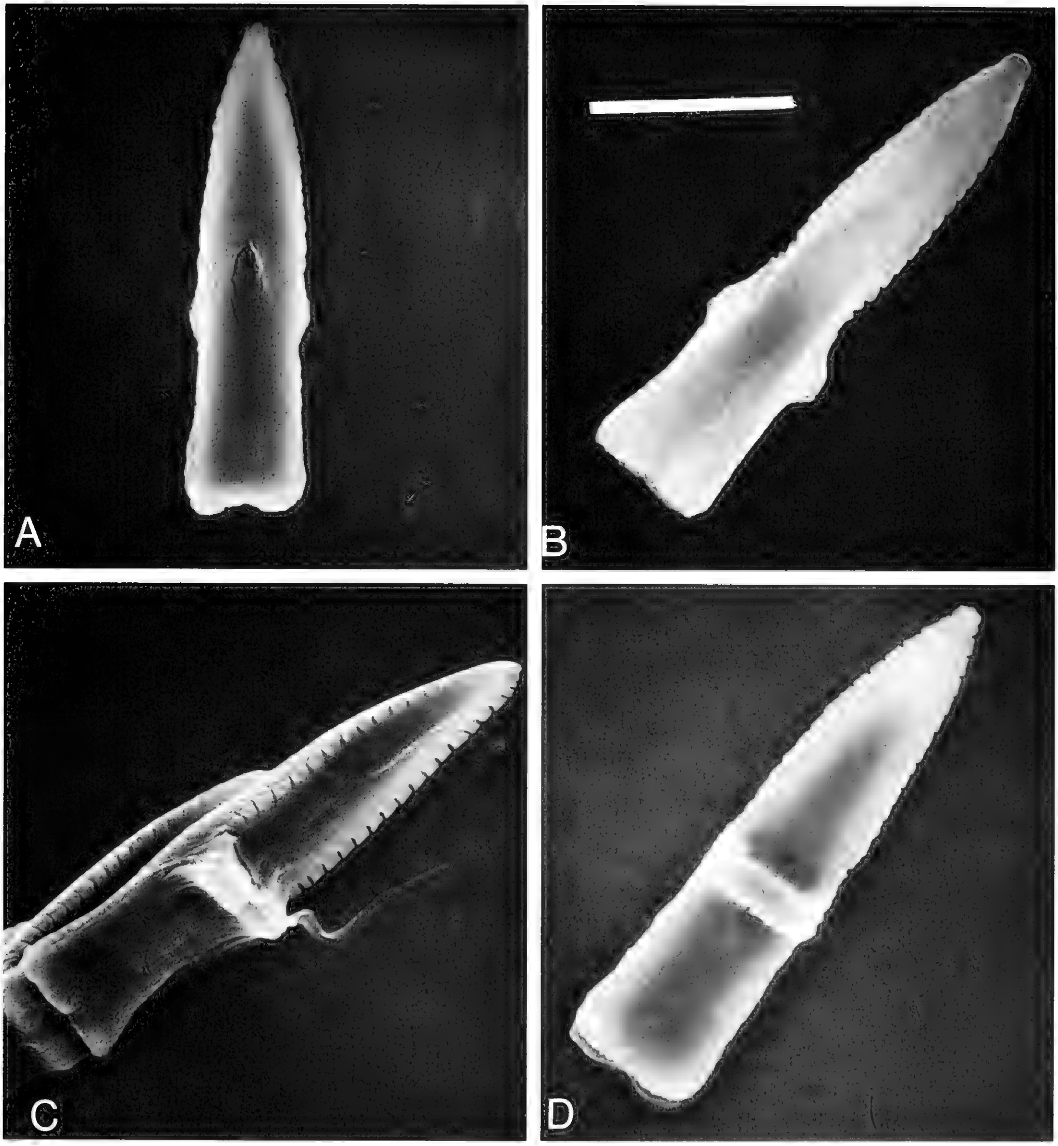

FIGURE 5. Radular teeth of specimen with color typical of *T. ratna*. A, B. Dorsal view of tooth of specimen from Palau, CASIZ 099058. A. scale = 15 μm. B. scale = 7.5 μm. C. Ventral view of tooth of specimen from Borneo, CASIZ 078470, scale = 15 μm. D. Ventral view of tooth of specimen from Palau, CASIZ 099058, scale = 10 μm.

Guinea (CASIZ 072919) examined had faint blue markings on the parapodia and head, but lacked any trace of blue on the foot. Another specimen from Australia (CASIZ 071469) and the specimen from the Maldives illustrated by Yonow (1994), had faint blue lines on the parapodia, but lacked any trace of blue on the head or foot. One specimen having no trace of blue markings has been found in the Indian Ocean (Yonow, 1994). Only a single specimen having coloration similar to *T. ratna* has been found from the western Indian Ocean. *Thuridilla* *ratna* is considered uncommon in Western Australia (Wells and Bryce, 1993) and, together with Jensen's (1992) record from Thailand, represents the only other record of this color form from the Indian Ocean.

Internally, there is little difference between *Thuridilla bayeri*, *T. ratna* and *T. splendens*. All three have paired lateral vessels from the pericardium and posterior vessels that originate from a common junction with the pericardium. There are fewer lateral branches in most specimens with the color pattern of *T. bayeri*, though there is considerable overlap in branching pattern with specimens typical of *T. ratna* and *T. splendens*. Jensen (1992) indicated that there are slight differences in the size of the pharyngeal pouch and shape of the radular teeth between *T. bayeri* and *T. ratna*. No consistent differences in the relative proportions of the muscular buccal mass and pharyngeal pouch and the shape and size of the radular teeth could be determined in the present material, with one exception. The pharyngeal pouch of *T. splendens* is slightly larger proportionately than the pouch of *T. bayeri* and *T. ratna*. The configuration of the reproductive system, including the shape of the bursa copulatrix and penial papilla, is virtually identical in the specimens typical of *T. bayeri*, *T. ratna* and *T. splendens* examined in this study.

Color photographs of more than 50 specimens of *Thuridilla bayeri* and *T. ratna* from a broad geographical area were compared in detail. No consistent difference in pattern could be discerned. The fact that some specimens had faint blue markings on the parapodia and entirely lacked blue markings on the head and foot, suggests that they are intermediate in coloration between that described for the two species. No consistent anatomical differences could be found in branching of the dorsal vessels, morphology of the buccal mass, radula or reproductive system that could be correlated with differences in coloration. All of these data strongly suggest that the described differences between *T. bayeri* and *T. ratna* are simply variation within a single species that is extremely variable in its coloration. Johnson and Boucher (1983) noted that the egg capsule size of *T. bayeri* and *T. ratna* was somewhat different. Possible developmental differences of the two color forms require further investigation. On this basis, *Thuridilla ratna* is regarded as a junior synonym of *T. bayeri*. Both species were described in the same paper (Marcus, 1965), but *T. bayeri* appears first in the text and is, therefore, regarded as the senior synonym.

As noted above, specimens of *Thuridilla splendens* are similar in coloration and internal anatomy to *T. bayeri*. However, specimens of *T. splendens* are consistently different in that they have yellow spots on the sides of the parapodia and foot which are absent in all variants of *T. bayeri*. In addition, the pharyngeal pouch is somewhat proportionately larger in *T. splendens*. On these bases, *T. splendens* is regarded as distinct from *T. bayeri*.

2. **Thuridilla lineolata** (Bergh, 1905)

Elysia? lineolata Bergh, 1905: 85, pl. 3, fig. 10, pl. 13, figs. 25, 26.
Thuridilla lineolata (Bergh) Jensen, 1992: 277.

MATERIAL EXAMINED. — CASIZ 070285, one specimen, Manado, Sulawesi, Indonesia, 0.5 m depth, 21 May 1989, Pauline Fiene-Severns. CASIZ 099059, two specimens, one dissected, Bunaken Island, Manado, Sulawesi, Indonesia, 3 m depth, 20 May 1990, Pauline Fiene-Severns.

DISTRIBUTION. — This species is known only from Indonesia (Bergh, 1905; present study).

EXTERNAL MORPHOLOGY. — The living animals (Fig. 1D) are light blue. The edge of the parapodia is lined with a band of bright orange. Immediately inside this band is a narrower black band. Two black lines and an orange band are present at the base of the parapodia, as well. There is a narrow black band surrounding the head, near the level of the eyes. A v-shaped black band is near the middle of each rhinophore and the rhinophores are tipped with orange. Orange pigment is present on the anterior margin of the foot.

PERICARDIUM AND DORSAL VESSELS (Fig. 6A). — There are paired lateral and posterior vessels. These vessels are thin compared to most other species. The anterior vessels are bifurcate near their tips. The more posterior vessels have separate origins from the pericardium and give rise to one or two short branches.

BUCCAL MASS AND RADULA. — The buccal mass (Fig. 6B, C) contains a large pharyngeal

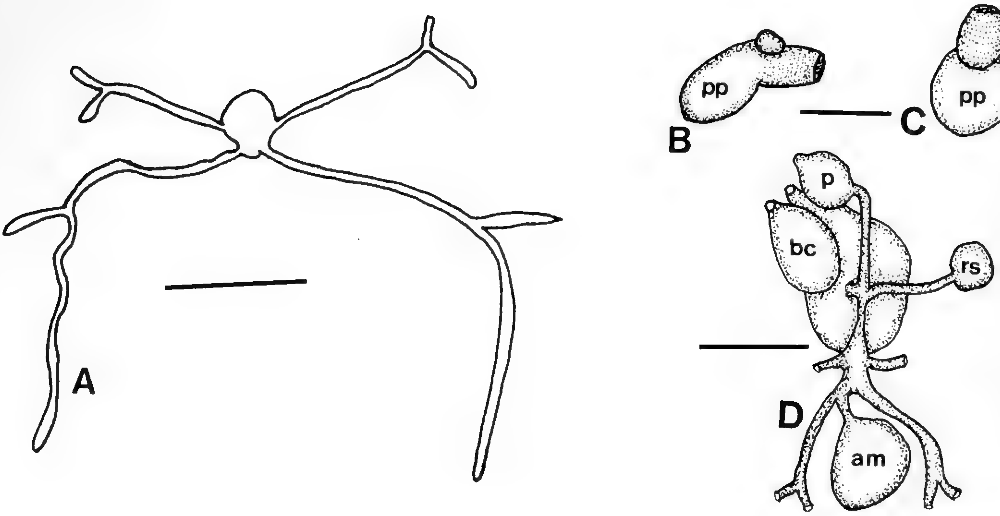

FIGURE 6. *Thuridilla lineolata* (Bergh, 1905). A. Branching of pericardial vessels, scale = 4.0 mm. B. Lateral view of buccal mass. C. Ventral view of buccal mass. B., C. pp = pharyngeal pouch, scale = 0.25 mm. D. Ventral view of distal reproductive organs: am = ampulla, bc = bursa copulatrix, p = penis, rs = receptaculum seminis, scale = 0.5 mm.

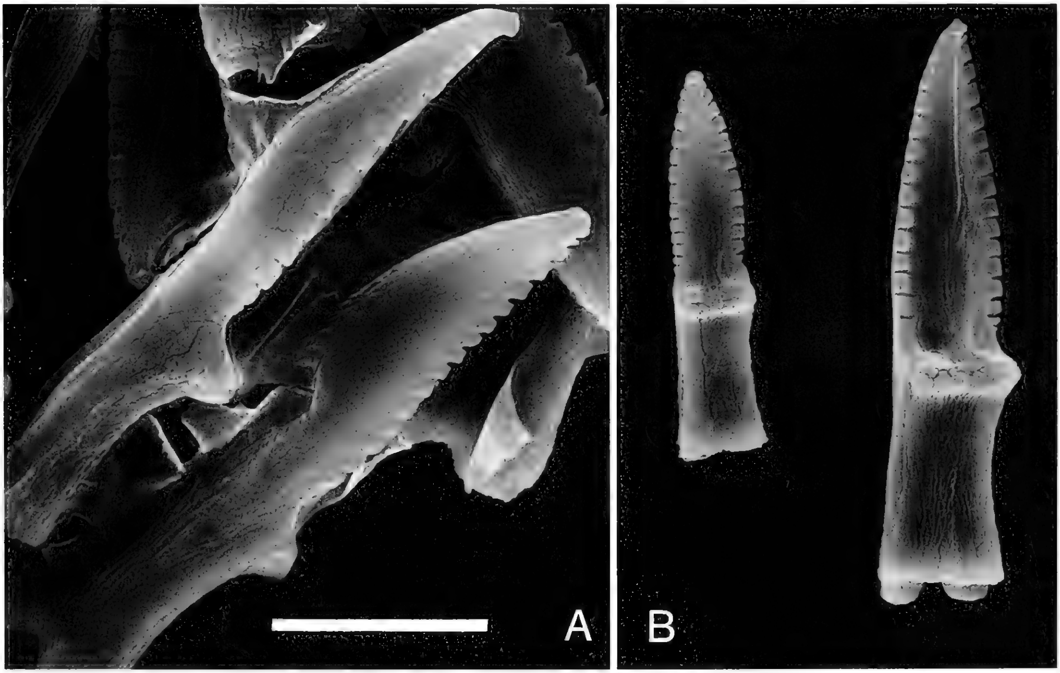

FIGURE 7. *Thuridilla lineolata* (Bergh, 1905). Radular teeth. A. Lateral view of specimen from Indonesia, CASIZ 099059, scale = 10 μm. B. Ventral view of same, scale = 15 μm.

pouch and a smaller muscular portion of the buccal mass. The radula contains 17 teeth (8 ventral teeth and 9 dorsal) with another 17 teeth in the ascus. The teeth (Fig. 7) bear 12–16 denticles.

REPRODUCTIVE SYSTEM (Fig. 6D). — The ovotestis, prostate and albumen glands are arranged as in *T. bayeri*. The ampulla enters the female gland mass anterior of the right hermaphroditic duct near its junction with the left hermaphroditic duct. A small spherical receptaculum seminis joins the large female gland mass by means of thin, elongate duct. The bursa copulatrix is thin and pyriform and exits near the female gonopore. The vas deferens branches from the female gland mass and enters the small, conical, unarmed penial papilla.

DISCUSSION. — This species has not been recorded since its original description (Bergh, 1905). Bergh figured this species in a color plate. The pattern of coloration he illustrated is identical to that found in the present material. There is no doubt that the present material is conspecific with Bergh's.

Eliot (1906: 689), in reviewing the status of Kelaart's Ceylonese nudibranchs, stated that *Elysia caerulea* Kelaart, 1858 "can hardly be anything but *Elysia lineolata* of Bergh, which has a similarly gorgeous coloration, though there are some differences in detail. For instance, in Kelaart's animal the rhinophores have not red tips, but a red ring below a black tip."

While Eliot was fairly certain that *T. lineolata* should be regarded as a junior synonym of *T. caerulea*, the differences in coloration between the two, though minor, appear consistent.

Another animal depicted by Wells and Bryce (1993: fig. 75) as *T.* sp. has similar coloration, but with more black pigment relative to orange and blue. It also appears to be distinct from either *T. lineolata* or *T. caerulea*. Pending detailed study of specimens from western Australia and Sri Lanka, it is preferable to retain *T. lineolata* as distinct from *T. caerulea*.

Morphologically, *T. lineolata* appears to be most closely related to *T. undula* sp. nov. The two differ in color, with *T. undula* having an undulating, orange parapodial marginal band, while the orange marginal band of *T. lineolata* is straight.

In *T. lineolata*, the lateral pericardial vessels are much less branched than in *T. undula* and the posterior vessels join the pericardium separately rather than from a common connection.

3. **Thuridilla livida** (Baba, 1955)

Elysia livida Baba, 1955: 12, fig. 13, pl. 4, fig. 10; Carlson and Hoff, 1978: 100, figs. 10c, d, 13; Gosliner, 1987: 53, fig. 44.

Thuridilla livida (Baba), Jensen, 1992: 277.

MATERIAL EXAMINED. — SAM A35280, one specimen, Mbibi, Sodwana Bay National Park, Natal, South Africa, 1 m depth, 6 May 1982, T. M. Gosliner. SAM A35271, one specimen, Adlams Reef, Sodwana Bay National Park, Natal, South Africa, 1 m depth, 7 May 1982, T. M. Gosliner. SAM A35272, one specimen, dissected, Mbibi, 2 m depth, 10 May 1982, T. M. Gosliner. CASIZ 074211, two specimens, Passe Femme, Aldabra Atoll, Seychelles, 2 m depth, 23 March 1986, T. M. Gosliner. CASIZ 070022, one specimen, radula removed, 1 km wnw of Onna Village, Horseshoe Cliffs, 3 m depth, 16 July 1989, R. F. Bolland.

DISTRIBUTION. — Enewetak, Marshall Islands (Johnson and Boucher, 1983), Okinawa (present study), Japan (Baba, 1955), Guam (Carlson and Hoff, 1978), Aldabra Atoll (present study), South Africa (Gosliner, 1987).

EXTERNAL MORPHOLOGY. — The living animals (Fig. 1C) are dark brown to black. The parapodia are lined with a series of longitudinal lines. The innermost line is black followed by lines of orange, black and bright blue. The head and rhinophores are black. The apical half of the rhinophores has varying amounts of opaque white pigment. Black, orange and blue lines are also present along the anterior margin of the foot.

PERICARDIUM AND DORSAL VESSELS (Fig. 8A–C). — The branching of the vessels was examined in three specimens. In two animals, there is only a single pair of posterior vessels with separate origins from the pericardium. In the third specimen, there is a second pair of lateral vessels. The lateral vessels are bifurcate. The posterior vessels may be unbranched or may have a few short branches.

BUCCAL MASS AND RADULA. — The pharyngeal pouch (Fig. 8D) is slightly larger than the muscular portion of the buccal mass. The radula consists of 28 teeth (8 in a coil, 13 in the ventral limb and 7 in the dorsal limb). The

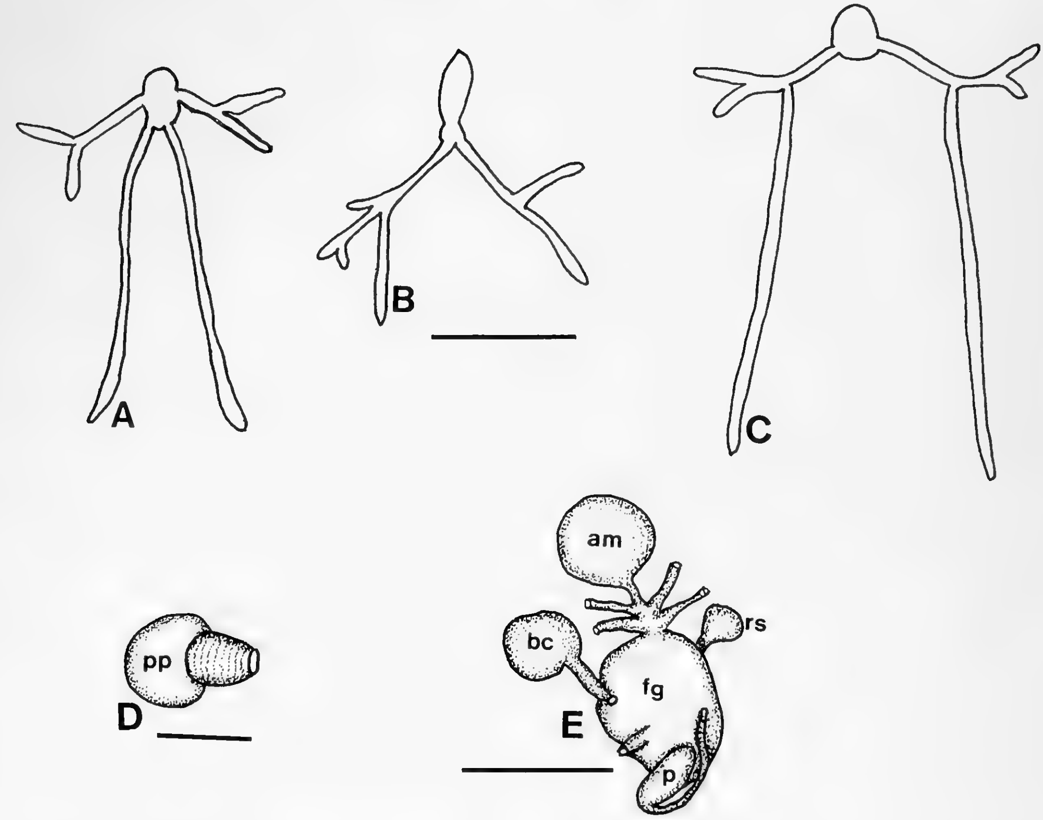

FIGURE 8. *Thuridilla livida* (Baba, 1955). A–C. Branching of pericardial vessels, scale = 4.0 mm. D. Ventral view of buccal mass, pp = pharyngeal pouch, scale = 0.25 mm. E. Distal reproductive organs: am = ampulla, bc = bursa copulatrix, fg = female gland mass, p = penis, rs = receptaculum seminis, scale = 1.0 mm.

teeth (Fig. 9) are triangular with a short base and longer cutting edge. The cutting edge contains approximately 15 coarse denticles per side. The denticles continue as distinct striations on to the dorsal surface of the teeth.

REPRODUCTIVE SYSTEM (Fig. 8E). — The diffuse ovotestis are identical to those described for *T. bayeri*. The ampulla is large and spherical. It enters the female gland mass immediately posterior to the ducts from the ovotestis, albumen and prostate glands. The female gland mass is large and irregular in shape. A spherical receptaculum seminis enters the gland mass via a short duct. The spherical bursa copulatrix exits from its own gonopore immediately posterior to the female gonopore, by means of an elongate duct. The vas deferens leads to the simple, ovoid, unarmed penial papilla.

DISCUSSION. — In their discussion of *Thuridilla livida*, Carlson and Hoff (1978) described the existence of a distinct species similar in coloration to *T. livida* and noted radular differences between the two. *Thuridilla livida* is most closely related to this species described here as *T. hoffae* sp. nov. and more distantly to other species with orange and blue parapodial markings. In addition to having this color pattern, all members of this species complex have prominent striations on the teeth that extend from the denticles to the dorsal surface of the tooth. The differences between *T. livida* and *T. hoffae* in coloration described by Carlson and Hoff are consistent in the present material. Principally, *T. livida* has a distinct narrow iridescent blue submarginal line while *T. hoffae* has a se-

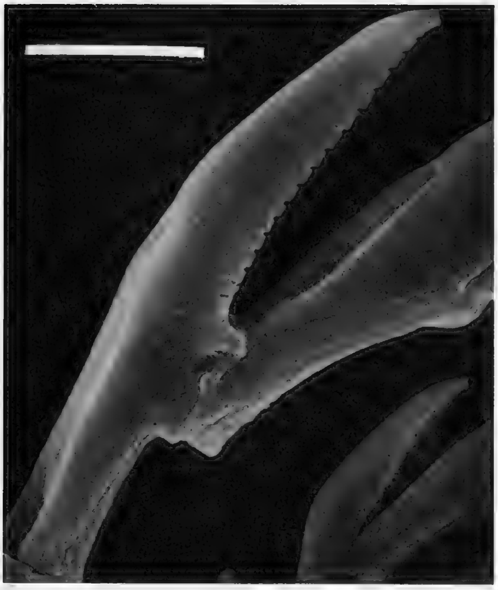

FIGURE 9. *Thuridilla livida* (Baba, 1955). Lateral view of radular teeth of specimen from South Africa, SAM A35272, scale = 10 μm.

ries of iridescent blue to blue green patches. *T. livida* has orange and blue lines on the anterior margin of the foot that are absent in *T. hoffae*. The general body color is darker in *T. hoffae* than in *T. livida*.

Carlson and Hoff stated that the radular teeth of *T. livida* are wider and more finely denticulate than those of *T. hoffae*. Those differences are also evident and consistent in the present material.

In addition to the color and radular differences described by Carlson and Hoff, other anatomical features differ between the two species. In *T. livida*, the two posterior vessels enter the pericardium separately, while in *T. hoffae* they have a common junction. The pharyngeal pouch of *T. livida* is proportionately smaller than that of *T. hoffae*, while the penial papilla is wider and less acute than that of *T. hoffae*.

4. **Thuridilla moebii** (Bergh, 1888)

Plakobranchus? moebii Bergh, 1888: 759, pl. 78, fig. 19.
Elysia moebii (Bergh) Gosliner, 1987: 53, fig. 42.
Thuridilla moebii (Bergh) Jensen, 1992: 277; Wells and Bryce, 1993: 67, fig. 74.

MATERIAL EXAMINED. — SAM A52166, one specimen, dissected, Mbibi, Sodwana Bay National Park, Natal, South Africa, 17 May 1981, T. M. Gosliner.

DISTRIBUTION. — Western Australia (Wells and Bryce, 1993), Mauritius (Bergh, 1888), Reunion Island and South Africa (Gosliner, 1987).

EXTERNAL MORPHOLOGY. — The body is bluish green (Fig. 1F). At the margin of the parapodia is an orange longitudinal band. Below this band is a black band. Both bands are covered with minute opaque white spots. The head is the same color as the rest of the body. The rhinophores and anterior margins of the foot contain the same sequence of orange and black pigment with white spotting as the parapodia.

PERICARDIUM AND DORSAL VESSELS. — The branching of the dorsal vessels could not be determined, owing to poor preservation of the single specimen.

BUCCAL MASS AND RADULA. — The pharyngeal pouch (Fig. 10A) is massive relative to the muscular portion. The radula contains 23 teeth (7 in the ascus, 8 in the ventral limb and 8 in the dorsal limb). The teeth (Fig. 11) bear approximately 18 coarse denticles on either side. The basal portion of the tooth is slightly shorter than the cutting portion.

REPRODUCTIVE SYSTEM (Fig. 10B). — The diffuse ovotestis is identical to that described for *T. bayeri*. The ampulla is large and spherical. It enters the female gland mass immediately posterior to the ducts from the ovotestis, albumen and prostate glands. The female gland mass is large and ovoid. The spherical receptaculum seminis enters the gland mass via a short duct. The spherical bursa copulatrix exits from its own gonopore immediately posterior to the female gonopore, by means of an extremely short duct. The short vas deferens leads to the simple, blunt, unarmed penial papilla.

DISCUSSION. — *Thuridilla moebii* is only known from four specimens, one each collected from Mauritius, Reunion Island, South Africa and the Houtman Abrolhos Islands off western Australia. Its color pattern is quite distinctive with a blue to greenish ground color and a burnt orange marginal band with scattered opaque white spots. It is a member of the clade of spe-

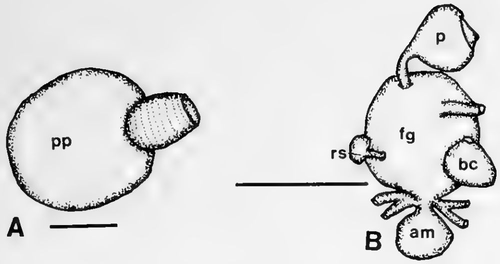

FIGURE 10. *Thuridilla moebii* (Bergh, 1888). A. Ventral view of buccal mass, pp= pharyngeal pouch, scale= 0.11 mm. B. Distal reproductive organs: am= ampulla, bc= bursa copulatrix, fg= female gland mass, p= penis, rs= receptaculum seminis, scale= 1.0 mm.

FIGURE 11. *Thuridilla moebii* (Bergh, 1888). Lateral view of radular tooth of specimen from South Africa, SAM A52166, scale= 15 µm.

cies that has an expanded pharyngeal pouch, and differs markedly from all other members of the clade by its distinct coloration. It differs from all members of the genus in its possession of a short, bulbous penial papilla. Details of the branching of the pericardial vessels remain unknown, owing to the poor preservation of the single specimen available.

5. **Thuridilla splendens** (Baba, 1949)

Elysia splendens Baba, 1949: 36, fig. 28, pl. 10, fig. 32.
Elysia sp. Willan and Coleman, 1984: 4, unnumbered figure.
Thuridilla splendens (Baba) Jensen, 1992: 277.

MATERIAL EXAMINED. — CASIZ 074697, one specimen, dissected, Seragaki Beach, 1.3 km ene of Maeki-zake, Okinawa, Ryukyu Islands, 3 m depth, 31 August 1989, R. F. Bolland. CASIZ 069993, one specimen, 2 km e of Oguma-saki, Okinawa, intertidal, 16 March 1987, R. F. Bolland. CASIZ 099060, two specimens, one specimen with radula removed, Tengan, Okinawa, 3 m depth, 5 March 1994, R. F. Bolland.

DISTRIBUTION. — Japan (Baba, 1949), Okinawa (present study), Guam (Carlson and Hoff, pers. comm.), Australia (Willan and Coleman, 1984 as *Elysia* sp.).

EXTERNAL MORPHOLOGY. — The body (Fig. 1E) is dark brown with a series of complete and interrupted bright yellow lines or series of spots. The margin of the parapodia consists of a red longitudinal band. Below this band is a black band with yellow spots. Below this band is a series of light blue ovoid spots. Often one or two additional series of spots are present below this level. The head has a whitish or blue mark. The rhinophores are black with yellow pigment basally and red apices. The anterior margins of the foot also have red, black with yellow spots, and blue pigment.

PERICARDIUM AND DORSAL VESSELS. — Branching of the vessels was observed in three specimens (Fig. 12A–C). Both lateral and posterior vessels are present. The lateral vessels are simple or bifurcate near their tips. The posterior vessels have a common origin from the pericardium with elongate posterior extensions. These posterior vessels have two undivided branches emanating from the primary vessels.

BUCCAL MASS AND RADULA. — The pharyngeal pouch (Fig. 12D) is larger than the more anterior muscular portion. The radula consists of 20 teeth (9 in the ventral limb, 6 in the dorsal limb and 5 in the ascus). The teeth (Fig. 13) are triangular with the cutting portion being slightly longer than the basal one. There are 14–18 coarse denticles along either side of the cutting margin.

REPRODUCTIVE SYSTEM (Fig. 12E). — The ovotestis, albumen and prostate glands are diffusely arranged as described for *T. bayeri*. The ampulla is spherical and joins with the ducts

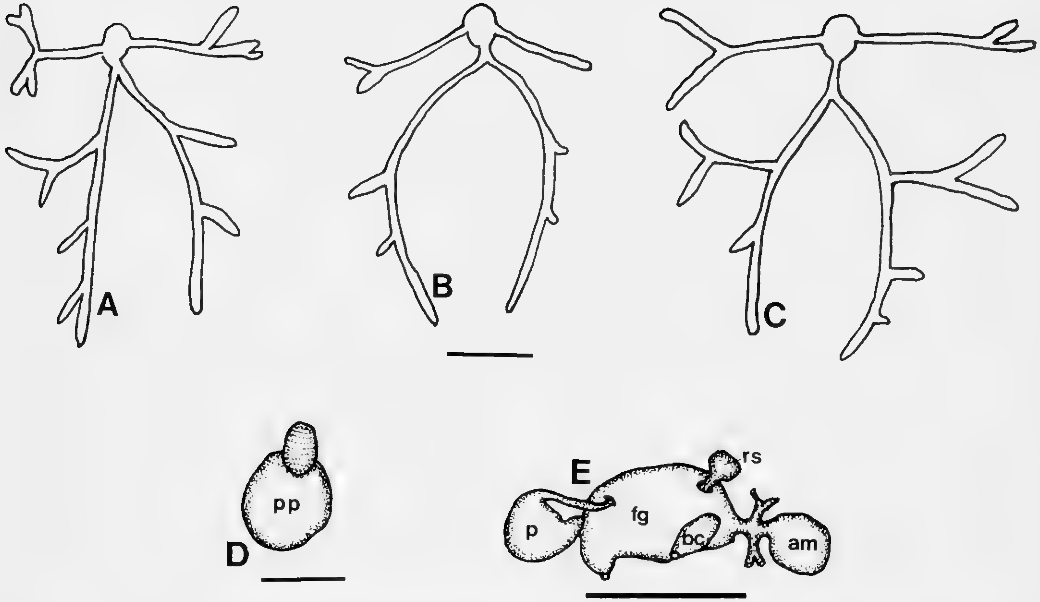

FIGURE 12. *Thuridilla splendens* (Baba, 1949). A–C. Branching of pericardial vessels, scale = 5.0 mm. D. Ventral view of buccal mass, pp = pharyngeal pouch, scale = 0.25 mm. E. Ventral view of distal reproductive organs: am = ampulla, bc = bursa copulatrix, fg = female gland mass, p = penis, rs =r eceptaculum seminis, scale = 1.0 mm.

from the ovotestis, albumen and prostate glands prior to entering the female gland mass. The spherical receptaculum seminis enters the posterior portion of the female gland mass, via a short duct. The pyriform bursa copulatrix exits, by means of its own gonopore, via a short duct. The vas deferens enters the penis. The unarmed penial papilla is curved and rounded. It exits adjacent to the female gonopore.

DISCUSSION. — The anatomy of this species and its similarity to *T. bayeri* and its junior synonym, *T. ratna*, are discussed in the discussion of *T. bayeri*. *Thuridilla splendens* is distinguished from *T. bayeri* by the yellow spots on the parapodia and foot and the expanded pharyngeal pouch.

6. **Thuridilla vatae** (Risbec, 1928)

Elysia vatae Risbec, 1928: 281, pl. 12, fig. 7; Carlson and Hoff, 1978: 108, figs 5c, 16f, g, 19; Gosliner, 1987: 53, fig. 43.
Thuridilla vatae (Risbec) Jensen, 1992: 273, figs. 14d, 16j–l, 18d.

MATERIAL EXAMINED. — SAM A35275, one specimen, Adlam's Reef, Sodwana Bay National Park, Natal, South Africa, 9 May 1982, T. M. Gosliner. CASIZ 073388, one specimen, Cement Mixer Reef, Madang Lagoon, Madang, Papua New Guinea, 2 m depth, 22 October 1986, T. M. Gosliner. CASIZ 070008, one specimen, Horseshoe Cliffs, 1 km, wnw of Onna Village, Okinawa, Ryukyu, Islands, 3 m depth, 16 July 1989, R. F. Bolland. CASIZ 088076, one specimen, 3 km e of Lighthouse near Dakak Resort, Mindanao, Philippines, 1 April 1993, T. M. Gosliner. CASIZ 065280, one specimen, barrier reef pinnacle, n. of Pig Island, Madang Lagoon, Papua New Guinea, 5 m. depth, 25 January 1988, J. Mizeu. CASIZ 065281, the Quarry, 1 km s of Cape Croiselles, Madang Province, Papua New Guinea, 4 m depth, 11 February 1988, J. Mizeu. CASIZ 065310, one specimen, Cement Mixer Reef, Madang Lagoon, Papua New Guinea, 19 January 1988, R. C. Willan. CASIZ 065337, one specimen, Rempi Lagoon, 20 km n of Madang, Papua New Guinea, 15 m depth, 3 February 1988, R. C. Willan. CASIZ 065349, one specimen, radula removed, the quarry, 1 km s of Cape Croiselles, Madang Province, Papua New Guinea, 11 February 1988, R. C. Willan. CASIZ 073030, one specimen, jetty, Christensen Research Institute, Madang Lagoon, Papua New

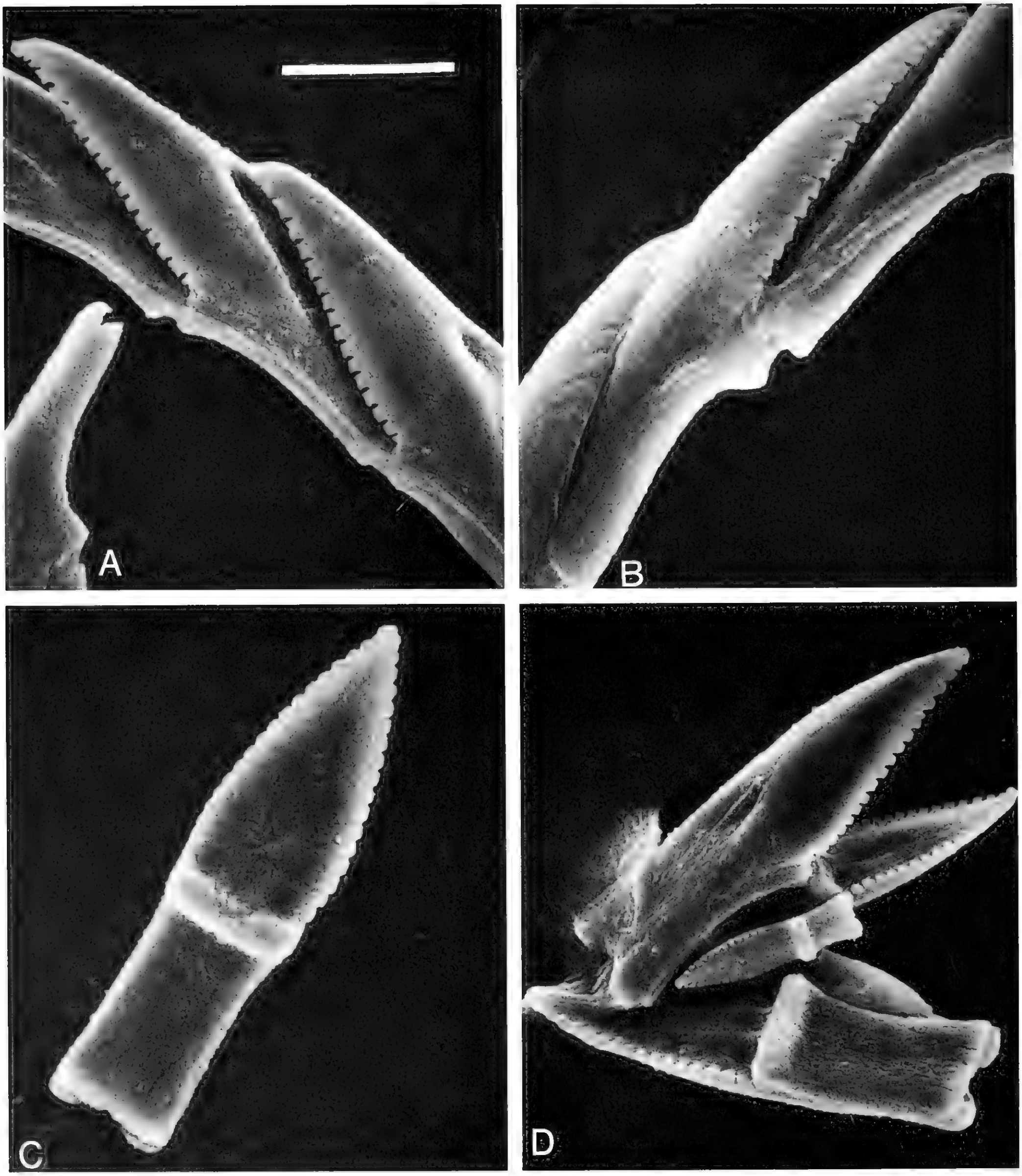

FIGURE 13. *Thuridilla splendens* (Baba, 1949). Radular teeth of specimen from Okinawa CASIZ 099060. A. Dorsolateral view, scale = 20 μm. B. Lateral view, scale = 10 μm. C. Ventral view, scale = 15 μm. D. Teeth from ascus, scale = 20 μm.

Guinea, 30 September, 1986, T. M. Gosliner. CASIZ 087158, one specimen, dissected, 2 km s of St. Gilles, Reunion, 2 m depth, 27 July 1977, M. L. Gosliner. CASIZ 099061, one specimen, dissected, Wongat Wall, Madang Lagoon, Madang, Papua New Guinea, 10 m depth, 30 August 1989, T. M. Gosliner. CASIZ 099062, one specimen, Bunaken Island, Manado, Sulawesi, Indonesia, under rock, 1.5 m depth, 20 May 1990, P. Fiene-Severns.

DISTRIBUTION. — New Caledonia (Risbec, 1928), Guam, Palau and Maug (Carlson and Hoff, 1978), Marshall Islands (Johnson and Boucher, 1983, Johnson, pers. comm.), Western

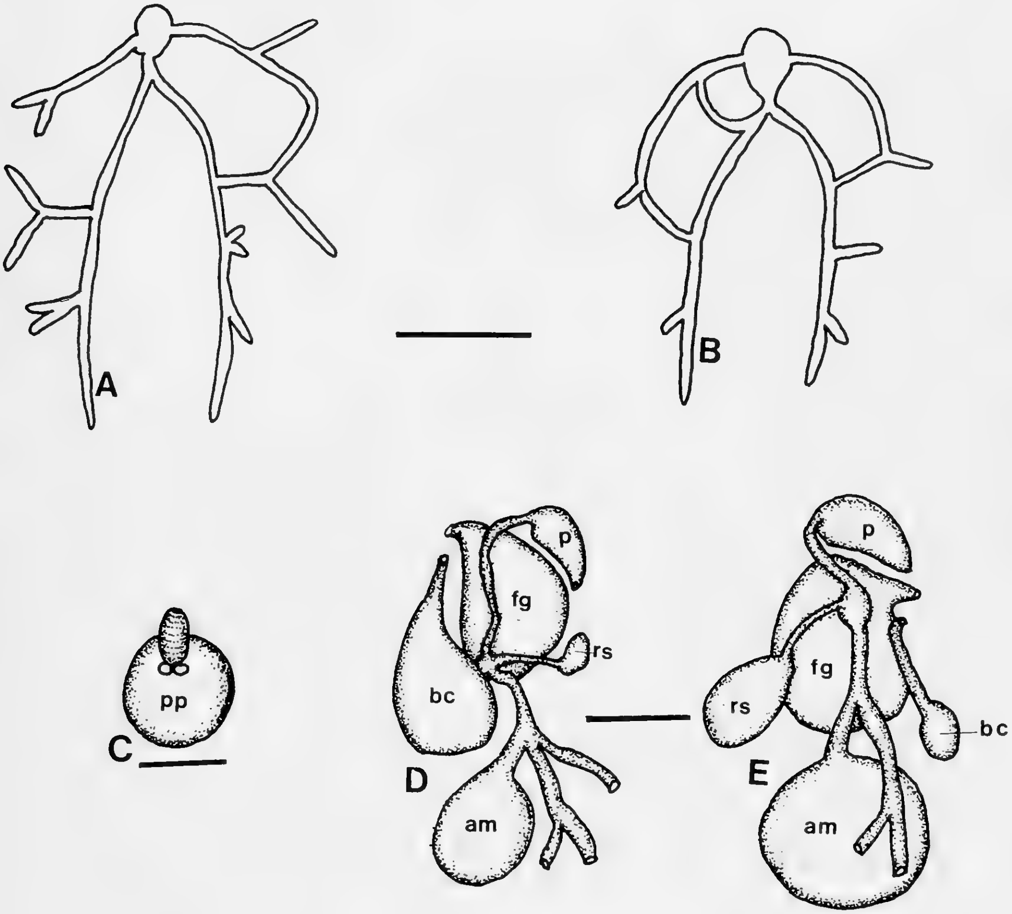

FIGURE 14. *Thuridilla vatae* (Risbec, 1928). A, B. Branching of pericardial vessels, scale = 4.0 mm. C. Ventral view of buccal mass, pp = pharyngeal pouch, scale = 0.25mm. D. Ventral view of distal reproductive organs, CASIZ 099061, Papua New Guinea. E. Distal reproductive organs, CASIZ 087158, Reunion Island. D., E. am = ampulla, bc = bursa copulatrix, fg = female gland mass, p = penis, rs = receptaculum seminis, scale = 0.5 mm.

Australia (Jensen, 1992), Indonesia (present study), Papua New Guinea (present study), Philippines (present study), Reunion Island (present study), Aldabra Atoll (present study), South Africa (Gosliner, 1987).

EXTERNAL MORPHOLOGY. — The body (Fig. 16A) is dark bluish with scattered black and yellow spots. The margin of the parapodia is cream to yellow, but this pigment does not form a distinct band as in other members of the genus. The head is the same color as the body with a y-shaped yellowish or white marking that extends onto most of the length of the rhinophores. The apex of the rhinophores is bright red. The anterior margin of the foot is the same color as the remainder of the body.

PERICARDIUM AND DORSAL VESSELS (Fig. 14 A, B). — Both lateral and posterior vessels are present. The lateral vessels are bifurcate for much of their length. The posterior vessels have a common origin with the pericardium and have a series of 2–3 bifurcate or undivided secondary branches. The right anteriormost branch is connected with the more posterior branch of the right lateral vessel.

BUCCAL MASS AND RADULA. — The pharyngeal pouch (Fig. 14C) is massive relative to the muscular portion. The radula consists of 22

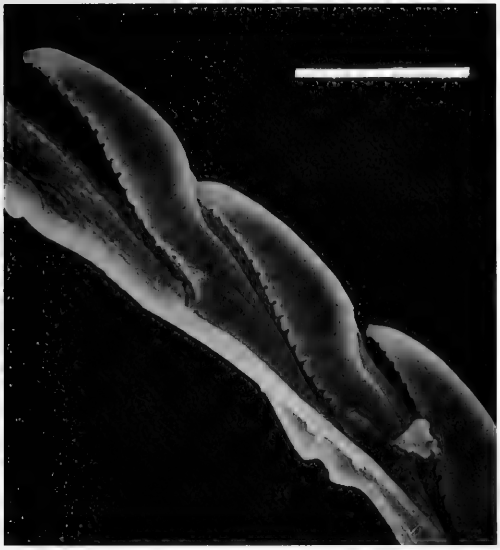

FIGURE 15. *Thuridilla vatae* (Risbec, 1928. Radular teeth. A. Lateral view of specimen from Papua New Guinea, CASIZ 099061, scale = 15 µm.

teeth (14 in the ventral limb, 8 in the dorsal limb and none present in the ascus). The radular teeth (Fig. 15) are triangular with 16–17 coarse denticles along either side of the cutting margin of the tooth. The basal portion is approximately equal in length to the cutting portion.

REPRODUCTIVE SYSTEM (Fig. 14D, E). — The arrangement of the diffuse ovotestis, albumen and prostate glands is identical to that described for *T. bayeri*. The ducts from these glands join the spherical ampulla and enter the female gland mass near the small membrane gland, situated near the posterior end of the large mucus gland. From this junction, the vas deferens emerges and enters the acutely pointed, unarmed penis. The spherical receptaculum seminis joins the female gland mass via an elongate duct. The pyriform bursa copulatrix is variable in size, but when fully developed, is as large as the female gland mass. It exits via its own gonopore, immediately posterior to the female gonopore. In the specimen from Reunion, it was minute, whereas in a specimen from Papua New Guinea, it was almost the same size as the female gland mass.

DISCUSSION. — *Thuridilla vatae* is most similar to *T. albopustulosa* sp. nov. Both species are unique among species of *Thuridilla* in having connections between the lateral and posterior pericardial vessels. The radular teeth of *T. vatae* appear to be more finely denticulate than those of *T. albopustulosa*. The penial papilla of one specimen of *T. albopustulosa* has a constriction in the middle of its length. At present, it is not known whether this is a consistent difference between the two species.

Aspects of the coloration of *T. vatae* differ consistently from that of *T. albopustulosa*. In *T. vatae*, the ground color is a dark gray to black while that of *T. albopustulosa* is blue. The parapodia of *T. vatae* are ornamented with black and yellow spots, while those of *T. albopustulosa* are white or cream. In *T. vatae*, white pigment covers most of the length of rhinophores and only the apex is red. In *T. albopustulosa*, the majority of the rhinophores are red rather than white. In *T. vatae*, the red pigment is a solid transverse band, while in *T. albopustulosa* the red is a diagonal band with white patches within the band.

7. **Thuridilla virgata** (Bergh, 1888)

Plakobranchus virgatus Bergh, 1888: 758, pl. 77, fig. 8, pl. 78, figs. 20–22.
Elysia virgata (Bergh) Gosliner, 1987: 52, fig. 41.
Thuridilla virgata (Bergh) Jensen, 1992: 277.

MATERIAL EXAMINED. — SAM A35274, six specimens, one dissected, one with radula removed, Mbibi, Sodwana Bay National Park, Natal, South Africa, 1–2 m depth, 6 May 1981, T. M. Gosliner. CASIZ 073973, one specimen, Mbibi, Sodwana Bay National Park, Natal, South Africa, 2 m depth, 18 May 1981, T. M. Gosliner. CASIZ 070336, one specimen, dissected, 2 km wsw of Mora Mora Resort, Ifaty, 20 km n. of Tulear, Madagascar, 3 m depth, 9 April 1989, T. M. Gosliner. CASIZ 102280, one specimen, Ras Nungwi, Zanzibar, Tanzania, 1 m depth, 6 November, 1994, T. M. Gosliner.

DISTRIBUTION. — Mauritius (Bergh, 1888), Madagascar (present study), South Africa (Gosliner, 1987), Tanzania (present study).

EXTERNAL MORPHOLOGY. — The body is blue to blue green (Fig. 16B). A series of broad, black longitudinal markings are present on the parapodia. The parapodial margin is the same color blue as the remainder of the body. The head is blue with black markings. A white

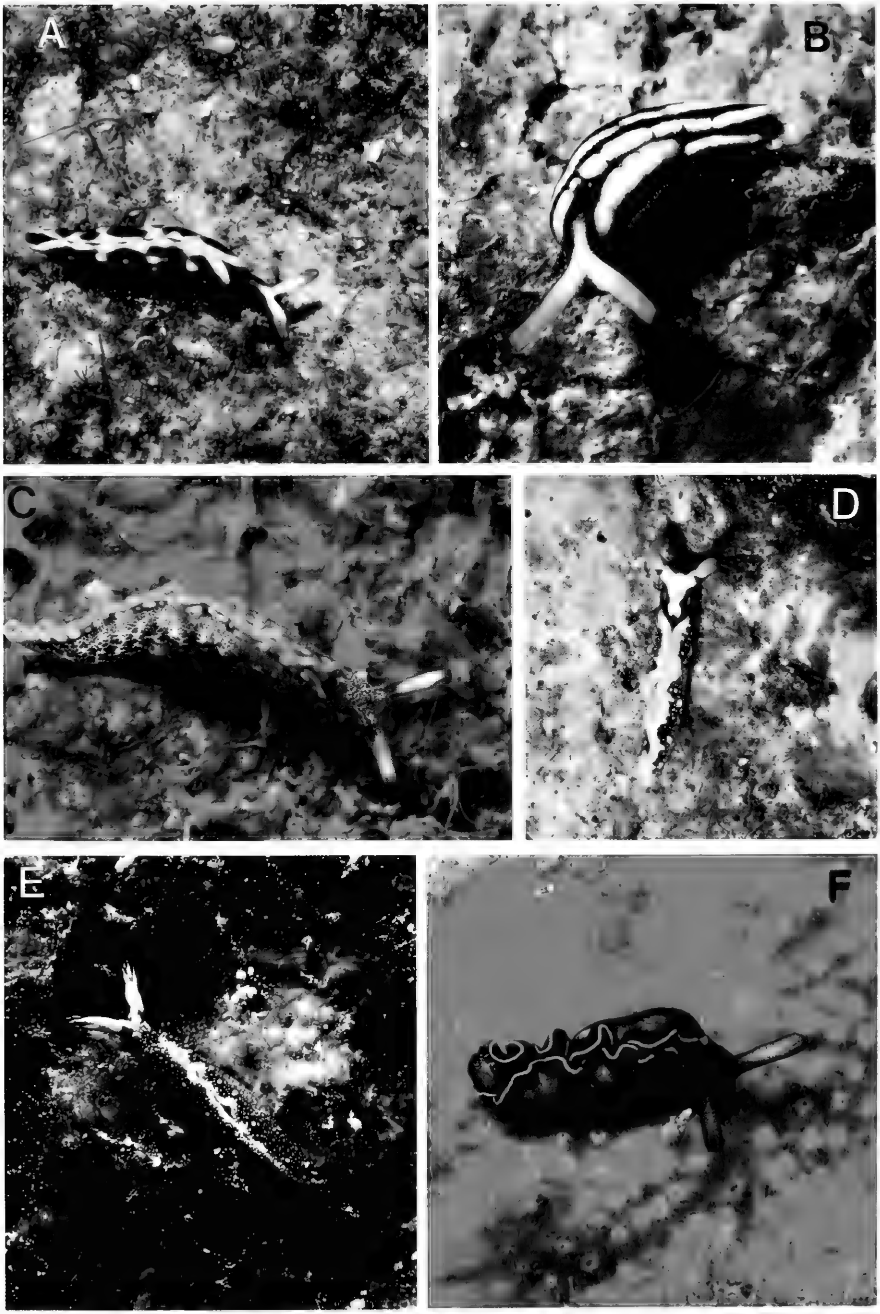

FIGURE 16. Living animals. A. *Thuridilla vatae* (Risbec, 1928), Madang, Papua New Guinea, 11 mm in length. B. *Thuridilla virgata* (Bergh, 1888), Tulear, Madagascar, 18 mm in length. C. *Thuridilla carlsoni* sp. nov., Madang, Papua New Guinea, 20 mm in length. D. *Thuridilla kathae* sp. nov., Tulear, Madagascar, 9 mm in length. E. *Thuridilla flavomaculata* sp. nov., Manado, Sulawesi, Indonesia, 11 mm in length, photo by Pauline Fiene-Severns. F. *Thuridilla hoffae* sp. nov, Madang, Papua New Guinea, 13 mm in length.

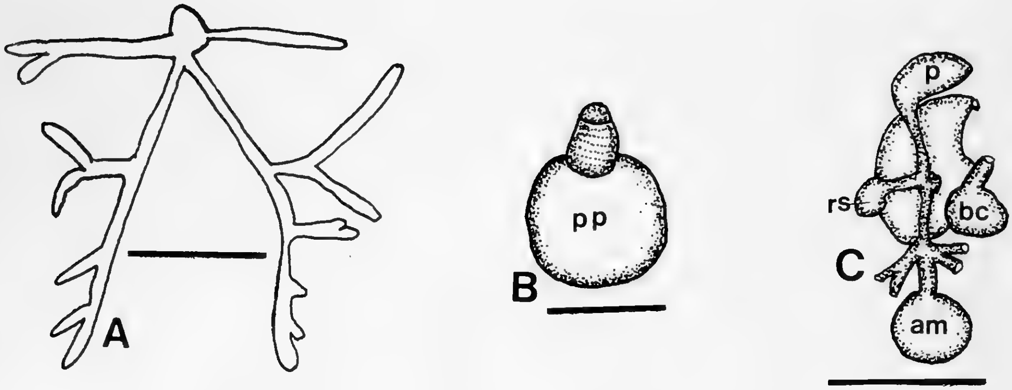

Figure 17. *Thuridilla virgata* (Bergh, 1888). A. Branching of pericardial vessels, scale = 4.0 mm. B. Ventral view of buccal mass, pp = pharyngeal pouch, scale = 0.25mm. C. Distal reproductive organs: am = ampulla, bc = bursa copulatrix, p = penis, rs = receptaculum seminis, scale = 1.0 mm.

marking extends from the anterior portion of the head to the base of the rhinophores. The apical two-thirds of the rhinophores is orange. The anterior margins of the foot are black.

Pericardium and Dorsal Vessels (Fig. 17A). — Paired lateral and posterior vessels are present. The lateral vessels are undivided or bifurcate at their tips. The posterior vessels have a common insertion with the pericardium. They give rise to 3–4 undivided or secondary vessels on either side.

Buccal Mass and Radula. — The pharyngeal pouch (Fig. 17B) is much larger than the muscular portion of the buccal mass. The radula of one specimen examined contained 20 teeth, with 11 in the ventral limb, 7 in the dorsal one and 3 in the ascus. The teeth (Fig. 18) bear 18–20 coarse denticles along the cutting margin. The basal portion of the tooth is approximately equal in length to the cutting portion.

Reproductive System (Fig. 17C). — The ovotestis, albumen and prostate glands are diffuse and occupy much of the tissue within the parapodia and are identical in form to that described for *T. bayeri*. Their ducts join the duct from the spherical ampulla and collectively enter the female gland mass. The small, spherical receptaculum seminis joins the female gland mass near the junction of the ampulla and associated ducts, by means of a short duct. The larger bursa copulatrix has a short duct that has its own gonopore. The vas deferens emerges from the junction of the ampulla and receptaculum seminis with the female gland mass. It continues anteriorly and enters the end of the simple unarmed penis.

Discussion. — *Thuridilla virgata* has a blue body with black parapodial bands and orange pigment on the rhinophores. This color pattern clearly distinguishes it from all other members of the genus. Morphologically, *T. virgata* is most closely related to *T. vatae*, *T. albopustulosa* and *T. moebii*. All of these species have an expanded pharyngeal pouch and a bluish body color. The duct of the receptaculum seminis appears shorter in *T. virgata* than in these other closely related species.

8. **Thuridilla carlsoni** sp. nov.

Elysia gracilis Carlson and Hoff, 1978, not Risbec, 1928: 95, figs. 6d, e, 8.
Thuridilla sp. Wells and Bryce, 1993: 67, fig. 71.

Type Material. — Holotype: CASIZ 075939, one specimen, the Quarry, 1 km s. of Cape Croiselles, Madang Province, Papua New Guinea, 28 November 1990, T. M. Gosliner.

Paratypes: CASIZ 078542, two specimens, under rock, Bunaken Island, Manado, Sulawesi, Indonesia, 3 m depth, 5 May 1991, P. Fiene-Severns. CASIZ 076447, four specimens, Hekili Point, Maui, Hawai-

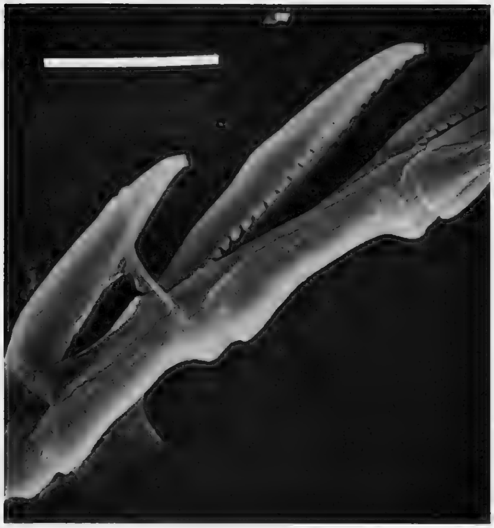

FIGURE 18. *Thuridilla virgata* (Bergh, 1888). Radular teeth. A. Lateral view of tooth, CASIZ 07336, Madagascar, scale = 15 µm.

ian Islands, 1 m depth, October 1990, C. Pittman. CASIZ 065784, two specimens, one dissected, the quarry, 1 km s. of Cape Croiselles, Madang Province, Papua New Guinea, 2 m depth, 11 February 1988, T. M. Gosliner. CASIZ 086365, one specimen, Molokini Island, Hawaiian Islands, 11 m depth, 16 December 1991, Pauline Fiene-Severns. CASIZ 099063, radula removed, Cocos Channel, off Merizo, Guam, 12 m depth, 30 August 1970, C. Carlson and P. Hoff. CASIZ 099065, four specimens, pinnacle, G. Buoy, Kwajelin Atoll, Marshall Islands, 6 m depth, 5 March 1994, S. Johnson. CASIZ 086659, one specimen, Maliko, Maui, crawling on algal turf, 3 m depth, 14 August 1992, P. Fiene-Severns.

ETYMOLOGY. — *Thuridilla carlsoni* is named for my colleague, Clay Carlson, who, together with Patty Jo Hoff, discovered this species.

DISTRIBUTION. — Hawaiian Islands (present study), Enewetak and Kwajelin, Marshall Islands (present study), Guam (Carlson and Hoff, 1978, as *Elysia gracilis*), Western Australia (Wells and Bryce, 1993), Papua New Guinea (present study).

EXTERNAL MORPHOLOGY. — The body color (Fig. 16C) consists of abundant irregular green pigment spots. The parapodia have anastomosing opaque white blotches covering much of the green pigment. The parapodial margin is light yellow. Immediately inside the marginal band is a series of opaque white spots. The head consists of opaque white with green pigment which extends on to the basal third of the rhinophores. The remainder of the rhinophore is covered with opaque white, except for the burnt orange apex. Opaque white pigment is also present at the anterior end of the foot and head. The inside of the parapodia contains a cream marginal line, followed by a band of opaque white and a broader band of black. Most of the internal surface of the parapodia is green with yellow-green longitudinal lines.

PERICARDIUM AND DORSAL VESSELS (Fig. 19A–C): The pericardium gives rise to paired lateral and posterior vessels. The lateral vessels are bifurcate or more highly branched. The posterior vessels have separate junctions with the pericardium. There are 4–5 multifid, bifid or undivided secondary branches. There may be connections between terminal branches of lateral and posterior vessels.

BUCCAL MASS AND RADULA. — The pharyngeal pouch (Fig. 19D) differs from other described species in being more highly muscularized. It is approximately the same size as the muscular portion of the buccal mass. The radula was examined in three specimens, one from Papua New Guinea, one from Guam and another from the Hawaiian Islands. There are 20–23 teeth with 35–38 fine denticles on either side of the cutting margin. In the Papua New Guinea specimen, there were 8 teeth in the ventral limb, 9 in the dorsal one and 6 teeth in the ascus. In the Hawaiian specimen, the different portions of the radula were not readily discernible. The teeth (Fig. 20) are broad and triangular, 105–115 µm in length. The numerous denticles are coarse and evenly spaced. They continue on to the dorsal surface of the tooth as fine striations. There is a deep triangular depression in the dorsal surface of the basal portion of the tooth in which the cutting portion of the more posterior tooth rests. The posterior end of the tooth is notched.

REPRODUCTIVE SYSTEM (Fig. 19E). — The ovotestis, prostate and albumen glands are diffuse and are arranged in the fashion described for *T. bayeri*. Their ducts join the spherical ampulla and the female gland mass. At this point, there is also a junction of the elongate duct of

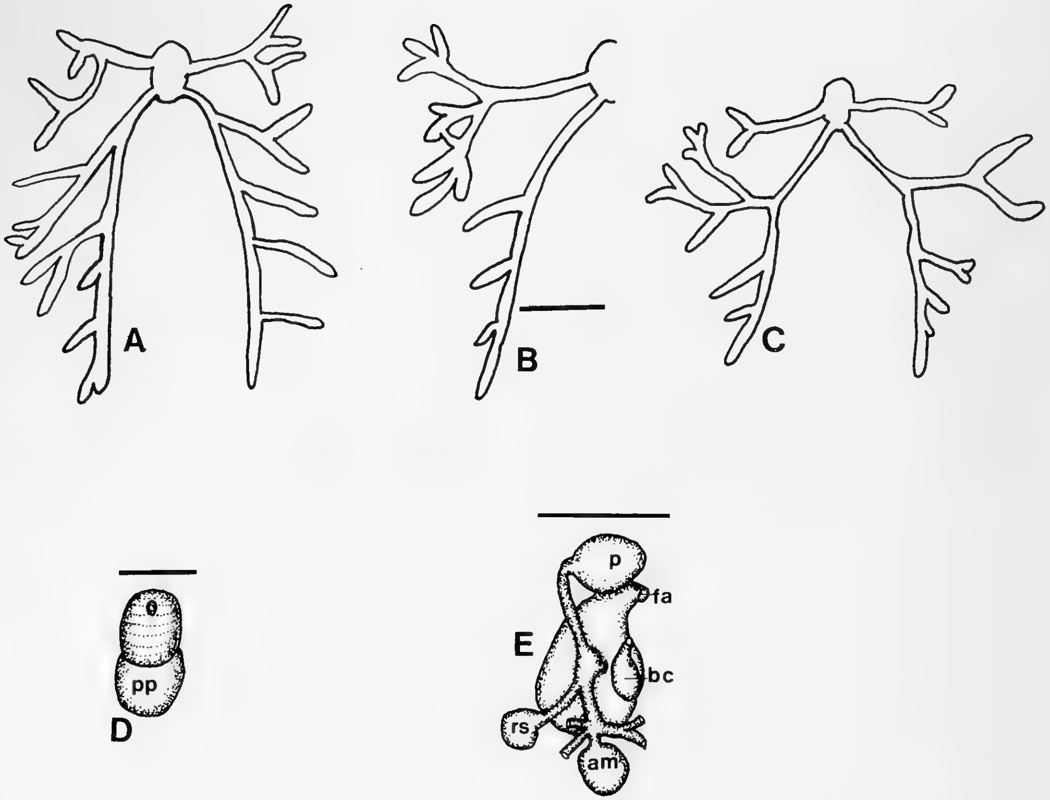

FIGURE 19. *Thuridilla carlsoni* sp. nov. A—C. Branching of pericardial vessels, scale = 5.0 mm. D. Ventral view of buccal mass, pp = pharyngeal pouch, scale = 0.25mm. E. Distal reproductive organs: am = ampulla, bc = bursa copulatrix, fa = female aperture, p = penis, rs = receptaculum seminis, scale = 1.0 mm.

the spherical receptaculum seminis. The small bursa copulatrix empties via a short duct into a separate gonopore. The vas deferens emerges near the junction of the ampulla and associated ducts and the receptaculum seminis. The vas deferens continues to the posterior end of the simple, unarmed, bulbous penis.

DISCUSSION. — This species was originally recorded from Guam as *Elysia gracilis* Risbec, 1928. However, from the original description of *T. gracilis* it is difficult to determine the identity of the species. The body is greenish with about 8 white longitudinal lines along the side of the parapodia. The edge of the parapodia, the edge of the foot and the anterior portion of the rhinophores are orange. These features suggest that this species may be a pale specimen of *T. bayeri*, but this is inconclusive. Risbec's specimen of *T. gracilis* had approximately ten denticles along either side of the radular tooth, far fewer denticles than any material studied here. Owing to differences in coloration and radular denticulation, the present material is described as a distinct species.

Thuridilla carlsoni differs from all other members of the genus in several regards. It is the least derived member of the genus, having almost all plesiomorphic features. The only derived feature is the numerous denticles along the cutting margin of the radular teeth, which is autapomorphic for the genus. It is most closely related to *T. multimarginata* n. sp., though the two differ in coloration and radular dentition. *Thuridilla carlsoni* has scattered green pigment granules while *T. multimarginata* has uniformly green body color. In

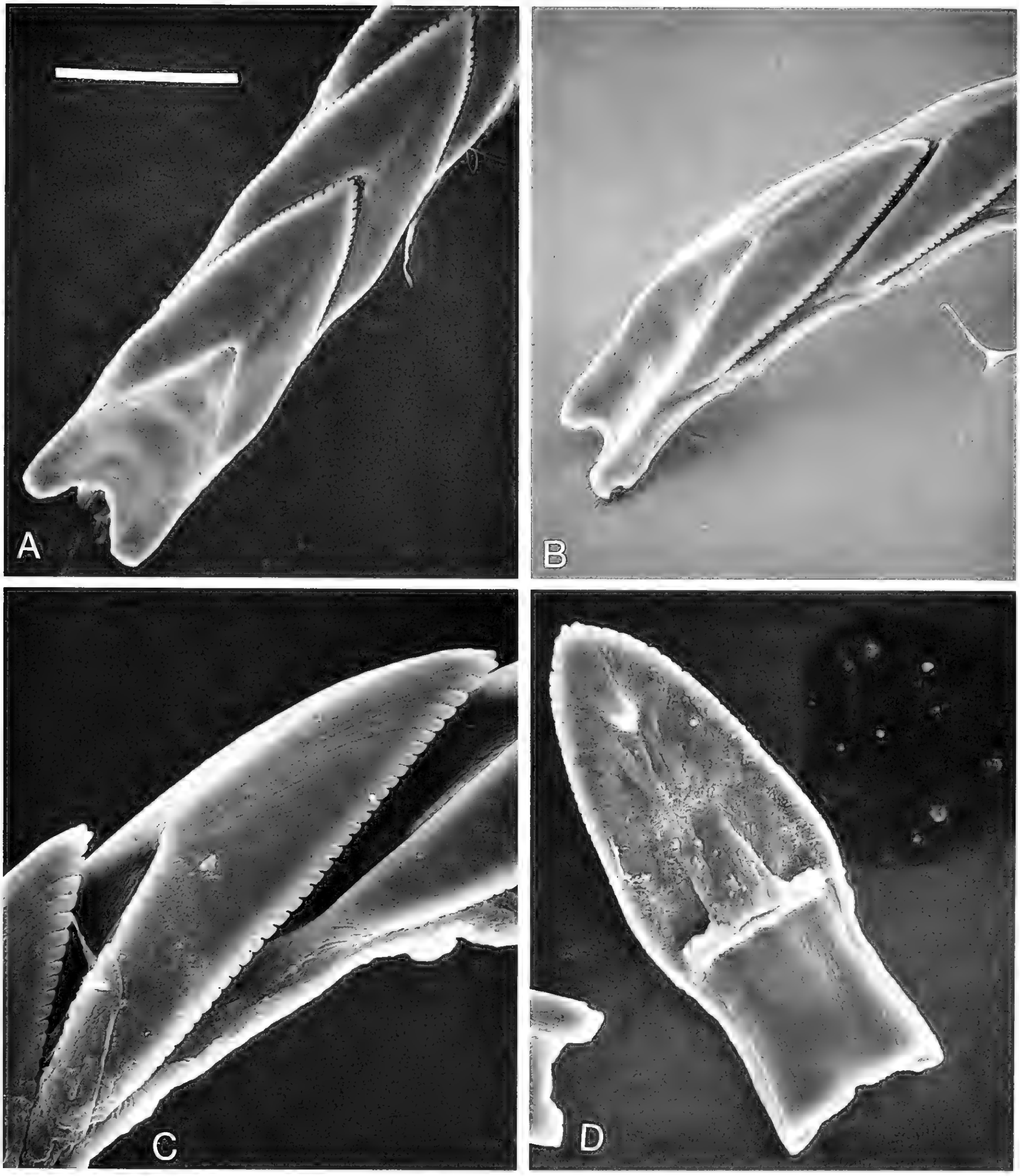

FIGURE 20. *Thuridilla carlsoni* sp. nov. Radular teeth. A. Dorsal view of specimen from Papua New Guinea, CASIZ 065784, scale = 43 µm. B. Lateral view of same specimen, scale= 43 µm. C. Lateral view of specimen from Guam, CASIZ 099063, scale = 20 um. D. Ventral view of same specimen, scale = 25 µm.

T. carlsoni, the parapodial margin is pale cream to yellow while *T. multimarginata* has a series of vividly colored white, orange blue and black bands. The radular teeth of *T. multimarginata* have far fewer denticles than those of *T. carlsoni*. The penis of *T. carlsoni* is bulbous throughout its length, while in *T. multimarginata* it is bulbous basally and narrows in

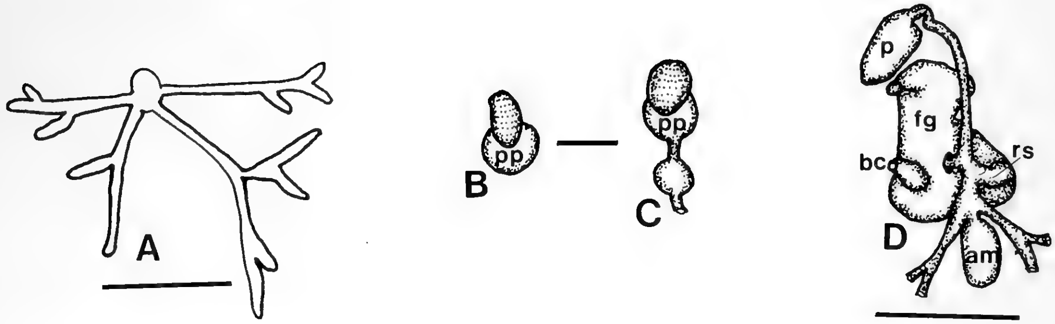

FIGURE 21. *Thuridilla kathae* sp. nov. A. Pericardial branching, scale = 3.0 mm. B. Dorsal view of buccal mass. C. Ventral view of buccal mass. B., C. pp = pharyngeal pouch, scale = 0.25mm. D. Ventral view of distal reproductive organs: am = ampulla, bc = bursa copulatrix, fg = female gland mass, p = penis, rs = receptaculum seminis, scale = 1.0 mm.

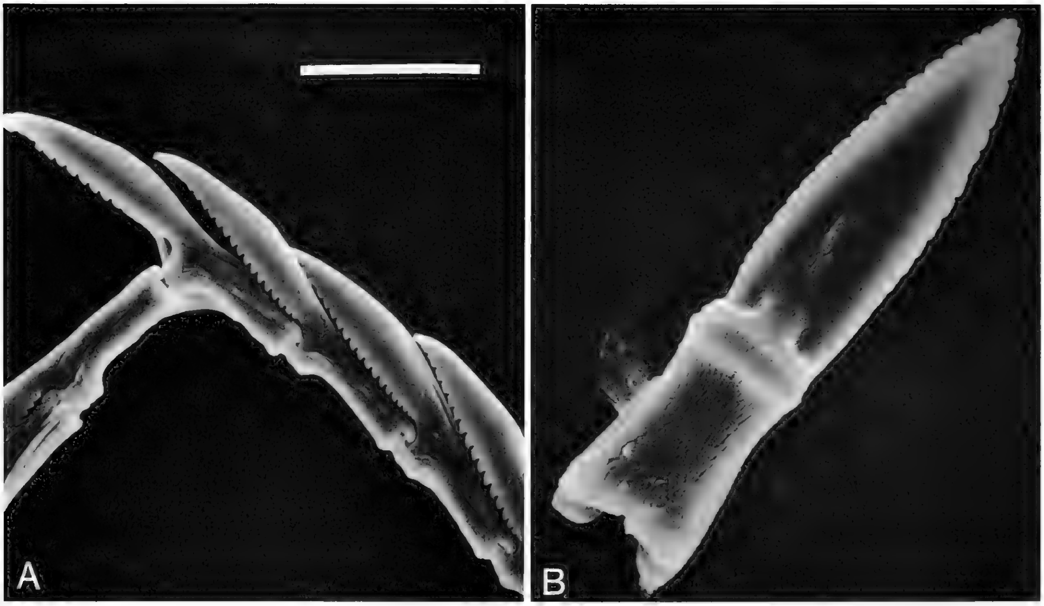

FIGURE 22. *Thuridilla kathae* sp. nov. Radular teeth of specimen from Indonesia, CASIZ 078575. A. Lateral view, scale = 30 µm. B. Ventral view, scale = 15 µm.

the distal half.

The color of *T. carlsoni* is most similar to *T. flavomaculata* n. sp. and *T. kathae* n. sp. All three of these species have green body color and a cream to yellowish parapodial margin. In *T. carlsoni* the green pigment is reticulated with white, while in the other two species the green is solid. Reticulate pigment is also present on the head, while in *T. flavomaculata* and *T. kathae* opaque white pigment patches are present on the head.

Thuridilla carlsoni has broad radular teeth while both *T. kathae* and *T. flavomaculata* have narrow teeth. The latter two species also have smaller radular teeth and also lack a prominent dorsal notch on the teeth.

9. **Thuridilla kathae** sp. nov.

TYPE MATERIAL. — Holotype: CASIZ 099064, 5 km wsw of Mora Mora Resort, 20 km n of Tulear, Madagascar, 2 m depth, 7 April 1989, T. M. Gosliner.

Paratypes: CASIZ 070278, two specimens, dissected, Manado, Sulawesi, Indonesia, 3 m depth, 28 May 1989, P. Fiene-Severns. CASIZ 078575, two specimens, one dissected, Bunaken Island, Manado, Sulawesi, Indonesia, 3 m depth, 11 May 1991, P. Fiene-Severns. CASIZ 085890, one specimen, dissected, Cemetery Beach, n. end Maricaban Island, off Luzon, Philippines, 2 m depth, 22 March, 1993, T. M. Gosliner. CASIZ 086705, one specimen, Lebantour, Flores, Indonesia, under rock, 2 m depth, 26 April 1992, P. Fiene-Severns. CASIZ 093951, two specimens, Bunaken Island, Sulawesi, Indonesia, 20 October 1993, P. Fiene-Severns.

ETYMOLOGY. — *Thuridilla kathae* is named for my colleague, Kathe Jensen, who has done much to advance our knowledge of the Sacoglossa and *Thuridilla*, in particular.

DISTRIBUTION. — Philippines, Indonesia and Madagascar (all present study).

EXTERNAL MORPHOLOGY. — The living animals (Fig. 16D) are a rich green with a scattering of large and small opaque white spots. The large spots form low papillae. The margin of the parapodia is cream to light yellow. There is a y-shaped opaque white mark on the head that extends on to the base of the rhinophores. This white is followed by an area of green and then a second patch of opaque white. The tips of the rhinophores are ornamented with orange. Orange pigment is also present on the anterior margin of the foot.

PERICARDIUM AND DORSAL VESSELS (Fig. 21A). — Paired lateral and posterior vessels emerge from the pericardium The lateral branches contain multiple secondary branches. The posterior branches originate separately from the pericardium and have one or two simple or bifid branches.

BUCCAL MASS AND RADULA. — The pharyngeal pouch (Fig. 21B, C), though larger than the muscular portion of the mass, is relatively smaller than most other species. The radula was examined in a single specimen from Indonesia. There are 24 teeth with 17–18 coarse denticles on either side of the cutting margin. There were 6 teeth in the ventral limb, 6 in the dorsal one and 12 teeth in the ascus. The teeth (Fig. 22) have a relatively short base and elongate triangular portion.

REPRODUCTIVE SYSTEM (Fig. 21D). — The ovotestis, prostate and albumen glands are diffuse and are arranged in the fashion described for *T. bayeri*. Their ducts join the ovoid ampulla and the female gland mass. At this point, there is also a junction of the short duct of the spherical receptaculum seminis. The small bursa copulatrix empties via a short duct into a separate gonopore. The oviduct empties at the anterior end of the female gland mass adjacent to the penis. The vas deferens emerges near the junction of the ampulla and associated ducts, female gland mass and the receptaculum seminis. The vas deferens continues to the posterior end of the simple, unarmed, bulbous penis.

DISCUSSION. — *Thuridilla kathae* is similar in appearance to *T. carlsoni* and *T. flavomaculata*, and is most closely related to *T. flavomaculata*. The differences between *T. carlsoni* and the other two species are enumerated in the previous discussion. In *T. kathae*, orange pigment is present on the distal portion of the rhinophores while in *T. flavomaculata* the distal portion is white with black longitudinal lines. *Thuridilla kathae* lacks yellow spots over the surface of the body that are present in *T. flavomaculata*. In addition to these consistent differences in coloration, *T. kathae* has less highly branched lateral pericardial vessels than does *T. flavomaculata*, but has somewhat more vesicular branching of the posterior vessels. The penial papilla of *T. kathae* is more bulbous than that of *T. flavomaculata*. Other than these relatively minor, but consistent, differences, the two species are similar in most other aspects of their anatomy and appear to be closely related.

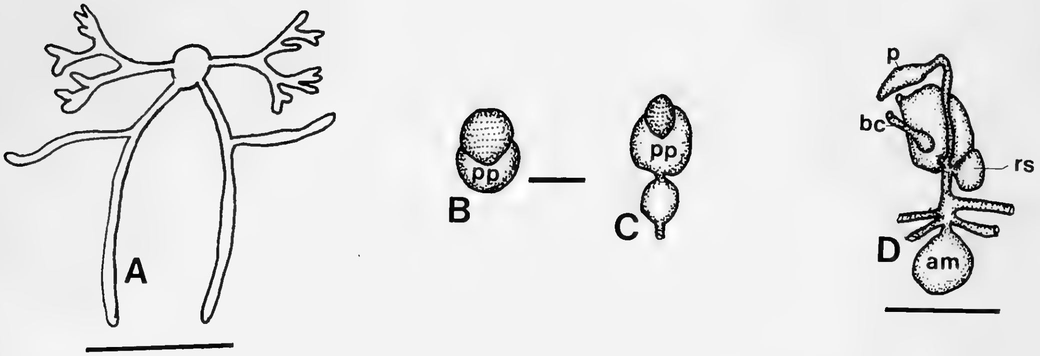

FIGURE 23. *Thuridilla flavomaculata* sp. nov. A. Branching of pericardial vessels, scale = 5.0 mm. B. Dorsal view of buccal mass. C. Ventral view of buccal mass. B., C. pp = pharyngeal pouch, scale = 0.25mm. D. Ventral view of distal reproductive organs: am = ampulla, bc = bursa copulatrix, p = penis, rs = receptaculum seminis, scale = 1.0 mm.

10. **Thuridilla flavomaculata** sp. nov.

TYPE MATERIAL. — Holotype: CASIZ 103557, The Head, Hamilo Bay, Luzon, Philippines, 9 m depth, 4 March 1995, Mel Segarra.

Paratypes: CASIZ 087367, Nain Island, Manado, Sulawesi, Indonesia, under rock, 1.5 m depth, 7 May 1990, P. Fiene-Severns. CASIZ 070278, one specimen, radula removed, Manado, Sulawesi, Indonesia, 3 m depth, 28 May 1989, P. Fiene-Severns. CASIZ 078583, one specimen, dissected, Bunaken Island, Manado, Sulawesi, Indonesia, 3 m depth, 13 May 1991, P. Fiene-Severns. CASIZ 099066, one specimen, radula removed, channel between Cocos Island and Merizo, Guam, 8 m depth, 27 September 1970, C. Carlson and P. Hoff.

ETYMOLOGY. — The epithet *flavomaculata* refers to the yellow spots that ornament the parapodia. This is the only species of *Thuridilla* with many scattered yellow spots.

DISTRIBUTION. — This species is known from Enewetak and Kwajelin, Marshall Islands (Scott Johnson pers. comm.), Indonesia, Luzon, Philippine Islands and Guam (present study).

EXTERNAL MORPHOLOGY. — The animal is green (Fig. 16E) with scattered opaque white and yellow spots. The edge of the parapodia is cream colored. The base of the rhinophores is opaque white with several longitudinal black lines extending along the outer third of the rhinophores.

PERICARDIUM AND DORSAL VESSELS. — Paired lateral and posterior vessels emerge from the pericardium (Fig. 23A). The lateral branches contain multiple secondary branches. The posterior branches originate separately from the pericardium and each have a single undivided branch.

BUCCAL MASS AND RADULA. — The pharyngeal pouch (Fig. 23B, C), is larger than the muscular portion of the mass, but is somewhat smaller than in other species. The esophageal pouch is muscular, smaller than the buccal mass. The radulae of two paratypes were examined, but the radula of one was lost during preparation. The precise number of teeth could not be determined, since the ascus and portions of the ventral limb of the radula were lost. There are 7 teeth forming the dorsal limb. Each triangular tooth (Fig. 24) has 18–21 coarse denticles along either side of the cutting margin. The cutting portion is slightly longer than the basal articulating surface.

REPRODUCTIVE SYSTEM (Fig. 23D). — The ovotestis, prostate and albumen glands are diffuse and are arranged in the fashion described for *T. bayeri*. Their ducts join the ovoid ampulla and join the female gland mass. At this point, there is also a junction of the short, spherical receptaculum seminis. The small bursa copulatrix exits via an elongate duct, into a separate gonopore. The oviduct empties at the anterior end of the female gland mass adjacent to the penis. The vas deferens emerges near the junction of the ampulla and associated ducts,

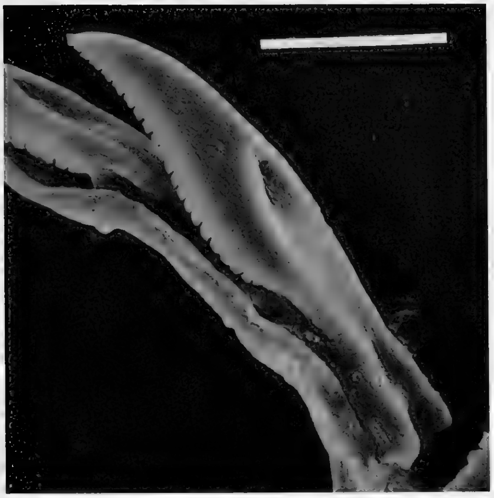

FIGURE 24. *Thuridilla flavomaculata* sp. nov. Radular teeth of specimen from Indonesia, CASIZ 070278, scale= 20 µm.

female gland mass and the receptaculum seminis. The vas deferens continues to the posterior end of the simple, unarmed, thin penis.

DISCUSSION. — The differences between this species, *T. carlsoni* and *T. kathae* are discussed in the sections dealing with those species. *Thuridilla flavomaculata* is readily distinguishable from other congeners by its green body color with scattered yellow spots and white apices of the rhinophores with black longitudinal lines.

11. **Thuridilla hoffae** sp. nov.

Elysia livida Carlson and Hoff, 1978, in part.
Elysia livida Johnson and Boucher, 1983, not Baba, 1955.

TYPE MATERIAL. — Holotype: CASIZ 065773, one specimen, the Quarry, 1 km s of Cape Croiselles, Madang Province, Papua New Guinea, 11 February 1988, T. M. Gosliner.

Paratypes: CASIZ 071248, one specimen, Planet Rock, 10 km s. of Madang, Papua New Guinea, 5 m depth, 16 February 1988, G. Williamson. CASIZ 071242, two specimens, one dissected, Barracuda Point, e side Pig Island, Madang Harbor, Madang, Papua New Guinea, 10 m depth, 8 February 1988, J. Mizeu. CASIZ 069936, one specimen, Horseshoe Cliffs, 1 km wnw of Onna Village, Okinawa, Ryukyu Islands, 10 m depth, 18 April 1987, R. F. Bolland. CASIZ 071241, one specimen, dissected, Madang Lighthouse, Papua New Guinea, 10 m depth, 15 January 1988, R. C. Willan. CASIZ 065361, one specimen, Barracuda Point, e side Pig Island, Madang Lagoon, Papua New Guinea, 15 m depth, 17 January 1988, R. C. Willan. CASIZ 071243, two specimens, se side Pig Island, Madang Lagoon, Papua New Guinea, 16 m depth, 24 January 1988, T. M. Gosliner. CASIZ 086486, one specimen, dissected, barrier reef between Pig Island and Rasch Passage, Madang Lagoon, Papua New Guinea, 8 June 1992, T. M. Gosliner. CASIZ 071247, Barracuda Point, e. side Pig Island, Madang Lagoon, Papua New Guinea, 8 m depth, 14 February 1988, R. C. Willan. CASIZ 073031, one specimen, Rasch Passage, Madang Lagoon, 25 October 1986, G. Williamson. CASIZ 089033, one specimen, Seragaki Beach, 1.3 km ene of Maeki-zaki, Okinawa, Ryukyu Islands, 2 m depth, 3 April 1993, R. F. Bolland. CASIZ 071248, one specimen, Planet Rock, Madang, Papua New Guinea, 12 m depth, 16 February 1988, G. Williamson.

ETYMOLOGY. — *Thuridilla hoffae* is named for my colleague Patty Jo Hoff who, together with Clay Carlson, first discovered this species.

DISTRIBUTION. — Enewetak, Marshall Islands (Johnson and Boucher, 1983, as *Elysia livida*, S. Johnson, pers. comm.), Guam (Carlson and Hoff, 1978, as *E. livida*, in part), Okinawa (present study), Papua New Guinea (present study).

EXTERNAL MORPHOLOGY. — The living animals (Fig. 16F) are black. The margin of the parapodia contains a vivid orange line of reflective granules. Below the margin, bright, reflective blue-green blotches cover most of the parapodia. The head is black with blue-green pigment covering most of the rhinophores. The anterior margin of the foot has an orange line.

PERICARDIUM AND DORSAL VESSELS. — Only posterior vessels were present in the three specimens examined (Fig. 25A–C). These have a common junction with the pericardium. Each posterior vessel has 2–3 secondary vessels with multifid, bifid or undivided branches.

BUCCAL MASS AND RADULA. — The pharyngeal pouch (Fig. 25D) is much larger than the muscular portion of the buccal mass. The radular teeth (Fig. 26) are triangular with 16–19 coarse denticles along either side of the cutting margin and continue on the dorsal tooth surface

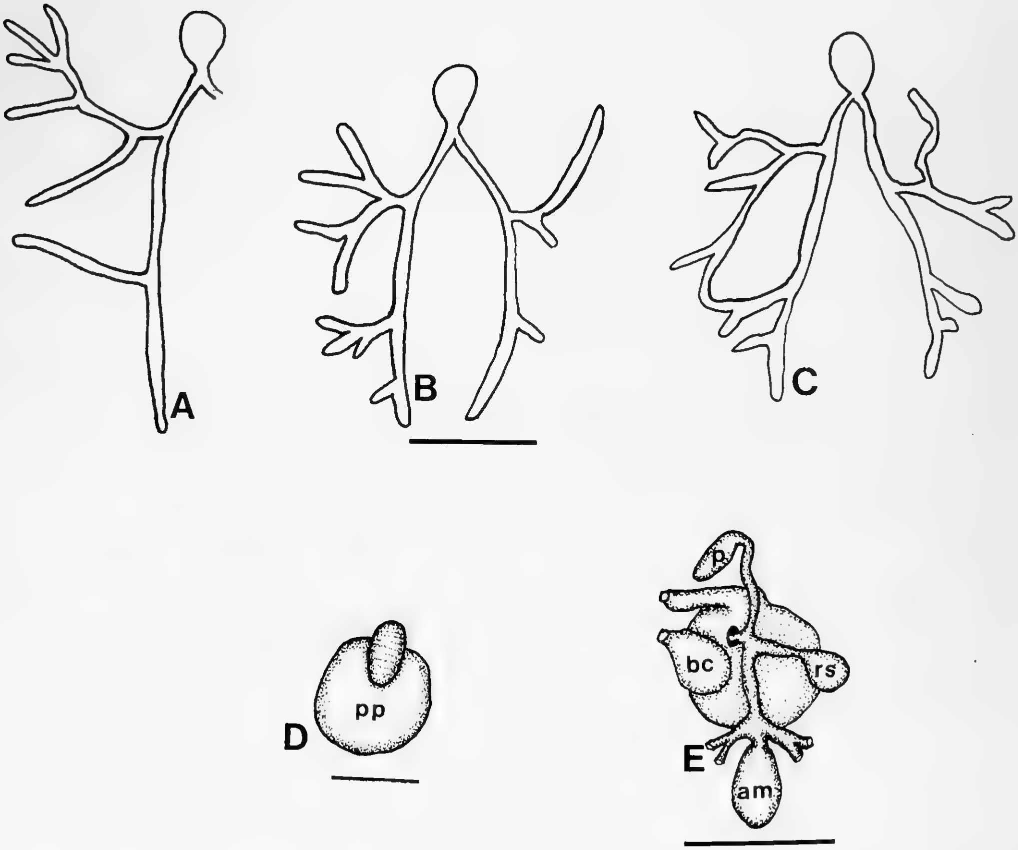

FIGURE 25. *Thuridilla hoffae* sp. nov. A.-C. Branching of pericardial vessels, scale = 5.0 mm. D. Ventral view of buccal mass, pp = pharyngeal pouch, scale = 0.25mm. E. Ventral view of distal reproductive organs: am = ampulla, bc = bursa copulatrix, p = penis, rs = receptaculum seminis, scale = 1.0 mm.

as striations.

REPRODUCTIVE SYSTEM (Fig. 25E). The ovotestis, prostate and albumen glands are diffuse and are arranged in the fashion described for *T. bayeri*. Their ducts join the ovoid ampulla and together join the female gland mass. At this point, there is also a junction of the elongate duct of the spherical receptaculum seminis. The pyriform bursa copulatrix exits via a short duct at a separate gonopore. The oviduct empties at the anterior end of the female gland mass adjacent to the penis, by means of an elongate duct. The vas deferens emerges near the junction of the ampulla and associated ducts, female gland mass and the receptaculum seminis. The vas deferens continues to the posterior end of the simple, unarmed, thin penis.

DISCUSSION. — This species is most similar in color to *T. livida* and is most closely related to this species. The important morphological distinctions between *T. hoffae* and *T. livida* were described previously in the discussion of *T. livida*.

12. Thuridilla albopustulosa sp. nov.

Elysia sp. 2 Gosliner, 1987: 54, fig. 47

TYPE MATERIAL. — Holotype: CASIZ 099068, one specimen, Cement Mixer Reef, Madang Lagoon, Papua New Guinea, 11 January 1988, R. C. Willan.

Paratypes: SAM A 35269, one specimen, dis-

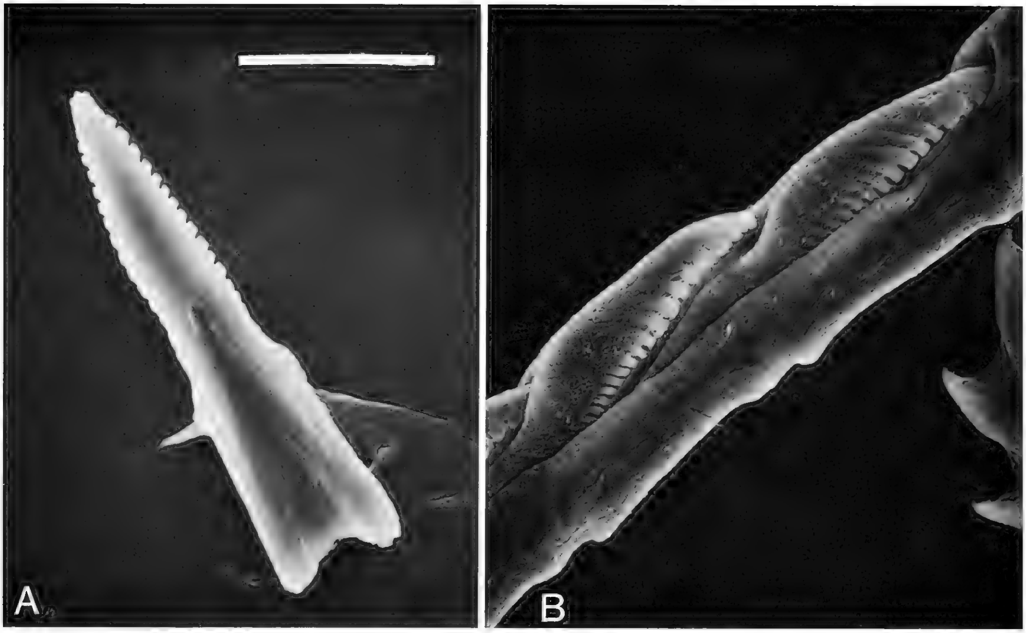

FIGURE 26. *Thuridilla hoffae* sp. nov. Radular teeth of specimens from Papua New Guinea. A. Dorsal view, CASIZ 086486, scale = 15 μm. B. Lateral view, CASIZ 071241, scale = 20 μm.

sected, Mbibi, Sodwana Bay National Park, Natal, South Africa, 6 May 1982, T. M. Gosliner. CASIZ 078564, one specimen, Bunaken Island, Manado, Sulawesi, Indonesia, 5 m depth, 20 May 1991, P. Fiene-Severns. CASIZ 074208, one specimen, Passe du Bois, Aldabra Atoll, Seychelles, 22 March 1986, T. M. Gosliner. CASIZ 099067, one specimen, Madang Resort, Papua New Guinea, 1 February 1988, R. C. Willan. CASIZ 085882, two specimens, one dissected, 3 km e of Lighthouse, near Dakak Resort, Mindinao, Philippines, 3 m depth, 1 April 1993, T. M. Gosliner. CASIZ 087034, one specimen, Bunaken Island, Manado, Sulawesi, Indonesia, under rock, 3 m depth, 20 May 1990, P. Fiene-Severns.

ETYMOLOGY. — The name *albopustulosa* is derived from the white pustules present on the parapodia.

DISTRIBUTION. — Philippines, Papua New Guinea, Indonesia, Aldabra Atoll (all present study), South Africa (Gosliner, 1987).

EXTERNAL MORPHOLOGY. — The living animals (Fig. 29B) are light blue with scattered black pigment especially near the foot at the base of the parapodia. The parapodial margin is opaque white. The parapodia are covered with scattered opaque white or cream spots or longitudinal bands. The head has diffuse black pigment along its margins. The basal third of the rhinophores is opaque white. The outer two-thirds is bright red with a scattered patch or two of opaque white in the middle of the red. The red pigment extends farther basally on the outer side of the rhinophore than on the inner side. This creates the appearance of a diagonal rather than transverse band. The anterior margin of the foot is blue.

PERICARDIUM AND DORSAL VESSELS. — The arrangement of the vessels was examined in four specimens (Fig. 27A–D). Both lateral and posterior vessels are present. The lateral vessels are undivided, bifurcate or trifurcate. The posterior vessels have a common origin from the posterior end of the pericardium. The anterior duct of the posterior vessel usually joins with the the lateral vessels.

BUCCAL MASS AND RADULA. — The pharyngeal pouch (Fig. 27E), is much larger than the

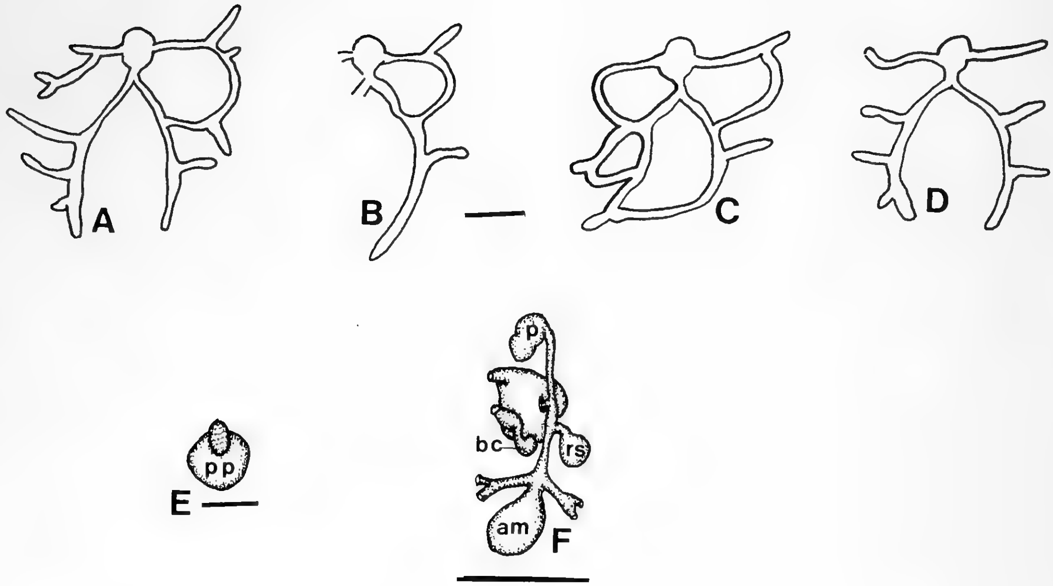

FIGURE 27. *Thuridilla albopustulosa* sp. nov. A.–D. Branching of pericardial vessels, scale = 3.0 mm. E. Dorsal view of buccal mass, pp = pharyngeal pouch, scale = 0.25 mm. F. Ventral view of distal reproductive organs: am = ampulla, bc = bursa copulatrix, p = penis, rs = receptaculum seminis, scale = 1.0 mm.

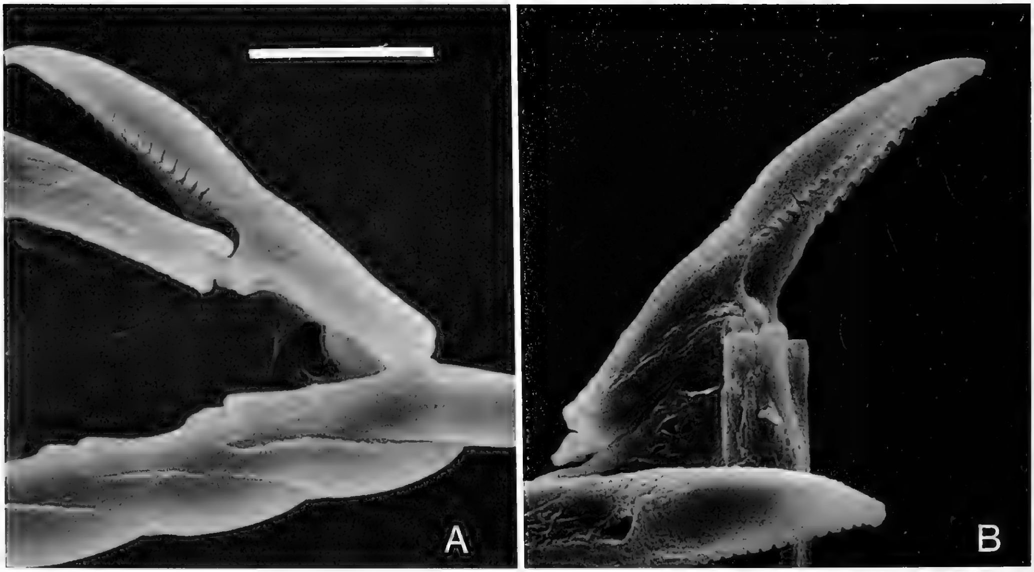

FIGURE 28. *Thuridilla albopustulosa* sp. nov. Radular teeth. A. Lateral view of specimen from South Africa, SAM A35269, scale = 10 μm. B. Lateral view of specimen from Philippines, CASIZ 085882, scale = 10 μm.

muscular portion of the mass. The radula consists of 16 teeth in one specimen from the Philippines and 21 teeth in a specimen from South Africa. There are 11–12 teeth in the ventral branch of the radula and 5–9 in the dorsal one. No discarded teeth were found in the ascus of either specimen examined. The individual teeth (Fig. 28) are triangular with 13–16 coarse denticles along the cutting margin. The cutting portion is slightly longer than the base of the tooth.

REPRODUCTIVE SYSTEM (Fig. 27F). — The ovotestis, prostate and albumen glands are diffuse and are arranged as in *T. bayeri*. Their ducts join the ovoid ampulla and the female gland mass. At this point, there is also a junction of the short duct of the spherical receptaculum seminis. The curved bursa copulatrix empties via an elongate duct at a separate gonopore. The oviduct empties at the anterior end of the female gland mass adjacent to the penis. The vas deferens emerges near the junction of the ampulla and associated ducts, female gland mass and the receptaculum seminis. The vas deferens continues to the posterior end of the simple, unarmed, bulbous penis.

DISCUSSION. — The similarity of *T. vatae* with *T. albopustulosa* is included in the discussion of the former species. The lighter bluish body color of *T. albospustulosa* with diagonal rather than transverse red pigment on the rhinophores clearly distinguishes it externally from *T. vatae*. It is also more distantly related to *T. virgata* and *T. moebii*, all of which share the derived feature of an enlarged pharyngeal pouch.

13. **Thuridilla undula** sp. nov.

Thuridilla sp. Yonow, 1994: 106, figs. 5B, 6B.

TYPE MATERIAL. — Holotype: CASIZ 099072, one specimen, Cement Mixer Reef, Madang Lagoon, 3 m depth, 21 August 1989, M. T. Ghiselin.

Paratypes: CASIZ 099071, one specimen, Rasch Passage, Madang Lagoon, Papua New Guinea, 10 m depth, 20 August 1989, M. T. Ghiselin. CASIZ 099070, one specimen, dissected, Hole in the Wall, n. of Cape Croiselles, Madang Province, Papua New Guinea, 1 m depth, 22 July 1989, T. M. Gosliner. CASIZ 099069, one specimen, buoy 7, Palau, 1 m depth, 21 July 1977, C. Carlson and P. Hoff. CASIZ 103558, one specimen, n. side of n.w. passage, Puerto Galera, Mindoro, Philippine Islands, 10 m depth, 28 February 1995, M. Miller.

ETYMOLOGY. — This species is named for the undulating bands along and below the parapodial margins.

DISTRIBUTION. — This species is known from Papua New Guinea, Guam, Palau and the Philippines (present study) and the Maldives (Yonow, 1994).

EXTERNAL MORPHOLOGY. — The living animals (Fig. 29A) are turquoise bluish green. The parapodial margin is a broad undulating band of burnt orange. Below that is a narrow undulating line of black. This is followed by an undulating region of vivid blue reflective pigment. There is black and reflective blue pigment on the head. The base of the rhinophores are the same color as the rest of the body. At about the middle of the rhinophores are narrow bands of blue and black. The apex has a broad orange band. Orange, black and blue bands are also present on the anterior margins of the foot.

PERICARDIUM AND DORSAL VESSELS. — There is considerable variation in the extent of branching of the vessels in the two specimens examined (Fig. 30A, B), but the basic pattern is similar. In both cases, lateral and posterior vessels are present. The lateral vessels are trifurcate or more highly branched. The posterior vessels have an elongate common origin from the pericardium. The posterior vessels may be undivided or may have 2–3 undivided or bifurcate branches.

BUCCAL MASS AND RADULA. The pharyngeal pouch (Fig. 30C, D) is larger than the more muscular portion of the buccal mass, although it is relatively smaller than that of some other species. The esophageal pouch is ovoid and more elongate than in other species. The radula was examined in a single specimen from Papua New Guinea. There are 28 teeth with 16–18 coarse denticles on either side of the cutting margin. There were 11 teeth in the ventral limb, 9 in the dorsal one and 8 teeth in the ascus. The base of the teeth (Fig. 31) is shorter than the elongate triangular portion.

REPRODUCTIVE SYSTEM (Fig. 30E). — The ovotestis, prostate and albumen glands are diffuse and are arranged in the fashion described for *T. bayeri*. Their ducts join the spherical ampulla and join the female gland mass. At this point, there is also a junction of the elongate

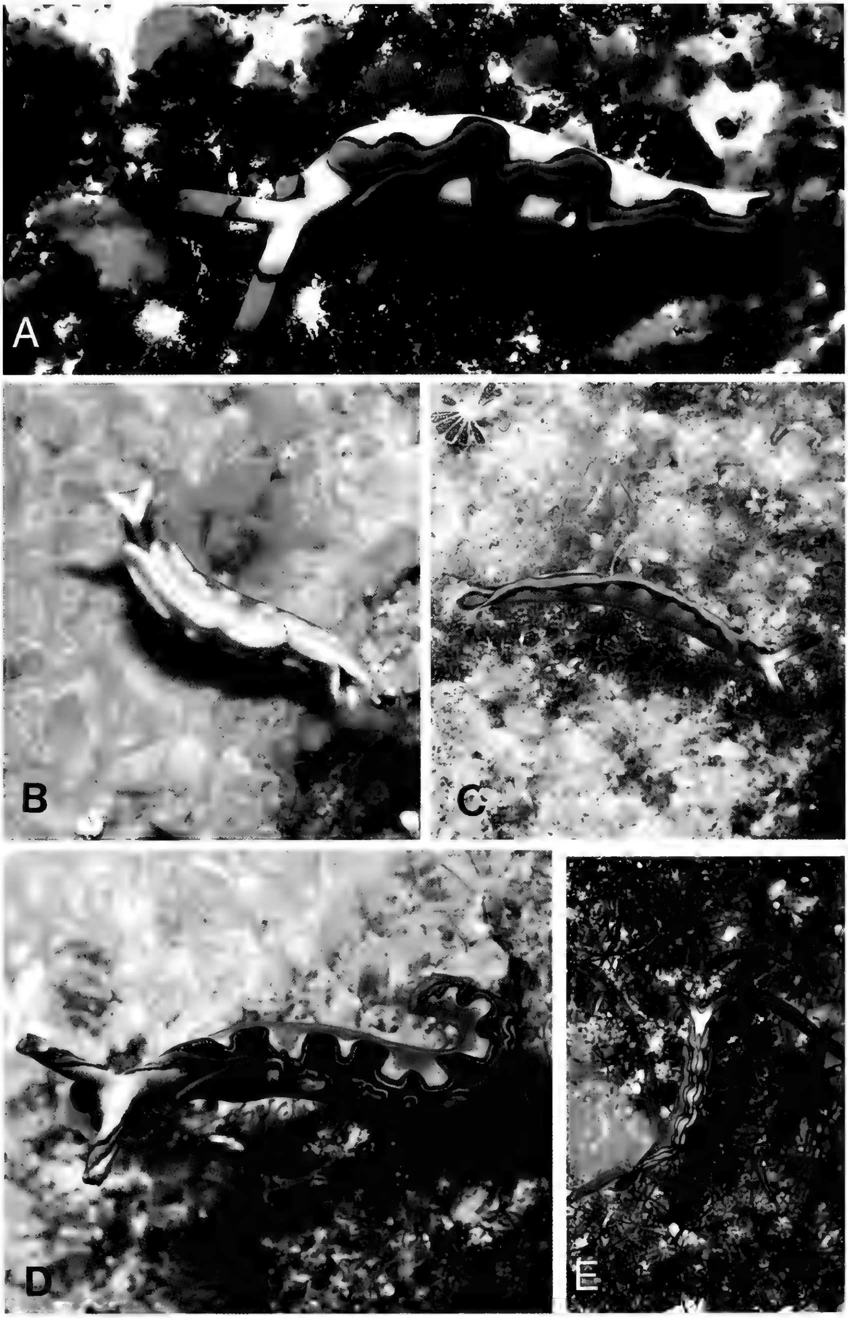

FIGURE 29. Living animals. A. *Thuridilla undula* sp. nov., Madang, Papua New Guinea, 25 mm in length. B. *Thuridilla albopustulosa* sp. nov., Madang, Papua New Guinea, 15 mm in length. C. *Thuridilla indopacifica* sp. nov., Sodwana Bay, South Africa, 18 mm in length. D. *Thuridilla neona* sp. nov., Midway Atoll, 22 mm in length. E. *Thuridilla multimarginata* sp. nov., Sodwana Bay, South Africa, 9 mm in length.

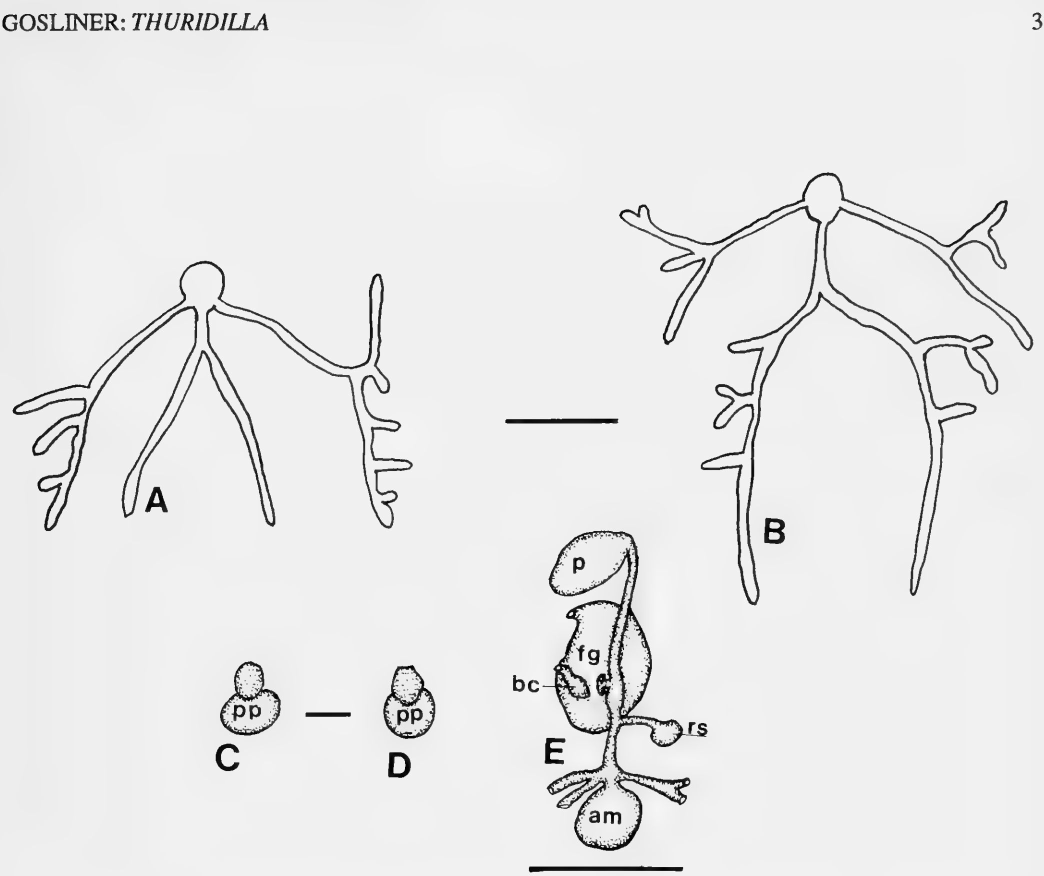

FIGURE 30. *Thuridilla undula* sp. nov. A., B. Branching of pericardial vessels, scale = 5.0 mm. C. Dorsal view of buccal mass. D. Ventral view of buccal mass. C., D. pp = pharyngeal pouch, scale = 0.20 mm. E. Ventral view of distal reproductive organs: am = ampulla, bc = bursa copulatrix, fg = female gland mass, p = penis, rs = receptaculum seminis, scale = 1.0 mm.

duct of the spherical receptaculum seminis. The small bursa copulatrix empties via a moderately long duct at a separate gonopore. The oviduct empties at the anterior end of the female gland mass adjacent to the penis. The vas deferens emerges near the junction of the ampulla and associated ducts, female gland mass and the receptaculum seminis. The vas deferens continues to the posterior end of the large, unarmed, bulbous penis.

DISCUSSION.—*Thuridilla undula* is a strikingly beautiful member of the genus. It is similar in coloration to *T. neona* sp. nov. Both species have a turquoise body with burnt orange, black and blue undulating parapodial bands. Despite these similarities in color, there are some consistent differences between the species. In *T. neona*, there are additional bright orange markings present on the parapodia, anterior margin of the foot and rhinophores. In *T. undula* the orange, blue and black markings on the rhinophores are transverse bands, while in *T. neona* they are diagonal.

The two species differ markedly in other aspects of their morphology. In *T. undula*, both lateral and posterior vessels emerge from the pericardium, while in *T. neona* only posterior vessels are present. The radular teeth of *T. undula* are narrower and have a deeper dorsal notch than do those of *T. neona*. Also, the denticles of *T. undula* do not continue as striations on the lateral and dorsal surfaces of the the teeth as they do in *T. neona*. In *T. undula*, the denticles extend below the level of the tooth margin, while in *T. neona* the denticles are flush with the margin.

Thuridilla undula appears to be most closely related to *T. lineolata*. The two have similar coloration and differ from other members of their clade by lacking an expanded pharyngeal

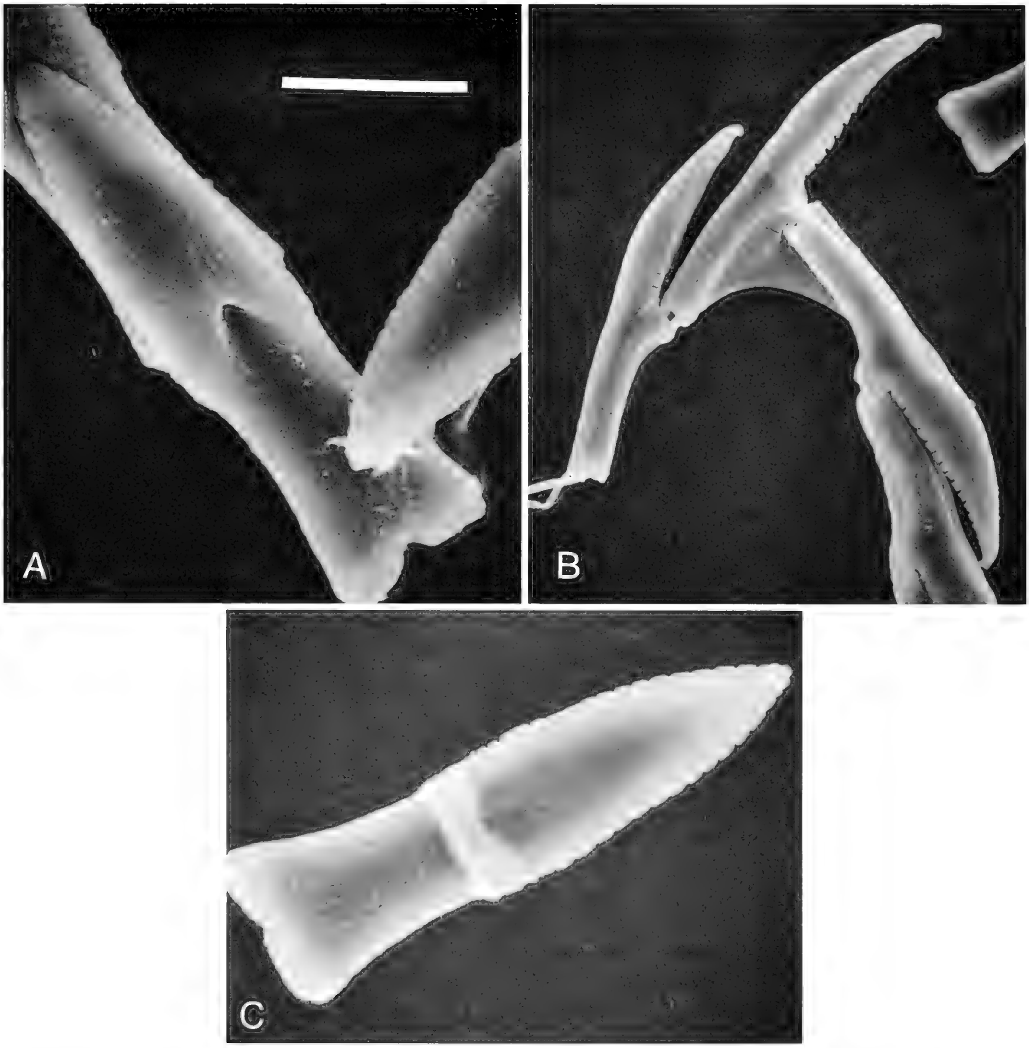

FIGURE 31. *Thuridilla undula* sp. nov. Radular teeth of specimen from Papua New Guinea, CASIZ 099070. A. Dorsal view. scale = 10 µm. B. Lateral view, scale = 20 µm. C. Ventral view, scale = 10 µm.

pouch or longitudinal white lines on the parapodia. In *T. undula* the lateral branches of the pericardium are highly ramified, while in *T. lineolata* they are only bifurcate. In *T. undula* the posterior vessels have a common junction prior to entering the pericardium while in *T. lineolata* they have separate insertions into the pericardium.

14. Thuridilla neona sp. nov.

TYPE MATERIAL. Holotype: CASIZ 074461, onespecimen, Lanai, Hawaiian Islands, July 1990, S. McLellan.

Paratypes: CASIZ 088551, one specimen, dissected, near white cross n. of harbor entrance, Sand Island, Midway Atoll, 5 June 1993, T. M. Gosliner. CASIZ 076462, three specimens, Hekili Point, Maui, Hawaiian Islands, on algal turf, 0.5 m depth, October

1990, C. Pittman.

ETYMOLOGY. — This species is named for the bright "electric" colors which adorn the parapodia, head and anterior margins of the foot.

DISTRIBUTION. — Windward and leeward Hawaiian Islands (present study; Scott Johnson, pers. comm.).

EXTERNAL MORPHOLOGY. — The living animals (Fig. 29D) are green with a slight bluish tinge. The margin of the parapodia is lined with a broad, undulating band of burnt orange. Inside of that are thin undulating bands of reflective bright orange, black and reflective bright blue. The head and base of the rhinophores are opaque white. The head has a series of lines. The lateral margin of the head has lines of reflective blue followed by black, reflective orange, and burnt orange. The rhinophores have a series of diagonal lines of reflective blue, black, reflective orange, burnt orange and white pigment. The apex of the rhinophores is orange. The anterior margin of the foot is burnt orange.

PERICARDIUM AND DORSAL VESSELS (Fig. 32A, B). — Lateral vessels are absent. The posterior vessels have separate origins from the pericardium. The specimen from Lanai had a single, undivided branch emerging from the middle of either vessel. The specimen from Midway has an asymmetrical and complex branching pattern with connections between adjacent branches.

BUCCAL MASS AND RADULA. — The pharyngeal pouch (Fig. 32C) is larger than the muscular portion, though not as large relatively as many other species. The radula was examined in one specimen from Midway Island and consists of 23 teeth. Eight teeth are present in the ascus, 6 in the ventral limb and 9 in the dorsal one. The teeth (Fig. 33) are triangular with 22–24 coarse denticles that continue dorsally as prominent striations. The denticles are unusual in that they do not extend below the level of the tooth margin. This is not owing to wear as this feature is present in newly formed teeth as well as older ones.

REPRODUCTIVE SYSTEM (Fig. 32D). — The ovotestis, prostate and albumen glands are diffuse and are arranged as in *T. bayeri*. Their ducts join the massive spherical ampulla and the female gland mass. At this point, there is also a junction of the elongate duct of the spherical receptaculum seminis. The moderately large bursa copulatrix empties via a short duct into a separate gonopore. The oviduct empties at the anterior end of the female gland mass adjacent to the penis. The vas deferens emerges near the junction of the ampulla and associated ducts, female gland mass and the receptaculum seminis. The vas deferens continues to the posterior end of the simple, unarmed, club-shaped penis.

DISCUSSION. — *Thuridilla neona* resembles *T. undula* in its coloration. The similarities and differences between these taxa are compared in the discussion of *T. undula*.

Thuridilla neona appears to be most closely related to *T. hopei* (Verany, 1853) from the Mediterranean. The two species differ markedly in their coloration (present study). *Thuridilla hopei* has a bluish body color, but lacks the burnt orange, black and blue lines around the parapodial margin that are present in *T. neona*.

Internally, *T. neona* appears to have wider teeth than *T. hopei*. The penial bulb in *T. neona* is widest distally, while that of *T. hopei* is widest proximally.

15. **Thuridilla indopacifica** sp. nov.

Elysia sp. 1 Gosliner, 1987: 54, fig. 46.
Thuridilla sp. Wells and Bryce, 1993: 67, fig. 73.

TYPE MATERIAL. — Holotype: CASIZ 099073, one specimen, Middle Camp, Aldabra Atoll, 2 m depth, 18 March 1986, T. M. Gosliner.

Paratypes: SAM A 35270, one specimen, Mbibi, Sodwana Bay National Park, Natal, South Africa, 1 m depth, 6 May 1981, T. M. Gosliner. SAM A 35294, five specimens, Mbibi, Sodwana Bay National Park, Natal, South Africa, 6 May 1981, T. M. Gosliner. SAM A 35279, two specimens, one dissected, Mbibi, Sodwana Bay National Park, Natal, South Africa, 2 m depth, 6 May 1981, T. M. Gosliner. SAM A 35277, one specimen, Mbibi, Sodwana Bay National Park, Natal, South Africa, T. M. Gosliner. CASIZ 073974, five specimens, Mbibi, Sodwana Bay National Park, Natal, South Africa, 6 May 1981, T. M. Gosliner. CASIZ 073972, one specimen, Mbibi, Sodwana Bay National Park, Natal, South Africa, May 1982, T. M. Gosliner. CASIZ 074240, two specimens, one dissected, Middle Camp, Aldabra Atoll, Seychelles, 18 March 1986, T. M. Gosliner.

ETYMOLOGY. — This species is named for

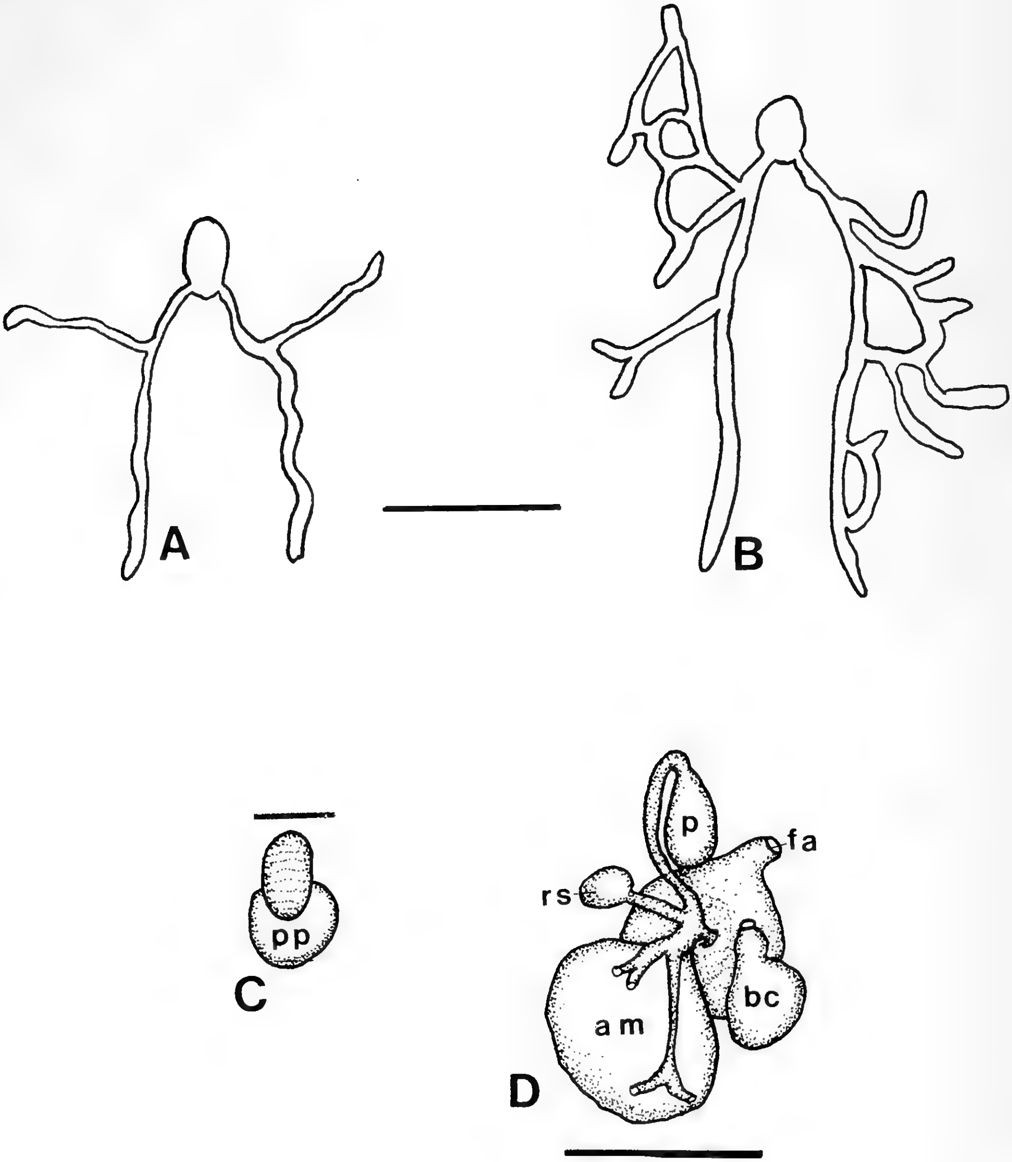

FIGURE 32. *Thuridilla neona* sp. nov. A., B. Branching of pericardial vessels, scale= 5.0 mm. C. Dorsal view of buccal mass, pp= pharyngeal pouch, scale = 0.25 mm. D. Distal reproductive organs: am = ampulla, bc = bursa copulatrix, fa = female aperture, p = penis, rs = receptaculum seminis, scale = 1.0 mm.

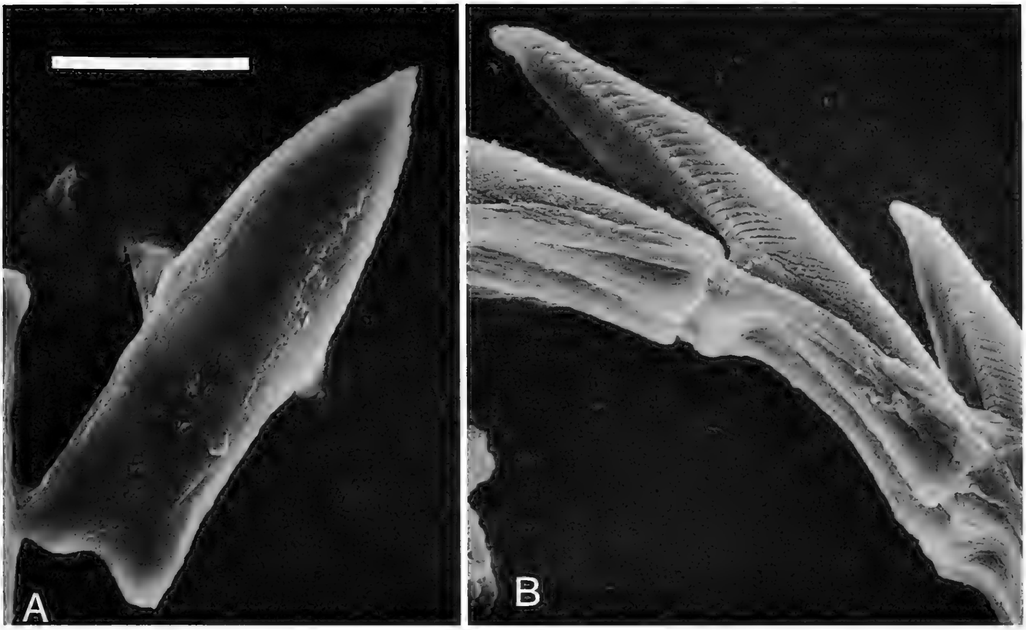

FIGURE 33. *Thuridilla neona* sp. nov. Radular teeth of specimen from Midway Atoll, CASIZ 088551. A. Dorsal view, scale = 15 µm. B. Lateral view, scale = 15 µm.

the Indo-Pacific tropics, the region where *Thuridilla* reaches its highest diversity.

DISTRIBUTION. — South Africa (Gosliner, 1987), Aldabra Atoll (present study), Western Australia (Wells and Bryce, 1993).

EXTERNAL MORPHOLOGY. — The body is green (Fig. 29C), covered with minute opaque white spots. The parapodia are lined with a thin band of black, followed by a broad band of orange, an irregular band of black with a series of ventral extensions of pigment. Between the black extensions are patches of reflective bright blue. The head is covered with opaque white, which extends on to the basal half of the rhinophores. Above this is a diffuse band of blue followed by black, orange and blue bands. The anterior margin of the foot has black, orange, black and blue bands.

PERICARDIUM AND DORSAL VESSELS. — Lateral vessels are absent (Fig. 34A, B). The posterior vessels have separate origins from the pericardium. Two to five undivided or bifurcate vessels emerge from each lateral vessel.

BUCCAL MASS AND RADULA. — The pharyngeal pouch (Fig. 34C, D), is much larger than the muscular portion of the mass. The radula, examined in a single specimen from South Africa, contains 29 teeth. There are 12 teeth in the ascus, 10 in the ventral limb and 7 in the dorsal one. The teeth (Fig. 35) are triangular with 17–19 coarse denticles that continue as prominent striations on to the dorsal surface of the teeth. The basal portion of the teeth is slightly shorter than the cutting margin.

REPRODUCTIVE SYSTEM (Fig. 34E). — The ovotestis, prostate and albumen glands are diffuse and are arranged in the fashion described for *T. bayeri*. Their ducts join the ovoid ampulla and together join the female gland mass. At this point, there is also a junction of the short duct of the spherical receptaculum seminis. The large bursa copulatrix empties via a short duct at a separate gonopore. The oviduct empties at the anterior end of the female gland mass adjacent to the penis. The vas deferens emerges near the junction of the ampulla and associated ducts, female gland mass and the receptaculum seminis. The vas deferens continues to the posterior end of the simple, unarmed, club-shaped penis.

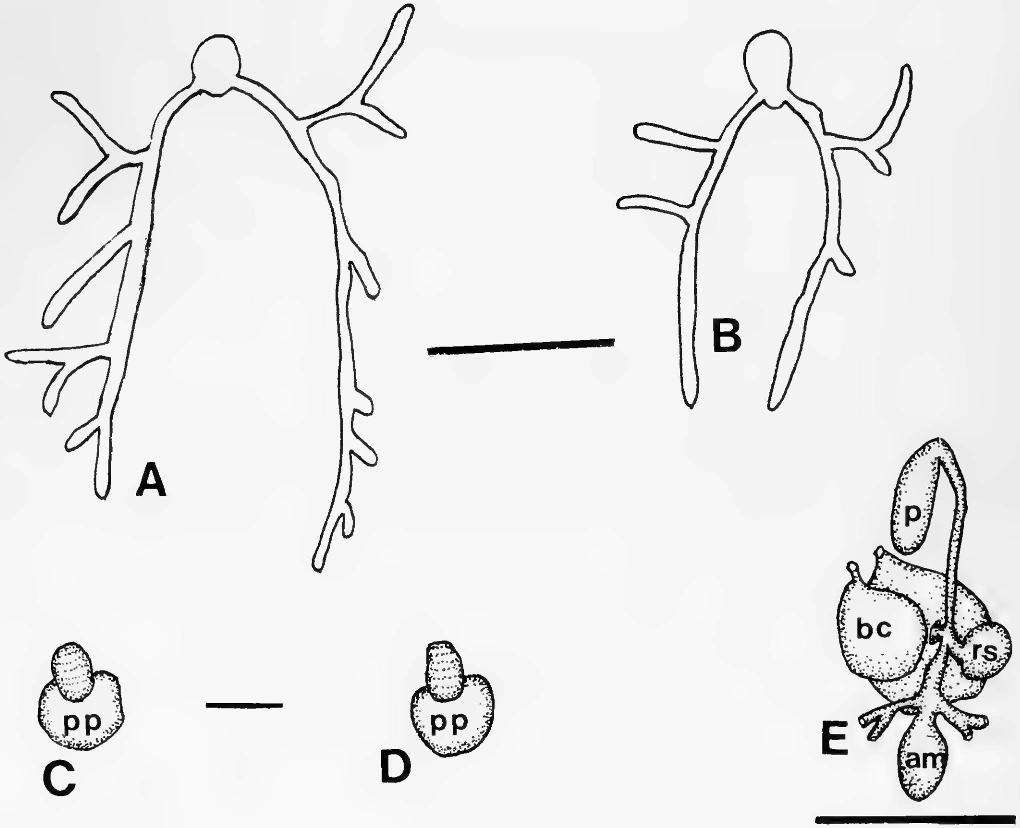

FIGURE 34. *Thuridilla indopacifica* sp. nov. A., B. Branching of pericardial vessels, scale = 5.0 mm. C. Dorsal view of buccal mass, pp = pharyngeal pouch, scale = 0.25 mm. D. Ventral view of buccal mass, pp= pharyngeal pouch, scale = 0.25 mm. E. Ventral view of distal reproductive organs: am = ampulla, bc = bursa copulatrix, p = penis, rs = receptaculum seminis, scale = 1.0 mm.

DISCUSSION. — *Thuridilla indopacifica* appears to be most closely related to *T. picta* (Verrill, 1901), which is known from the tropical Atlantic (Marcus and Marcus, 1967, as *E. duis*; Ortea, Luque and Templado, 1988). Both species have a greenish body color with orange and blue marking on the parapodia. *Thuridilla indopacifica* also has a black parapodial line that is sometimes absent in *T. picta.* The parapodial lines of *T. picta* are far more undulating than in *T. indopacifica. T. indopacifica* also has more white pigment on the head than does *T. picta.*

The branching of the pericardial vessels is similar in the two species. Both lack lateral vessels and have only paired posterior vessels with separate insertions into the pericardium. In *T. indopacifica*, the radular teeth have denticles that extend well below the margin of the tooth, while in *T. picta* they are flush with the margin. The penis of *T. indopacifica* is club- shaped, while it is far more bulbous in *T. picta.*

16. **Thuridilla multimarginata** sp. nov.

Elysia sp. 3 Gosliner, 1987: 55, fig. 48.

TYPE MATERIAL. — Holotype: CASIZ 088426, patch reef inside lagoon, n of Sand Island, Midway Atoll, 3 m depth, 1 June 1993, Pauline Fiene-Severns.

Paratypes: SAM A35282, one specimen, radula re-

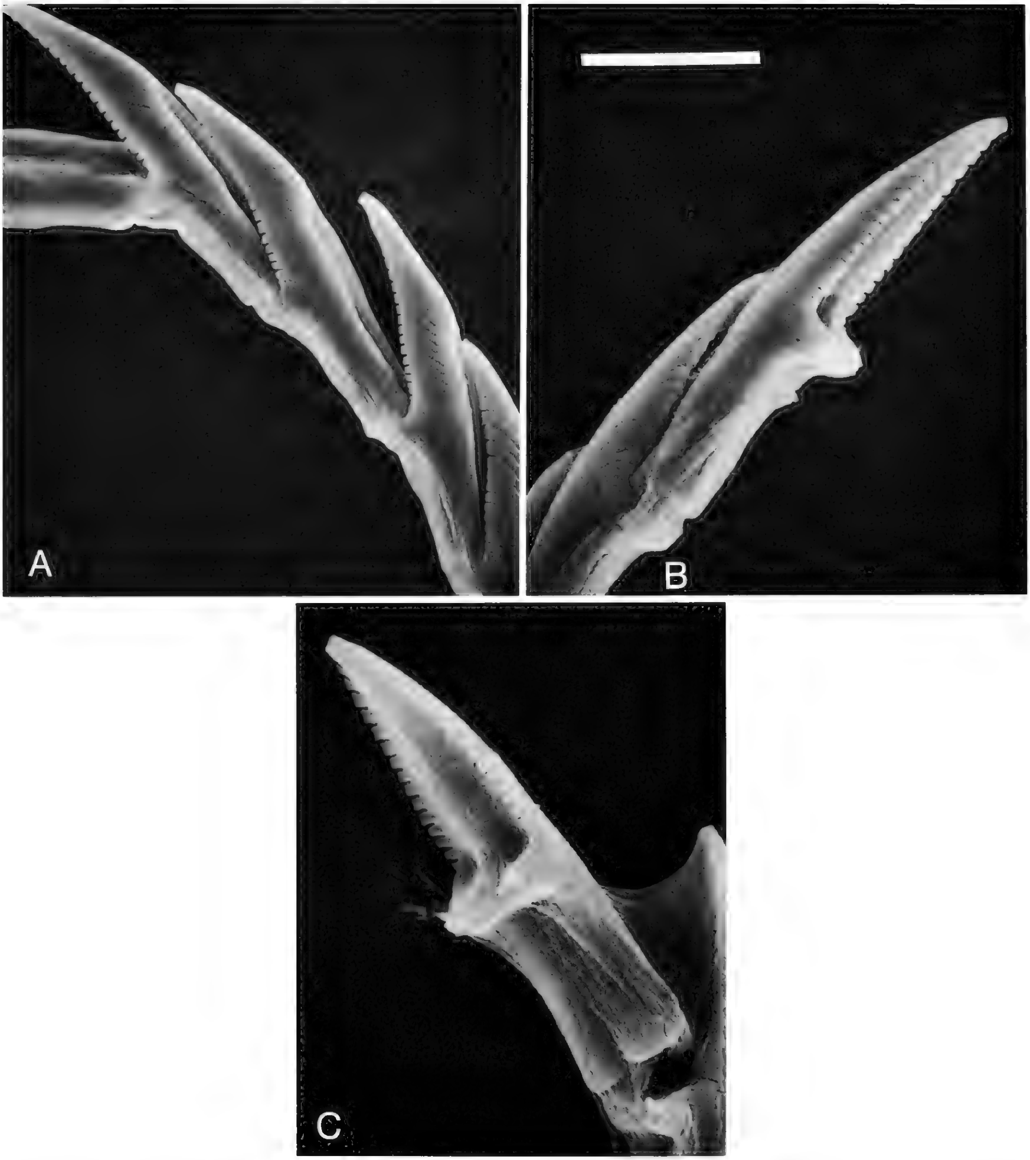

FIGURE 35. *Thuridilla indopacifica* sp. nov. Radular teeth of specimen from South Africa, SAM A35279. A. Dorsal view, scale = 20 µm. B. Lateral view, scale = 15 µm. C. Ventral view, scale = 10 µm.

moved, Adlam's Reef, Sodwana Bay National Park, Natal, South Africa, 1 m depth, 9 May 1982, T. M. Gosliner. CASIZ 078647, one specimen, dissected, Hekili Point, Maui, Hawaiian Islands, 1 m depth, 22 May 1991, C. Pittman.

ETYMOLOGY. — This species is named for the multiple bands of pigment found on and below the parapodial margins.

DISTRIBUTION. — South Africa (Gosliner, 1987), windward and leeward Hawaiian Islands (present study).

EXTERNAL MORPHOLOGY. — The living an-

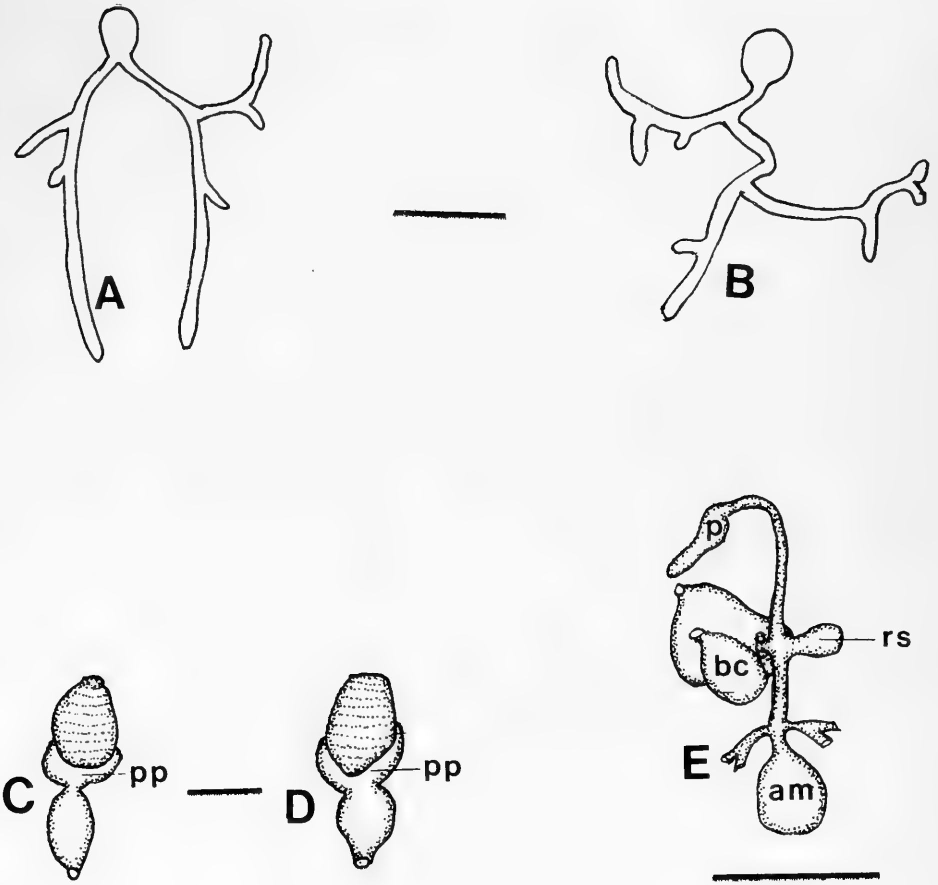

FIGURE 36. *Thuridilla multimarginata* sp. nov. A., B. Branching of pericardial vessels, scale = 5.0 mm. C. Dorsal view of buccal mass. D. Ventral view of buccal mass. C., D. pp = pharyngeal pouch, scale = 0.25 mm. E. Ventral view of distal reproductive organs, am = ampulla, bc = bursa copulatrix, p = penis, rs = receptaculum seminis, scale = 1.0 mm.

imals (Fig. 29E) are light to dark green. The parapodia contain a sequence of several undulating bands or series of interrupted bands. The margin contains interrupted spots of opaque white. Below that, is a series of interrupted patches of bright orange. Ventral to this level, are a series of thin undulating bands of black, reflective blue and black. The head and most of the rhinophores have opaque white pigment with a black tip. The specimen from southern Africa has more diffuse black pigment while the Hawaiian specimens have some green and opaque white on most of the rhinophores with black at the apex. The anterior margin of the foot has orange, black, blue and black lines.

PERICARDIUM AND DORSAL VESSELS. — Lateral vessels are absent (Figure 36A, B). The posterior vessels have a common origin from the pericardium. In the South African specimen, there are 2 undivided or bifurcate vessels emerging from each posterior vessel. In the Hawaiian specimen, the branching pattern is irregular and asymmetrical, with three undivided to trifid branches.

BUCCAL MASS AND RADULA. — The pharyngeal pouch (Fig. 36C, D) is much smaller than the muscular portion and is barely visible when viewed dorsally. The esophageal pouch

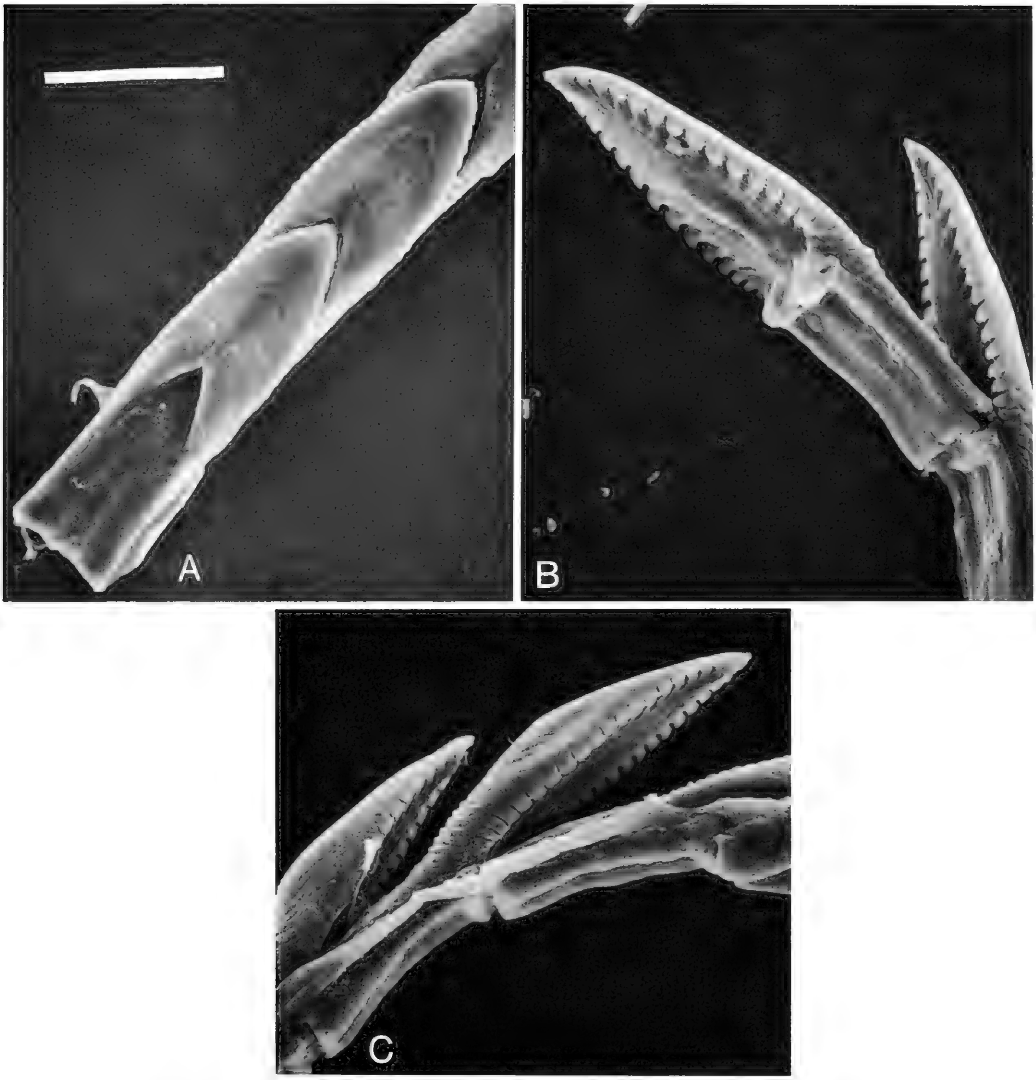

FIGURE 37. *Thuridilla multimarginata* sp. nov. Radular teeth. A. Dorsal view of specimen from South Africa, SAM A35282, scale = 43 µm. B. Lateral view of same specimen, scale = 30 µm. C. Ventral view of specimen from Hawaii, CASIZ 078647, scale = 25 µm.

is ovoid, almost as large as the buccal mass. The radula was examined in one specimen from South Africa and one from Hawaii and consists of 24–29 teeth. Neither specimen had any teeth in the ascus. The ventral limb had 18 and 22 teeth and the dorsal one had 6 or 7 teeth. The teeth (Fig. 37) are 83–103 µm in length. They are broad and triangular with 18–21 coarse denticles along either side of the cutting margin. The denticles continue dorsally as striations. The dorsal surface of the tooth (Fig. 37A) has a prominent triangular cavity where the cutting portion of the adjacent tooth fits snugly. The basal portion of the tooth is slightly shorter than the cutting one. The posterior end of the tooth is largely flat, without a distinct indentation.

REPRODUCTIVE SYSTEM (Fig. 36E). — The ovotestis, prostate and albumen glands are diffuse and are arranged as in *T. bayeri*. Their ducts join the spherical ampulla and the female gland mass. At this point, there is also a junction of the short duct of the spherical receptaculum seminis. The large bursa copulatrix empties via a short duct into a separate gonopore and contained large masses of spermatozoa in both specimens examined. The oviduct empties at the anterior end of the female gland mass adjacent to the penis. The vas deferens emerges near the junction of the ampulla and associated ducts, female gland mass and the receptaculum seminis. The vas deferens continues to the posterior end of the simple, unarmed penis. The penis is wider proximally and abruptly narrows near the middle of its length.

DISCUSSION. —*Thuridilla multimarginata* retains some of the least derived anatomical features. The buccal mass is highly muscularized with a proportionately small pharyngeal pouch. It has large, wide radular teeth with a prominent dorsal notch. Other aspects of its morphology are highly derived. The lateral pericardial vessels have been lost and the posterior vessels have a common insertion with the pericardium. The radular teeth have striations that extend from the denticles on to the surface of the tooth. The duct of the receptaculum seminis is elongate.

In its external morphology, *T. multimarginata* most closely resembles *T. indopacifica* and *T. livida*. All three species have orange, black and blue parapodial lines. *Thuridilla multimarginata* has additional white pigment and an additional black and orange line that are not present in either other species. In addition, *T. indopacifica* and *T. livida* lack the plesiomorphic features described above for *T. multimarginata*.

DISCUSSION

Phylogeny of the Elysiidae

The systematics and phylogeny of the Indo-Pacific Elysiidae have been recently discussed by Jensen (1992). She critically discussed the morphological variability and polarity of some forty characters within the Elysiidae. Many of these characters are autapomorphic within elysiid taxa or may be resolved within sacoglossan clades below the level of the Elysiidae. Characters which are informative in resolving elysiid phylogeny are listed in Table 1. Their polarities have been discussed by Jensen and will not be repeated here. In some cases, characters have been excluded from consideration since they cannot be adequately polarized using the stiligeroids as an outgroup. For example, Jensen considered a dorsal anus plesiomorphic within the Elysiidae, as the majority of stiligeroid genera have a dorsal anus. However, species of several genera including *Mourgona* and *Caliphylla* have a lateral anus. One cannot resolve the polarity of this character within the Elysiidae using the stiligeroids as an outgroup in the absence of a stiligeroid phylogeny. Presence of a feature in the majority of the outgroup is not sufficient to consider it plesiomorphic. Within the Elysiidae, a dorsal anus is present only in *Placobranchus*. In the resulting phylogeny of the Elysiidae (Fig. 38), it is less parsimonious to consider the dorsal anus plesiomorphic than apomorphic. For the dorsal anus to be considered plesiomorphic requires three steps within the tree, while considering it apomorphic requires a single step.

In addition to the characters considered by Jensen, two others were included in the present analysis. In the branching of the vessels of the pericardium there may be multiple vessels, few vessels or no vessels. In stiligeroids, there are 3 or more vessels emanating from either side of the pericardium. This is considered the plesiomorphic arrangement for the Elysiidae. In elysiids, the radular teeth may have denticles or entirely lack them. When present, the denticles may be small serrations or large rectangular cusps. Rectangular cusps are not found in stiligeroids, though the denticles of some species of *Cyerce* are more broadly triangular. Rectangular cusps are considered apomorphic within the Elysiidae.

Species of *Elysia* are variable for several characters. For this reason, four different species of *Elysia* which depict the range of variation were included in the analysis.

The condition of the parapodia is treated here as the only multistate character. In *Bosellia*, parapodia are absent while in *Elysiella* the parapodia are reduced. In the remainder of taxa, the parapodia are well developed. This character was treated as unordered and no *a priori* judgments were made as to whether the absence of

Table 1. Characters and states for the phylogeny of the Elysiidae

Character	plesiomorphic	apomorphic
1. parapodia	wide	short, absent
2. dorsal lamellae	absent	present
3. foot sole	with margin	indistinct margin
4. pericardium	short	elongate
5. pericardial vessels	3 or more	2 or less
6. ascus muscle	short	long
7. pharynx	large	small
8. pharyngeal pouch	present	absent
9. tooth shape	triangular	blade-shaped
10. denticles	small	large
11. penial stylet	present	absent
12. ampulla	hermaphroditic duct	separate duct

Character #	1	2	3	4	5	6	7	8	9	10	11	12
ancestor	0	0	0	0	0	0	0	0	0	0	0	0
E. papillosa	0	0	0	0	0	1	0	1	1	0	0	1
E. timida	0	0	0	0	1	1	0	1	1	0	1	1
E. ornata	0	0	1	0	0	1	0	1	1	0	1	1
E. trisinuata	0	0	0	1	0	1	0	1	1	0	1	1
Tridachia	0	0	0	0	0	1	0	1	1	0	1	1
Tridachiella	0	0	0	0	0	1	0	1	1	0	1	1
Elysiella	1	0	0	1	0	1	0	1	1	0	1	1
Pattyclaya	0	1	0	1	0	1	0	1	1	0	1	1
Thuridilla	0	0	1	0	1	0	1	0	0	1	1	1
Placobranchus	0	1	1	0	1	0	1	0	0	1	0	1
Bosellia	2	0	0	0	0	0	0	0	0	0	0	0

parapodia in *Bosellia* is plesiomorphic or due to secondary loss.

In her analysis of the Elysiidae, Jensen focused on Indo-Pacific taxa and did not consider the genera *Tridachia* and *Tridachiella* in her detailed discussion of phylogenetic relationships. For the purposes of this discussion, these taxa are considered in addition to the taxa treated by Jensen. Specimens of *Tridachia crispata* Mörch, 1863 (CASIZ 067560, Roatan) and *Tridachiella diomdedea* (Bergh, 1894) (CASIZ 066938, Bahía de los Angeles, Baja California) were examined to compare with the described anatomy of these species.

Jensen (1992) considered *Bosellia* as a member of the same clade as the elysiids. However, she contended that it should not be considered as a member of the Elysiidae, since it lacks parapodia, a separate ampulla or a highly branched prostate, all obvious apomorphic characters of the family. Jensen noted that while lacking parapodia, species of *Bosellia* have a densely branched digestive gland and a ciliated groove that continues across the foot sole and considered these as synapomorphies of *Bosellia* plus the Elysiidae. Whether one considers the Elysiidae to be diagnosed by the possession of densely branched digestive gland or parapodia is entirely arbitrary. However, the fact remains that *Bosellia* is more closely related to other elysiids than to any other sacoglossan. Rather than include the genus *Bosellia* in its own

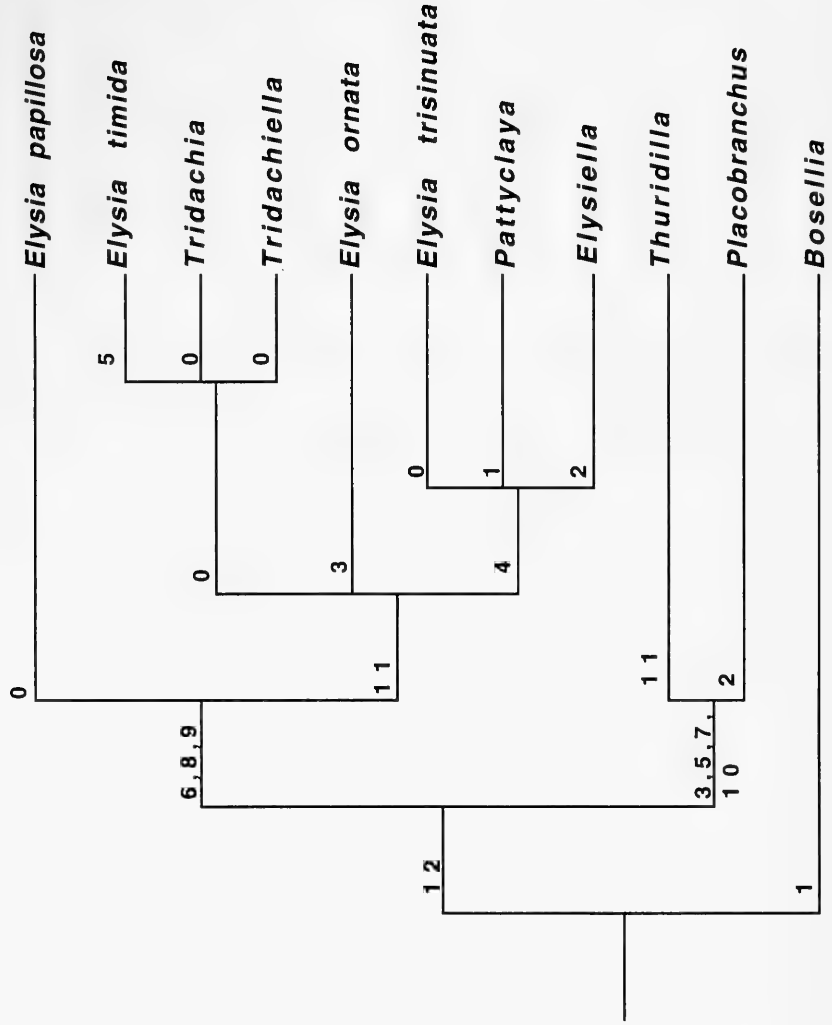

FIGURE 38. Phylogeny of the Elysiidae, numbers refer to characters listed in Table 1.

monogeneric taxon, I prefer to consider all of the descendants of the common ancestor with densely branched digestive gland and ciliated groove expanded to form a foot sole to represent the Elysiidae.

When the characters listed in Table 1 were analyzed using PAUP version 3.1, a single tree was produced (Fig. 38). The thirteen variations of the tree produced using this version of PAUP are all resolved into the single tree depicted here when branches not supported by apomorphies are collapsed. This tree has a consistency index of 0.722. From this tree several things regarding the phylogeny of the Elysiidae are evident. *Bosellia* is the least derived member of the clade, in that the ampulla is plesiomorphic. *Placobranchus* and *Thuridilla* represent a well-supported clade that is clearly distinct from the other well-supported clade containing *Elysia*, *Elysiella*, *Pattyclaya*, *Tridachia* and *Tridachiella*.

Within the second clade, there is little resolution of phylogeny. However, separation of the genera *Pattyclaya* and *Elysiella* renders *Elysia* paraphyletic since no apomorphic characters are shared by all members of *Elysia*. This fact was first noted by Jensen (1992) and is also the case in the present analysis based largely upon her investigation. *Tridachia* and *Tridachiella* have been separated from *Elysia* on the basis of their undulate parapodia. MacFarland (1924) described *Tridachiella* as distinct from *Tridachia*, as the parapodia were not joined anteriorly. However, all other elysiids with parapodia have them unjoined, and this is clearly plesiomorphic. MacFarland indicated that the anus of *Tridachiella* was situated near the pericardium rather than laterally, but did not discuss the systematic relevance of this apparent difference. Re-examination of *Tridachiella diomedea* here indicates that MacFarland was in error. The anus of *T. diomedea* is lateral, as in all elysiids other than species of *Placobranchus*. Maintenance of *Tridachia* as a distinct genus renders *Tridachiella* paraphyletic, as there are no autapomorphic features which support it. Jensen (1992) noted that these genera are all monotypic except for *Pattyclaya*, which includes two species. Based on the present phylogenetic analysis, *Tridachiella*, *Tridachia*, *Elysiella* and *Pattyclaya* are regarded as synonyms of *Elysia*, as this is the oldest name for the most inclusive monophyletic group. *Elysia* represents a large and morphologically diverse taxon. Further phylogenetic analysis of this taxon is needed to ascertain whether monophyletic subclades do in fact exist.

The monophyletic group containing *Thuridilla* and *Placobranchus* is supported by four apomorphies, a modified foot sole, reduced lateral pericardial vessels, a small pharynx and presence of rectangular denticles on the teeth. The latter two of these are unique to members of this clade, while the first two have also arisen independently within *Elysia*. *Placobranchus* has several synapomorphies shared by members of the taxon including: a broad head, well-developed longitudinal dorsal lamellae, median eyes, dorsal anus, and reduced pericardial vessels. *Placobranchus* has been regarded as a monotypic genus containing only *P. ocellatus* van Hasselt, 1824 and its many synonyms. Another undescribed species has been found in the western Pacific and will be treated in a separate paper.

Species of *Thuridilla* also share several apomorphic features: elongate rhinophores, single, thick, darkly pigmented ampulla, non-muscular, unarmed penis, bursa copulatrix with separate gonopore and orange or red eggs. Bright coloration, indicated as an autapomorphy of *Thuridilla* by Jensen (1992), is not an autapomorphy for the taxon, as some species are more drably colored (see subsequent discussion of *Thuridilla*), thus retaining the plesiomorphic state. The above phylogeny and the autapomorphic features described for *Thuridilla* indicate that it is indeed a monophyletic taxon within the Elysiidae.

Aspects of the ecology of these species are interesting in light of the hypothesis of phylogeny presented here. Virtually all of the least derived sacoglossans are intimately associated with siphonaceous chlorophytes of the genus *Caulerpa*. Several workers (Gosliner, 1987; Clark and DeFreese, 1987) have suggested that the sacoglossans have undergone most of their adaptive radiation on *Caulerpa*. Most species of *Elysia* (including species originally considered as *Tridachia*, *Tridachiella*, *Elysiella* and *Pattyclaya* but here included in *Elysia*) are intimately associated with their algal food and are usually cryptic upon their food. Species are not often observed crawling away from their preferred food. In contrast, species of *Placobranchus* and *Thuridilla* are generally observed crawling freely in the open, and have not been observed in association with particular algae. *Placobranchus* spp. are found crawling partially buried under fine silty sediment while species of *Thuridilla* are found on shallow reefs. It appears that the morphological divergence noted in the proposed phylogeny is mirrored in their ecological radiation. Little is known about the relative palatability of *Elysia*, *Placobranchus* and *Thuridilla*, but species of *Thuridilla* are brightly colored and readily observed in the open, while species of *Elysia* and *Placobranchus* are generally cryptic. This might suggest that species of *Thuridilla* have better developed chemical defense mechanisms

Table 2. Tooth length in *Thuridilla* species

Species	Tooth length (in µm)
bayeri	40-50
lineolata	27-40
livida	40
moebi	43
splendens	40-60
vatae	40-60
virgata	50
carlsoni	105-115
kathe	52-59
flavomaculata	60
hoffae	50
albopustulosa	30
undula	33-47
indopacifica	30-44
multimarginata	83-103
neona	45-50
picta	56
hopei	45-60
decorata	34

and may be employing aposematic warning coloration. This hypothesis certainly requires testing in both field and laboratory situations.

Morphological variability in *Thuridilla* and polarity of characters.

In examining the morphological variability within *Thuridilla*, species of *Placobranchus* and *Elysia* were considered as outgroups for determination of polarity. Twenty-three characters were determined to be informative, though two were autapomorphic and were excluded from cladistic analysis. Data from the literature (primarily from the recent work of Jensen (1992)) was used for *T. hopei* (Verany, 1853) and *T. decorata* (Heller and Thompson, 1983). The remaining species were examined from specimens in the collections of the California Academy of Sciences. In addition to the species described here, a specimen of *T. picta* (Verrill, 1901) was examined, as its anatomy had not been completely described. Anatomical data was available for all known species of *Thuridilla* with the exceptions of *T. caerulea* (Kelaart, 1858), *T. gracilis* (Risbec, 1928) and *T.* sp. 75 of Wells and Bryce (1993). The following characters were considered:

1. Ground color. — Virtually all species of *Elysia* and *Placobranchus* have a uniformly green body color. Several species of *Thuridilla* are greenish while others have brightly colored general body color. This is also true of most other sacoglossans. Here green is considered plesiomorphic while other colors are considered derived.

2. Tooth size. — In virtually all species of *Elysia* and *Placobranchus*, the radular teeth are large, more than 100 µm in length. Within the *Thuridilla*, only *Thuridilla carlsoni* and *T. multimarginata* have teeth of this size. In the remaining species, the teeth are smaller than 75 µm (Table 2). This latter state is considered apomorphic.

3. Buccal mass size. — In all species of *Elysia* a pharyngeal pouch is absent. In *Placobranchus*, the anterior muscular portion of the buccal mass is larger than the pharyngeal pouch. This is also the case in *T. carlsoni*, *T. multimarginata* and *T. kathae* and *T. flavomaculata*. In the remaining species of *Thuridilla*, the muscular portion is equal to or smaller than the pharyngeal pouch. A proportionately larger pharyngeal pouch is considered derived.

4. Dorsal notch. — Most species of *Elysia* have a prominent notch on the dorsal surface of the tooth where the acute end of the adjacent tooth abuts. A notched tooth is present in most stiligeroids as well. The radular teeth of *Placobranchus* lack a deep notch. In *Thuridilla carlsoni* and *T. multimarginata*, a prominent dorsal notch is present. This is considered plesiomorphic in *Thuridilla*. In the remaining species, the notch is reduced or entirely absent and is considered apomorphic.

5. Lateral pericardial vessels. — In many species of stiligeroids and most species of *Elysia* there are three or more pairs of lateral vessels emanating from the pericardium. In some species of *Elysia*, the number of vessels is smaller. In *Elysia timida*, for example, only the posterior pair of vessels is present. In *Placobranchus*, no vessels are present. In species of *Thuridilla*, two pairs of vessels may be present or only the pos-

terior pair remains. A single pair of vessels is considered apomorphic, although the character is variable within *T. livida*.

6. Branching of lateral vessels. — In species of *Thuridilla* the lateral vessels from the pericardium, when present, may be highly branched or poorly ramified. Both conditions occur in species of *Elysia*. As there is a trend towards reduction in the degree of branching of the vessels in stiligeroids and species of *Elysia*, reduction in branching or complete loss of lateral vessels are considered apomorphic for *Thuridilla*.

7. Insertion of posterior vessels. — In most *Elysia* and all stiligeroids, the right and left posterior vessels enter the pericardium separately. This condition also occurs in several species of *Thuridilla*, although it may vary in species such as *T. bayeri* and *T. hopei*. In some species of *Thuridilla*, the vessels join and have a common insertion into the pericardium. This configuration is unique to these species of *Thuridilla* and is considered apomorphic.

8. Posterior end of radular tooth. — All species of *Elysia* and *Placobranchus* have a distinctly indented posterior margin of the tooth. This is also true of species of *Thuridilla*, with the exception of *T. multimarginata*, which has a straight posterior margin. Presence of a straight margin is considered autapomorphic and was not included in the phylogenetic analysis of *Thuridilla*.

9. Articulating lobes on radular teeth. — In species of *Elysia* and *Placobranchus* the posterodorsal portion of the tooth has a simply rounded surface. This is also the case in the radular teeth of *Thuridilla carlsoni* and *T. multimarginata*. In the remaining species of *Thuridilla*, the posterior portion of each tooth is expanded into a pair of rounded articulating lobes with a separtion of the posterodorsal and posteroventral portions of each tooth. This is considered apomorphic for these members of the genus.

10. Number of denticles on radular teeth. — Some species of *Elysia* have numerous minute denticles on the sides of the cutting margin of the teeth, while others have smooth margins. Most members of this genus have a row of small medial denticles. In species of *Placobranchus* and *Thuridilla*, the denticles are wide and rectangular. This character is a synapomorphy for these taxa. In species of *Placobranchus*, there are about 8–15 denticles on either margin of the tooth. In most species of *Thuridilla*, there are about 20 denticles on either side of the cutting margin. In *T. carlsoni* there are 35–38 denticles on either side of the tooth. This is considered autapomorphic for this species and is excluded from the cladistic analysis.

11. Striations on teeth. — In some species of *Thuridilla*, the spaces between the denticles continue as linear depressions that extend onto the lateral and dorsal surface of the teeth, creating striated teeth. Other species of *Thuridilla* lack these striations as do all species of *Elysia* and *Placobranchus*. Therefore, presence of striations on the teeth of some species of *Thuridilla* is considered apomorphic.

12. Extension of denticles on cutting margin of tooth. — In several species of *Elysia*, both *Placobranchus* and most species of *Thuridilla*, the denticles on the tooth extend from the lateral margin of the tooth and continue ventrally as extended denticles. In a few species of *Thuridilla*, such as *T. neona* (Fig. 33B), the distal end of denticles is flush with the lateral margin of the tooth. This is considered apomorphic for these species of *Thuridilla*.

13. Relative size of buccal mass and pharyngeal pouch. — In character 3, a muscular portion of the buccal mass was larger than or equal to the pharyngeal pouch in the plesiomorphic state, while in other derived species the buccal mass was smaller than than the pharyngeal pouch. In this transformation, based on the sizes of the muscular portion of the buccal mass and pharyngeal pouch, it appears that the buccal mass retains its original size and that the pharyngeal pouch becomes slightly larger. In some species of *Thuridilla* the pharyngeal pouch is much larger than the buccal mass. This appears to be due to additional enlargement of the pharyngeal pouch coupled with reduction in the size of the muscular portion. Since this occurs

by both enlargement of the pharyngeal pouch and reduction of the muscular portion of the buccal mass, it is considered as a character transformation distinct from simple enlargement of the pharyngeal pouch. This increase in relative and actual size of the pharyngeal pouch is considered apomorphic.

14. Receptaculum seminis duct. — The organ for storage of sperm in most Elysiidae that connects to the female gland mass has been considered by Sanders-Esser (1984) and Jensen (1992) as a genital receptaculum rather than a receptaculum seminis, since it does not contain oriented spermatozoa. However, its position in most species of *Elysia* and *Placobranchus*, entering the junction of the ampulla the female gland mass and vas deferens, is identical to that of the receptaculum seminis of other sacoglossans and many other opisthobranchs. It appears to be a structure homologous to the receptaculum owing to its similar position, though its function may have been altered. Because of the likely homology, it is referred to as a receptaculum seminis in this study. Jensen (1992) also considered the stalked structure found in *Elysiella pusilla* a genital receptacle. It differs from the other genital receptacle in that it is situated at the distal end of the female gland mass, near the female genital aperture. This is far more likely homologous with the bursa copulatrix of less derived sacoglossans such as *Volvatella*, despite its histological similarity to the more proximal receptical of all other elysiids.

The structure referred to as a bursa copulatrix by Jensen (1992) and here may not be homologous to the bursa copulatrix of other sacoglossans such as *Volvatella*, with a less derived reproductive system and that described above for *Elysiella pusilla*. The bursa of *Thuridilla* differs from that of all other sacoglossans in that it opens via a separate gonopore adjacent to the female gland mass. It also appears to be permanently present in mature individuals while other bursae in other elysiids are transitory and appear only following copulation. These secondary bursae have been found only in species with hypodermic impregnation (Jensen, 1992). Certainly more detailed study of the various genital receptacles found in the Sacoglossa is necessary to more firmly establish homology.

In species of *Thuridilla*, the duct of the receptaculum seminis may be long or short. Species of *Placobranchus* and *Elysia* have elongate receptaculum ducts. An elongate duct in *Thuridilla* is considered plesiomorphic.

15. Cream or yellow parapodial marginal band. — No species of *Elysia* or *Placobranchus* have a cream or yellow band along the margin of the parapodia. In *Thuridilla carlsoni*, *T. kathae* and *T. flavomaculata*, a band that varies from cream to yellow to orange-yellow may be present. This is not found in other species of *Thuridilla* and is considered apomorphic for the genus.

16. Orange, black and blue parapodial marginal bands. — No species of *Elysia* or *Placobranchus* has a combination of these three colored bands, yet they are present in several species of *Thuridilla*. Two species of *Elysia*, *E. ornata* and *E. grandifolia*, have orange and black marginal lines. However, it is apparent from the phylogenetic analysis presented in (Fig. 38) that *E. ornata* is a more derived species of *Elysia*. Presence of the orange, black and blue lines in the same sequence is considered apomorphic for species of *Thuridilla*. Three other species have orange, black and blue pigment on the parapodia. In *T. lineolata*, the blue is a light blue color rather than the "electric" reflective pigment found in other species of *Thuridilla*. In *T. undula* and *T. neona*, the orange is a subdued burnt orange undulating band rather than a straight line composed of reflective granules. Owing to these deferences, these three species are not consdered apomorphic for this character, as this appears to be a non-homologous similarity.

17. White longitudinal parapodial lines. — No species of *Elysia* or *Placobranchus* have a series of white longitudinal lines on the surface of the parapodia. Such lines are present in *T. bayeri* and *T. splendens* and are considered apomorphic.

18. Bluish body color. — All species of *Elysia* and *Placobranchus* have a basically green body color. Several species of *Thuridilla* have a bluish body color. This is considered

apomorphic.

19. White head with orange or red rhinophores. — This feature is only found in a few species of *Thuridilla* and in no other elysiids. Presence of this pigment combination is considered apomorphic.

20. Connections between lateral and posterior vessels. — In some species of *Thuridilla* branches of the lateral pericardial vessels join with branches of the posterior vessels. This condition also occurs in a few species of *Elysia* with an elongate pericardium. As an elongate pericardium is probably a derived feature within the Elysiidae, it is logical to assume that connections between vessels are also apomorphic. Having connections of the lateral and posterior vessels is also considered apomorphic within *Thuridilla.*

21. Orange undulating margin of the parapodia. — No species of *Elysia* or *Placobranchus* have an undulating burnt orange margin to the parapodia. Thus, this condition found in *Thuridilla undula* and *T. neona* is considered apomorphic.

22. Black body color. — *Thuridilla livida* and *T. hoffae* are the only elysiids with a black body color. Presence of this pigment is considered apomorphic for these species.

23. Width of teeth. — The radular teeth of *Placobranchus* are of moderate width. Also the radular teeth of most caliphyllid stiligerids (excluding *Caliphylla*) are wide. Wide teeth occur in *Thuridilla carlsoni*, *T. multimarginata* and *T. neona.* Narrow teeth are found in the remainder of species and are considered apomorphic within *Thuridilla.*

Phylogeny of *Thuridilla*

Based on the polarities discussed above, the distribution of plesiomorphic and apomorphic character states is found in Table 3. These data were analyzed using PAUP version 3.1. A single most parsimonious tree was found (Fig. 39). This tree had a consistency index of 0.477 and a length of 44 steps. A consistency index of 0.477 means that more than half of the characters were subject to at least one instance of homoplasy, either parallelism or reversal. Several apomorphies exhibit no instance of parallelism or reversal. They include: reduction of tooth size, increase in size of the pharyngeal pouch, reduction of the dorsal notch of the radular teeth, presence of articulating lobes on posterior end of radular teeth, denticles flush with cutting edge of tooth, buccal mass reduced in size, presence of opaque white lines on body, head white with orange or red tentacles, lateral vessels connecting with posterior ones and body black. The following characters exhibit parallelism in the apomorphic state: ground color other than green, lateral pericardial vessels lost, posterior vessels with a common insertion into the pericardium, striations present on dorsal surface of tooth, duct of receptaculum seminis short, cream or yellow parapodial margin present, orange, black and blue parapodial margins present, body bluish, orange undulating band present.

Five characters exhibit one instance of reversal to the plesiomorphic state: lateral pericardial vessels many, separate insertion of posterior vessels, length duct of receptaculum long, orange, black, and blue parapodial bands absent and radular teeth wide.

Use of characteristics of color patterns is controversial in phylogenetic reconstruction. For this reason, a separate phylogeny was produced, which excluded all characters that are related to color. The basic topology of the tree is very similar to the tree produced using characteristics of color pattern. The primary difference is that there is poor resolution of taxa within the two large clades that are determined by apomorphies of character 18 and characters 5, 11 and 16. The fact that the tree topology is essentially the same in the absence of color data increases the confidence in adding additional data to enhance resolution, particularly in taxa such as *Thuridilla*, that are not especially character rich.

The pattern of species cladogenesis observed in *Thuridilla*, where there is little adaptive radiation in the lower branches of the tree and more derived clades tend to undergo much more speciation than lower clades, is similar to that found in other opisthobranch lineages. Within the distantly related opisthobranch genera *Flabellina* and *Hallaxa*, the same pattern

Table 3. Character states in *Thuridilla* taxa

character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
bayeri	1	1	1	1	0	1	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1
lineolata	1	1	1	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	1
livida	1	1	1	1	1	1	0	0	1	0	1	0	0	1	0	1	0	0	0	0	0	1	1
moebii	1	1	1	1	0	1	1	0	1	0	0	0	1	9	0	0	0	1	0	0	0	0	1
splendens	1	1	1	1	0	1	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1
vatae	1	1	1	1	0	1	1	0	1	0	0	0	1	0	0	0	0	1	1	1	0	0	1
virgata	1	1	1	1	0	1	1	0	1	0	0	0	1	1	0	0	0	1	1	0	0	0	1
carlsoni	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0
kathe	0	1	0	1	0	1	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	1
flavomaculata	0	1	0	1	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	1
hoffae	1	1	1	1	1	1	1	0	1	0	1	0	1	0	0	1	0	0	0	0	0	1	1
albopustulosa	1	1	1	1	0	1	1	0	1	0	0	0	1	1	0	0	0	1	1	1	0	0	1
undula	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	1
indopacifica	0	1	1	1	1	1	0	0	1	0	1	0	0	1	0	1	0	0	0	0	0	0	1
multimarginata	0	0	0	0	1	1	1	1	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0
neona	1	1	1	1	1	1	0	0	1	0	1	1	0	0	0	0	0	1	0	0	1	0	0
picta	0	1	1	1	1	1	0	0	1	0	1	1	0	0	0	1	0	0	0	0	0	0	1
hopei	1	1	1	1	1	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1
decorata	0	1	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1

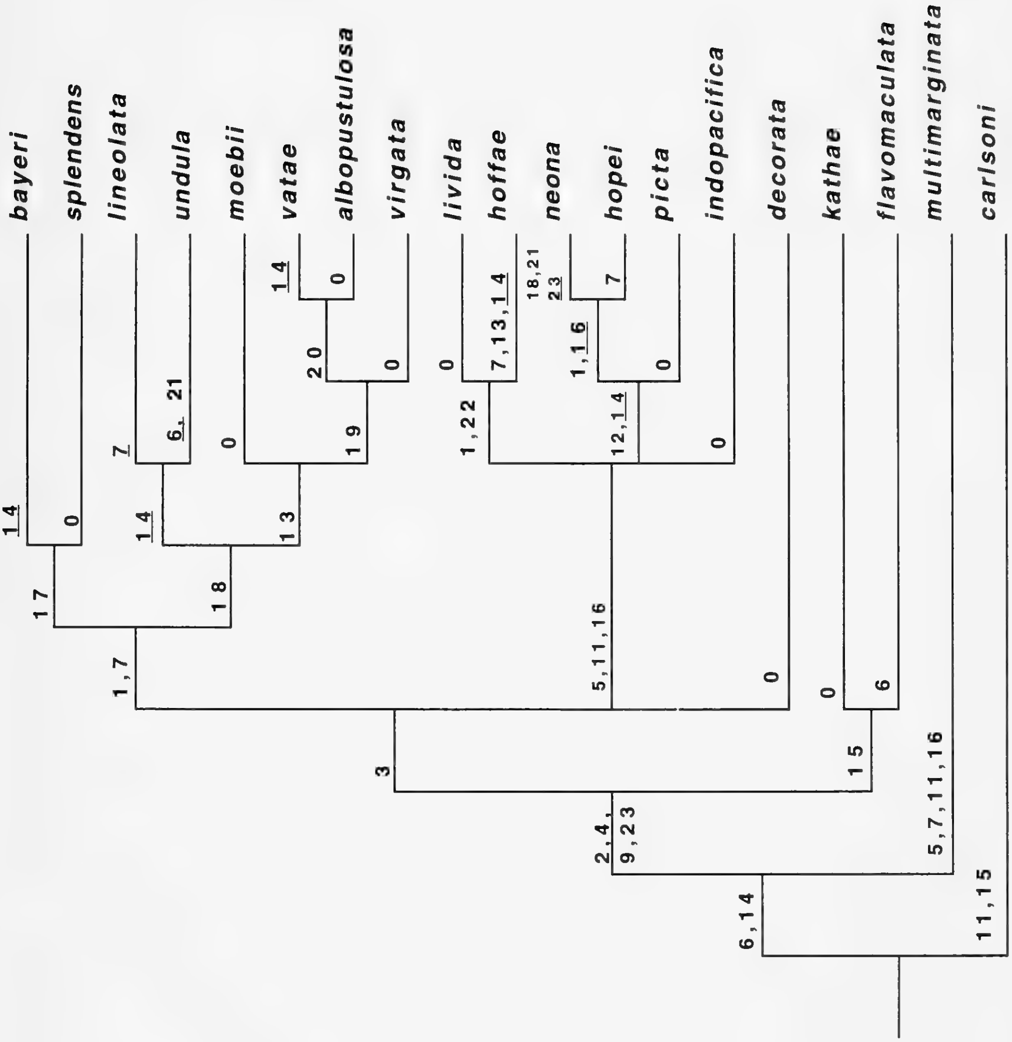

FIGURE 39. Phylogeny of *Thuridilla*, numbers refer to characters discussed in text and present in Table 3. Underlined numbers refer to characters that have undergone reversal.

of speciation tends to occur (Gosliner and Willan, 1991; Gosliner and Johnson, 1994). In *Flabellina*, most of the less derived taxa are polar or temperate, while the clades that have undergone a great deal of adaptive radiation are strictly tropical. This pattern is not as obvious in *Hallaxa*, where some of the less derived taxa are tropical. *Thuridilla*, in contrast is exclusively tropical. Most of the least derived sacoglossans are tropical and some members of more derived clades are present in temperate habitats.

Biogeographical relationships

Previous studies on the phylogenetics of Indo-Pacific opisthobranchs (Gosliner, 1989; Gosliner and Willan, 1991; Gosliner and John-

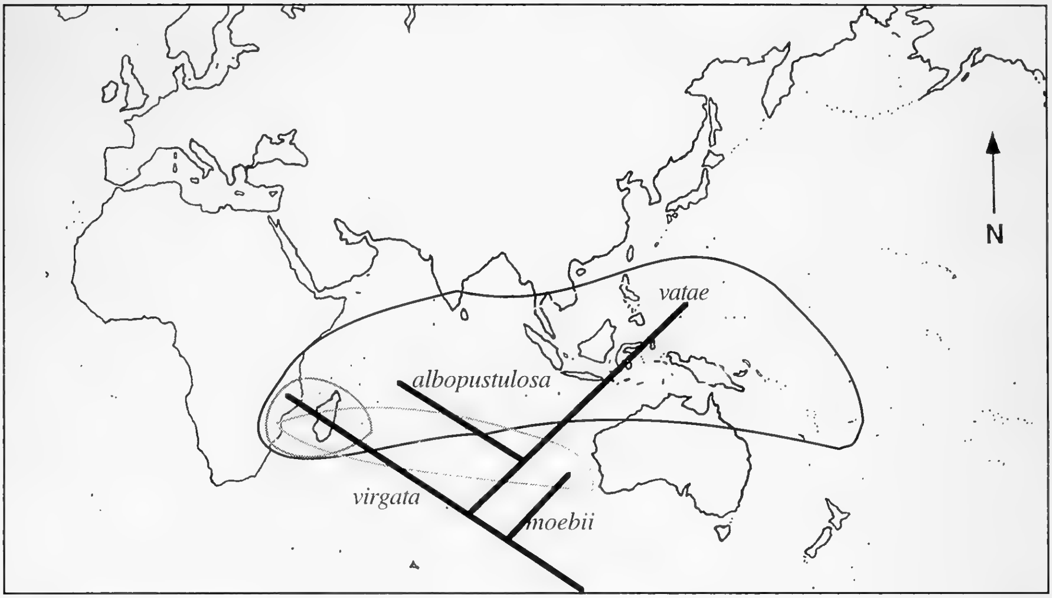

FIGURE 40. Area cladogram of four species of *Thuridilla.*

son, 1994) have demonstrated that sister taxa exhibit little or no vicariance in their present distributions.

When sister species of *Thuridilla* are compared geographically, two clear cut cases of vicariance are apparent. *Thuridilla hopei* from the Mediterranean has an Indo-Pacific sister species (*T. neona*), while *T. picta* from both the eastern and western Atlantic is the sister taxon of *T. hopei* plus *T. neona*. Springer (1982) demonstrated that in Indo-Pacific reef fishes sister species had marked areas of vicariance related to plate boundaries. For example, a species found in the Indian Ocean to the western margin of the Pacific Plate would likely have its sister species restricted to the non-marginal portions of the Pacific Plate. In no instance does that occur within *Thuridilla*. The only species restricted to the non-marginal portions of the Pacific Plate is *T. neona* whose sister species is Mediterranean. Three additional species are apparently somewhat restricted in their distributions. *Thuridilla decorata* is known only from the Red Sea. *Thuridilla lineolata* is known only from Indonesia. The distribution of *T. virgata* is thus far known only from the south western Indian Ocean. Two of these, *T. decorata* and *T. virgata*, have no clear-cut sister species, but are rather the sister taxa to a larger clade. In the case of *T. decorata*, it is the sister taxon to the clade that includes 14 species of *Thuridilla. Thuridilla lineolata* is the sister taxon to *T. undula* which has been found from the Maldives, Papua New Guinea, Palau, the Philippines and Guam. *Thuridilla virgata* is the sister species to a clade containing two other species, *T. vatae* and *T. albopustulosa.* All three of these species completely overlap in their distributions in the western Indian Ocean (Figure 40), although the latter two species are more widely distributed to the east. In the remaining cases where sister species are well defined, the species are presently overlapping for most of their ranges. *Thuridilla bayeri* is found from the western Indian Ocean to the Marshall Islands in the central Pacific, while its sister species, *T. splendens* is found only in the western Pacific. The ranges of *T. vatae* and *T. albopustulosa* are shown in Fig. 40, and are almost completely overlapping, except that *T.*

vatae has been found in the Marshall Islands while *T. albopustulosa* has not been found east of the western Pacific margin. *Thuridilla livida* has been found from the western Indian Ocean to the Marshall Islands while its sister species, *T. hoffae* is known from the western Pacific to the Marshalls. *Thuridilla kathae* is known from the western Indian Ocean to the western Pacific, while its sister species, *T. flavomaculata* has been found from the western Pacific to the Marshalls.

Clearly no consistent pattern emerges from these examples. Present distributions have probably expanded from original vicariant ones and this subsequent dispersal masks any early separation of founder populations. Though many of the ranges of these species are probably incomplete, subsequent additional records can only serve to increase the area of overlap for sister taxa.

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THE EELPOUT GENERA *LYCENCHELYS* GILL AND *TARANETZELLA* ANDRIASHEV (TELEOSTEI: ZOARCIDAE) IN THE EASTERN PACIFIC, WITH DESCRIPTIONS OF NINE NEW SPECIES

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Abstract: The 26 species of the eelpout genus *Lycenchelys* Gill, 1884 in the eastern Pacific Ocean are described from a total of 628 specimens. Nine are new to science: *L. callista* (Oregon and California), *L. chauliodus* (Peru), *L. folletti* (Mexico), *L. hadrogeneia* (Ecuador), *L. lonchoura* (Peru), *L. pearcyi* (Oregon to Mexico), *L. pentactina* (Peru), *L. pequenoi* (Peru and Chile) and *L. peruana* (Peru). The closely related *Taranetzella lyoderma* Andriashev, 1952 is included and redescribed on the basis of all 18 known specimens. Lectotypes are designated for *Lycodes anguis* Garman, 1899 and *Lycodes incisus* Garman, 1899. A key to all the species of *Lycenchelys* in the eastern Pacific is given and includes three from the Kuril-Kamchatka Trench that may occur within the area: *L. albeola*, *L. uschakovi* and *L. vitiazi*.

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Introduction

The eelpout genus *Lycenchelys* was erected by Gill (1884) "for Collett's second group which have 'the body elongate'..." to distinguish four boreal Atlantic species (*L. muraena*, *L. paxilla*, *L. sarsi* and *L. verrillii*) from the more robust *Lycodes* Reinhardt. Gill did not designate a type species for *Lycenchelys*, but Jordan (1885) placed Goode and Bean's (1877) *Lycodes verrillii* in Gill's new genus. A type species (*Lycodes muraena* Collett, 1878) was finally designated by Jordan (1920). Andriashev (1955) redefined *Lycenchelys*, again on characters that separate it from *Lycodes*, chiefly: 1) large head pore size; 2) absence of mental crests (cartilage lamina under the dentary bones); 3) presence of oral valve (palatine membrane); 4) inferior mouth; 5) teeth present on jaws, vomer and usually palatine bones; 6) lower jaw teeth in irregular series anteriorly. The first three characters have only limited validity, the others none, and Anderson (1994) expanded the generic description and redefined *Lycenchelys* on the basis of 76, mostly osteological, characters. The genus presently comprises some 56–57 species of derived lycodines with a reduced palatopterygoid series and without autapomorphies, and with or without large head pores, vomerine and palatine teeth, lateral line, pelvic fins, pseudobranch or pyloric caeca.

Many undescribed species of *Lycenchelys* from the eastern Pacific have been known in museum collections for about the last 30 years, but efforts to diagnose every species in the region have been impeded until now. Most of the material described here was collected on oceanographic expeditions under the auspices of the Smithsonian Institution (most collections housed at the Los Angeles County Museum of Natural History), the Scripps Institution of Oceanography, Oregon State University, and the Moss Landing Marine Laboratories. Other specimens were made available from the Russian Academy of Sciences, Japanese and Peruvian fisheries vessels, and research cruises of the American yacht *Te Vega*. Previous papers on eastern Pacific eelpouts in a similar style include Peden and Anderson (1978) and Anderson and Peden (1988).

This paper treats all 26 species of *Lycenchelys* found in the eastern Pacific Ocean. As most species that are adequately known are broadly distributed, the entire Bering Sea is covered, from the Kamchatka Peninsula, around the North Pacific rim (including the Aleutian Islands), to Tierra del Fuego, Chile. Three abyssal species from the northern Kuril-Kamchatka Trench, *L. albeola, L. uschakovi* and *L. vitiazi*, still only known from the holotypes, are included in the key to species, as they probably occur throughout the Aleutian Basin (Bering Sea abyss). In previous papers on North Pacific lycodines (Andriashev, 1955; Fedorov, 1976; Toyoshima, 1985) genera related to *Lycenchelys* have been treated and I follow that tradition with the one remaining genus requiring updating, *Taranetzella* Andriashev, 1952 (*Embryx* Jordan and Evermann, 1898 was synonymized with *Lycenchelys* by Anderson, 1988). Anderson (1994) also diagnosed *Taranetzella* and other genera related to *Lycenchelys* in the eastern Pacific (*Derepodichthys, Eucryphycus, Lyconema*, and *Ophthalmolycus*).

Authors have treated the gender of *Lycenchelys* as masculine. However, the Greek root noun ενχεχυσ (eel) is feminine, thus species-group adjectival suffices are emended here as required (see Anderson, 1982a:210). Specific names accepted as nouns include *crotalinus, hippopotamus* and *scaurus*.

METHODS AND MATERIALS

Measurements were made with dial calipers to the nearest 0.1 mm. Definitions of characters and measurements follow Anderson (1982a, 1994). Head pore terminology follows Gosztonyi (1977), the first to identify and name canals, and number their pores sequentially in an English language publication; however, his system was preceded by Fedorov (1976) in Russian. Gostonyi's system was modified slightly by Anderson (1982b; see also Anderson, 1994, fig. 4). Lateral line pattern terminology follows Andriashev (1954, fig. 142). Some discrepancies will be noticed when comparing morphometric characters in this paper with those published by previous authors who used total length in calculating some ratios; standard length (SL) is used herein, as SL is not subject to the vagaries of caudal fin wear in these often delicate, pliable fishes. Eye diameter in relation to head length (HL) is a measure of the entire spectacle, not just the pupil, and this affects snout length as well. Interorbital width of Fedorov (1976) and Toyoshima (1985) is more akin to interpupillary width here; my interorbital is the narrower bony distance. Some species of *Lycenchelys* have a ventral abdominal skinfold ("plica"), which can be white or blue. In previous publications I termed ray-less, dorsal-fin pterygiophores as "free" pterygiophores, also termed interneurals by authors, but here I refer to them as supraneurals following Mabee (1988). Institutional abbreviations follow Leviton et al. (1985), or as emended by Leviton and Gibbs (1988).

This review is based on 636 specimens, 49–428 mm SL, housed in 11 museums (listed by abbreviation in each account; specimen lengths are in SL). All type specimens were examined with the exception of the holotype of *Lycenchelys antarctica* (but see Anderson, 1988). Lectotypes of *Lycodes insisus* Garman, 1899 (valid) and *Lycodes anguis* Garman, 1899 (junior synonym of *Lycenchelys porifer* [Gilbert, 1890]) are designated. For ease of identification, diagnoses include some variable characters in addition to those that are important in combination or unique for a species. Expanded diagnoses only are given for two species, *Lycenchelys antarctica* and *L. monstrosa*, as these were fully described elsewhere (Anderson, 1982a, 1988, 1990). Species accounts are presented alphabetically.

KEY TO SPECIES OF EASTERN PACIFIC *LYCENCHELYS*

This key is intended for late juvenile to adult specimens, as several characters, such as gill raker and tooth counts, or characters of the axial skeleton and fins are either not completely expressed or difficult to observe in small juveniles. One difficulty with zoarcids is that many good characters are skeletal, thus radiographs are essential for counts and fin characters in these variable fishes. Specimens with distorted or damaged skin will add to difficulties because of the importance of head pores and their positions. Data transposition errors were discovered for previously published pelvic ray counts in *L. antarctica* (3 rays, not 2–3; Anderson, 1988, 1990) and head length in *L. monstrosa* (13.7%–15.3% SL, not 5.0%–6.2% SL; Anderson, 1982a).

1a. Occipital pores absent 10
1b. Occipital pores present (rarely all absent in *L. scaurus*) 2
2a. Vomerine and palatine teeth present .. 4
2b. Vomerine and palatine teeth absent ... 3
3a. Preoperculomandibular pores nine; interorbital pores absent; lateral line double, with mediolateral and ventral branches; gill rakers 15–21; pectoral fin rays 18–21; gill slit extending anterior to pelvic fins; chin without fleshy lobe (PANAMA—CHILE) ....*Lycenchelys scaurus* (Garman)
3b. Preoperculomandibular pores eight; interorbital pore present; lateral line with mediolateral branch only; gill rakers 11–13; pectoral fin rays 17 (±); gill slit extending to just above lower end of pectoral base; chin with large fleshy lobe (ECUADOR) ....*Lycenchelys hadrogeneia* sp. n.
4a. Pelvic fin rays three 7
4b. Pelvic fin rays two 5
5a. Nostril tube not reaching upper lip; interorbital pore absent (rarely present in *L. callista*) 6
5b. Nostril tube reaching or overhanging upper lip; interorbital pore present (OKHOTSK AND BERING SEAS) ....*Lycenchelys rassi* Andriashev
6a. Gill slit extending ventrally to lower end of pectoral base and not extending forward dorsally; ventral abdominal fold (plica) present;dorsal fin origin associated with vertebrae 6–8 (OREGON AND CALIFORNIA) ....*Lycenchelys callista* sp. n.
6b. Gill slit extending ventrally to just above lower end of pectoral base and continuing forward dorsally about one-third eye diameter; ventral abdominal plica absent; dorsal fin origin associated with vertebrae 5–6 (PERU) .... *Lycenchelys peruana* sp. n.
7a. Suborbital pores 8–10; predorsal length longer than head length; dorsal fin origin associated with vertebrae 3–5; total vertebrae 106–137; gill rakers 8–17 .. 8
7b. Suborbital pores six (5 + 1); predorsal length shorter than head length; dorsal fin origin associated with vertebra two; total vertebrae 88; gill rakers 8–9 (ALEUTIAN ISLANDS) .... *Lycenchelys alta* Toyoshima
8a. Total vertebrae 106–115; 2–3 suborbital pores arising from ascending ramus of bone chain behind eye; first suborbital pore mesial to, or anteromesial to, nostril tube 9
8b. Total vertebrae 132–137; 0–1 pore arising from ascending ramus of suborbital bone chain behind eye; first suborbital pore anterior to (under) nostril tube (OKHOTSK AND BERING SEAS) .... *Lycenchelys hippopotamus* Shmidt
9a. Gill rakers 13–14; lateral line with mediolateral and ventral branches; first suborbital pore directly mesial to nostril tube (MEXICO—CHILE) ....*Lycenchelys incisa* (Garman)
9b. Gill rakers 8–11; lateral line with ventral branch only; first suborbital pore anteromesial to nostril tube (KURIL ISLAND AND BERING SEA) ....*Lycenchelys ratmanovi* Andriashev
10a. Scales absent on nape and cheeks .. 12
10b. Scales present on nape and cheeks . 11
11a. Vomerine and palatine teeth absent; lateral line single, coursing ventrally on abdomen, then rising to mediolateral position on tail; first suborbital pore anterior to (under) nostril tube; P 15–18; pseudobranch filaments 5–7 (BERING

SEA—CALIFORNIA) ....*Lycenchelys crotalinus* (Gilbert)

11b. Vomerine and palatine teeth present; lateral line ventral on body and tail; first suborbital pore anteromesial to nostril tube; P 12–15; pseudobranch filaments 4–5 (BERING SEA—MEXICO) ... *Lycenchelys camchatica* (Gilbert and Burke)

12a. Pelvic fin rays three 19

12b. Pelvic fin rays two, or fin absent .. 13

13a. Postorbital pores 1–2; precaudal vertebrae 26–30; dorsal fin origin associated with vertebrae 6–18; supraneurals 1-13 15

13b. Postorbital pores 4–5; precaudal vertebrae 23–25; dorsal fin origin associated with vertebra four; no supraneurals 14

14a. Interorbital pore present; nostril tube overhanging upper lip; mouth terminal; first suborbital pore mesial to nostril (PERU) ....*Lycenchelys chauliodus* sp. n.

14b. Interorbital pore absent; nostril tube not reaching upper lip; mouth subterminal; first suborbital pore anteromesial to nostril (PERU AND CHILE) .... *Lycenchelys pequenoi* sp. n.

15a. Lateral line with ventral branch only 17

15b. Lateral line with ventral and mediolateral branches 16

16a. White abdominal fold (plica) present on abdomen; pelvic fin length 19%–24% HL (NW PACIFIC) ....*Lycenchelys plicifera* Andriashev

16b. No abdominal plica; pelvic fins absent, or fin length 12% HL (MEXICO—PANAMA) ....*Lycenchelys monstrosa* Anderson

17a. Gill slit extending ventrally to opposite pelvic base; dorsal fin origin associated with vertebrae 11–18; supraneurals 7–13 18

17b. Gill slit extending ventrally to lower end of pectoral base; dorsal fin origin associated with vertebrae 6–7; supraneurals 1–3 (OREGON—MEXICO) .... *Lycenchelys pearcyi* sp. n.

18a. Interorbital pore absent; nostril tube not reaching upper lip; pyloric caeca present (KURIL-KAMCHATKA TRENCH) .... *Lycenchelys uschakovi* Andriashev

18b. Interorbital pore present; nostril tube reaching upper lip; pyloric caeca absent (BERING SEA) .... *Lycenchelys volki* Andriashev

19a. Total vertebrae 113–138 21

19b. Total vertebrae 109 or less 20

20a. Vomerine and palatine teeth present; nostril tube reaching upper lip; pectoral fin rays 18; gill slit extending ventrally to opposite pelvic base; mouth terminal; pyloric caeca absent; pseudobranch filaments six (PERU) ....*Lycenchelys lonchoura* sp. n.

20b. Vomerine and palatine teeth absent; nostril tube not reaching upper lip; pectoral fin rays 14–15; gill slit extending ventrally to just above lower end of pectoral base; mouth inferior; pyloric caeca present; pseudobranch filaments 3–4 (MEXICO) ....*Lycenchelys folletti* sp. n.

21a. Color dark, with tones of black, brown, dark blue, or red; palatine teeth present; lateral line either ventral, mediolateral, both, or absent 22

21b. Color white; palatine teeth absent; lateral line dorsolateral (KURIL-KAMCHATKA TRENCH) .... *Lycenchelys albeola* Andriashev

22a. Color black or brown (abdomen usually dark blue); lateral line present; caudal fin rays 6–10; dorsal fin origin associated with vertebrae 4–21 23

22b. Color red; lateral line absent; caudal fin rays 10–11; dorsal fin origin associated with vertebra two (ALEUTIAN ISLANDS) .... *Lycenchelys rosea* Toyoshima

23a. Lateral line double, with ventral and mediolateral branches 26

23b. Lateral line single, with ventral branch running to tail tip, or short, mediolateral branch 24

24a. Branchiostegal rays six (rarely seven); postorbital pores 1–3; dorsal fin origin associated with vertebrae 8–21; nostril tube not reaching upper lip; gill slit extending ventrally below lower end of pectoral base; first suborbital pore anteromesial to nostril tube 25

24b. Branchiostegal rays five; postorbital pores five; dorsal fin origin associated with vertebra four; nostril tube overhanging upper lip; gill slit extending ventrally to just above lower end of pectoral base; first suborbital pore directly mesial to nostril tube (PERU) ....*Lycenchelys pentactina* sp. n.

25a. Interorbital pore absent; postorbital pores 1–2; lateral line ventral, complete to tail tip; supraneurals 6–16; ventral abdominal plica absent (CHILE—ANTARCTICA) .... *Lycenchelys antarctica* Regan

25b. Interorbital pore present; postorbital pores three; lateral line mediolateral, running only on body; one supraneural; abdominal plica present (KURIL-KAMCHATKA TRENCH) ....*Lycenchelys vitiazi* Andriashev

26a. Ventral abdominal plica present; first suborbital pore anteromesial to nostril tube; mouth terminal or subterminal 28

26b. Abdominal plica absent; first suborbital pore directly mesial to nostril tube; mouth inferior 27

27a. Precaudal vertebrae 23–26; nostril tube not reaching upper lip; pseudobranch filaments 3–7 (MEXICO—PERU) .... *Lycenchelys cicatrifer* (Garman)

27b. Precaudal vertebrae 27–30; nostril tube overhanging upper lip; pseudobranch filaments 0–4 (BERING SEA—MEXICO) .. ....*Lycenchelys micropora* Andriashev

28a. Mouth terminal; gill slit extending ventrally to opposite pelvic base; total vertebrae 128–133 (ALASKA—MEXICO) .. ... *Lycenchelys jordani* (Evermann and Goldsborough)

28b. Mouth subterminal; gill slit extending ventrally to lower end of pectoral base; total vertebrae 113–120 (MEXICO—PERU) .... *Lycenchelys porifer* (Gilbert)

DESCRIPTIONS

Lycenchelys alta Toyoshima, 1985

Lycenchelys altus Toyoshima, 1985:158–159, figs. 14–15 (original description. Type locality: off Buldir Isl., Aleutian Islands).

Lycenchelys alta Anderson, 1994:117.

DIAGNOSIS. — Vertebrae 21 + 67 = 88; suborbital pores 5 + 1; postorbital pores five; occipital pores two; interorbital pore present; lateral line ventral; dorsal fin origin associated with vertebra two; predorsal length less than head length; total gill rakers 8–9.

COUNTS AND MEASUREMENTS. — Vertebrae 21 + 67 = 88; D 84; A 71; C 9; P 18; pelvic 3; vomerine teeth 5; palatine teeth 7–10; gill rakers 1 + 7/1 + 8; branchiostegal rays 6; pseudobranch filaments 3. Following measurements in percent SL: head length 19.9; head width 7.5; head depth 8.1; pectoral fin length 10.6; predorsal length 18.1; preanal length 40.5; body height 8.3; gill slit length 6.1. Following measurements in percent HL: head width 38.0; head depth 41.3; upper jaw length 49.6; pectoral fin length 53.7; snout length 21.9; eye diameter 23.6; gill slit length 31.0; interorbital width 6.6; interpupillary width 17.8; pelvic fin length 17.8; caudal fin length 8.3. Pectoral base/length ratio 47.7.

DESCRIPTION. — Only holotype known. Head elongate, ovoid; dorsal profile convex, evenly sloping from snout to nape. Scales absent on head, nape, pectoral fin and base, and in pectoral axil. Scales present on body, abdomen to isthmus, tail and on unpaired fins, extending to about 60%–75% of their height. Eye ovoid, not entering dorsal profile of head. Gill slit extending ventrally nearly to pelvic fin base. Opercular flap at upper margin of gill slit well-developed, angular; slit extending anteriorly about half eye diameter. Pectoral fin origin slightly below body midline, insertion on abdomen; posterior margin of fin evenly rounded, ray tips very slightly exserted, more so ventrally; ventralmost six rays thickened.

Mouth subterminal, upper jaw extending well behind posterior margin of eye. Nostril tube small, not reaching half way from its base to upper lip when pressed forward. Upper lip poorly delimited, adnate to snout tip. Labial lobe of lower jaw well-developed. Inner surface of lower jaw with large, swollen, papilliform lining. Oral valve not coalesced with sides of palate, and not reaching edge of vomer. Jaw teeth conical, sharp; upper jaw with two anterior tooth rows, lower jaw with four irregular tooth rows; teeth in outer row in both jaws caniniform, retrorse, four times as large as inner row. Vomerine teeth in small patch; palatine teeth in single row.

Cephalic lateralis system with five postorbital pores, arising from frontal, sphenotic, two from pterotic and lateral extrascapulars (positions 1–5). Two pairs of anterior supraorbital (nasal) pores, one set mesial to small nostril tube, the other dorsoposteriorly. Six suborbital bones and pores, five pores arising from ventral ramus of bone chain under eye and one from ascending ramus behind eye just posteroventral to first postorbital pore (formula 5 + 1). Eight preoperculomandibular pores, four arising from dentary, one from anguloarticular and three from preopercle. Interorbital pore present, set between middle of pupils. Occipital pores two (left and right laterals). Body lateral line ventral, complete, traceable as few groups of neuromasts to tail tip.

Dorsal fin origin associated with vertebra two, resulting in predorsal length shorter than head; no supraneurals. Anal fin origin associated with ultimate precaudal vertebra (21), with three ray-bearing pterygiophores inserted anterior to haemal spine of first caudal vertebra. Pterygiophore of last dorsal ray associated with fourth preural vertebra; pterygiophore of last anal ray associated with second preural vertebra, with two rays articulating with its haemal spine. Caudal fin with two epural, four upper and three lower hypural rays.

Gill rakers 1 + 7 (right) and 1 + 8 (left), only dorsalmost on lower limb developed, others regressed, triangular or acute. Pseudobranch filaments short. Pyloric caeca two nublike swellings, poorly delimited owing to full stomach.

Color in alcohol dark reddish-brown. Head region dorsally, around opercle and on branchiostegal membranes black. Dorsal fin reddish brown. Anal fin dusky anteriorly. Pectoral fin base dusky, fin blackish proximally. Lining of orobranchial chamber black. Peritoneum dark brown, undoubtedly black in life. Stomach pale (unpigmented).

The single specimen measured 125 mm TL.

DISTRIBUTION. — Known only from the western Aleutian Islands in 336 m.

REMARKS. — Toyoshima (1985, fig. 15) mislabeled the first nasal and first suborbital ("infraorbital," or IFP) head pores as the two nasal pores. He also labeled the sixth suborbital pore (as IFP), but stated that only five are present in his description (twice). The upper jaw in the holotype is very long, but is not included in the diagnosis as the specimen is a mature male and females of *Lycenchelys* usually have shorter jaws than males, especially among the more primitive species, like *L. alta*. Characters indicating the primitiveness of *L. alta* are its few vertebrae, few suborbital pores, robust body, 18 pectoral rays and anteriorly placed dorsal fin origin. Also not included in the diagnosis, but requiring scrutiny when more specimens are available, is the low number of gill rakers and their development, and the specimen's small size for being a ripe male (is this a dwarf species?). Unusual in this specimen, but also not verifiable for the species, is the combination of five lower suborbital pores and five postorbital pores (which will show some variation). In other species there are more suborbital pores than postorbitals.

MATERIAL EXAMINED. — HUMZ 88704 (holotype, 123 mm SL male); So. of Buldir Isl., Aleutian Islands; 52°03.7'N, 175°39.0'E; Japanese fisheries trawler; 336 m; 14 Aug. 1980.

Lycenchelys antarctica Regan, 1913

Lycenchelys antarcticus Regan, 1913:242, pl. IX, fig. 3 (original description. Type locality: off South Georgia Isl.). Grey, 1956:197.
Lycenchelys sp.: Parin and Makushok, 1973:175.
Lycenchelys atacamensis Andriashev, 1980:1105, figs. 1–4 (Peru-Chile Trench).
Lycenchelys antarctica: Anderson, 1988:88, fig. 28. Anderson, 1990:258, fig. 2. Anderson, 1994:65, 117, fig. 118.

DIAGNOSIS. — Vertebrae 26–29 + 92–109 = 120–138; D 102(?)–116; A 98–112; C 6–9; P 15–17; pelvic 3; vomerine teeth 2–12; palatine teeth 0–11; gill rakers 2–3 + 10–13 = 13–16; branchiostegal rays 6–7; pseudobranch filaments 0–4, small; pyloric caeca absent or present as low swellings only; dorsal fin origin associated with vertebrae 12–21, with 6–16 supraneurals; head 14.1%–18.0% SL, pectoral fin 8.0%–10.7% SL; predorsal length 27.1%–33.0% SL; body height 4.5%–7.0% SL; upper jaw 31.1%–44.3% HL; pelvic length 9.1%–16.3% HL; preoperculomandibular pores usually nine, but with poorly developed septum between pores five and six in some, producing one large pore giving a count of eight; postorbital pores 1–2; suborbital pores 7–9; occipital and interorbital pores absent; body lateral line ventral, complete.

DISTRIBUTION. — Peru-Chile Trench in 4855–5320 m, Scotia Sea in 1976–3870 m, and Weddell Sea in 2037 m (MNHN 1990-645).

MATERIAL EXAMINED. — See Anderson (1988). Weddell Sea record (above) is a range extension.

Lycenchelys callista sp. nov.
(Fig. 1)

Lycenchelys "A" sp. n. Pearcy et al., 1982:387.

HOLOTYPE .— CAS 55412 (male, 190 mm); California, off Pt. Sur; 36°15.1'N, 122°25.5'W; *Cayuse* sta. SLS-16; 1580–1622 m; 0837–0907 hrs.; 26 July 1984; W. Wakefield, M. E. Anderson and party.

PARATYPES. — Oregon: OS 14376; (8; 119–174 mm); 44°24.1'N, 125°07.2'W; *Yaquina* sta. OTB-313; 1285 m; 2134–2220 hrs.; 19 Feb. 1970. California, off Farallon Isl.: CAS 39849 (5; 162–200 m); *Velero IV*, US EPA; 1464 m; Sept. 1977. California, off Pt. Sur: CAS 80630 (29; 148–190 mm); same coll. as holotype. CAS 55062 (2; 110–172 mm); 36°23.8'N, 122°14.6'W; *Cayuse* sta. SLS-12; 1200 m; 0743–0800 hrs.; 11 May 1984. SIO 84-249 (21; 123–190 mm); 36°29.2'N, 122°19.1'W; *Cayuse* sta. SLS-21; 1409–1429 m; 1037–1107 hrs.; 3 Oct. 1984. SIO 85-51 (22; 124–193 mm); 36°30.7'N, 122°19.2'W; *Cayuse* sta. SLS-12; 1410–1510 m; 0903–1003 hrs.; 7 Nov. 1984. California, Tanner Basin: SIO 71-141 (3; 133–163 mm); 32°47.0'N, 119°28.5'W; sta. R-41; 1390 m; 13 July 1971.

ADDITIONAL MATERIAL. — SIO 60-476 (1; 123 mm); California, off Farallon Isl.; U.S. Atomic Energy Commission; 1830 m; 11 Nov. 1960. Trawl damaged.

DIAGNOSIS. — Vertebrae 23–25 + 102–112 = 126–136; suborbital pores 7–9 + 1 = 8–10; postorbital pores three; occipital pores two; interorbital pore usually absent; lateral line ventral; dorsal fin origin associated with vertebrae 6–8; pelvic fin rays two; total gill rakers 12–15.

COUNTS AND MEASUREMENTS. — Values for holotype first, followed by range of paratypes in parentheses: vertebrae 23 + 108 = 131 (23–25 + 102–112 = 126–136); D 125 (118–127); A 112 (108–118); C 8 (8–10); P 16 (14–16); pelvic 2 (2); vomerine teeth 4 (1–10); palatine teeth 1/2 (1–6); gill rakers 2 + 11 (2–3 + 9–12 = 12–15); branchiostegal rays 6 (6); pseudobranch filaments 4 (4–5). Following measurements in percent SL: head length 13.3 (12.2–15.5); head width 6.3 (4.4–6.1); head depth 5.4 (4.4–5.6); pectoral fin length 7.0 (6.7–9.7); predorsal length 18.0 (17.2–19.1); preanal length 29.7 (28.0–30.8); body height 5.6 (4.9–5.9); gill slit length 3.9 (3.3–4.4). Following measurements in percent HL: head width 47.3 (35.5–46.0); head depth 40.2 (34.6–40.6); upper jaw length 40.7 (29.1–41.5); pectoral fin length 52.7 (46.3–65.1); snout length 24.5 (19.1–26.9); eye diameter 20.3 (21.3–26.3); gill slit length 29.1 (26.7–34.1); interorbital width 7.3 (5.6–7.9); interpupillary width 25.7 (20.3–26.4); pelvic fin length 17.1 (17.4–22.3); caudal fin length 8.4 (6.7–12.4). Pectoral base/length ratio 43.3 (31.4–41.2).

DESCRIPTION. — Based on 92 known adults and juveniles. Head elongate, ovoid; dorsal profile gently convex or nearly flattened from anterior margin of eye to nape. Head somewhat longer in males than in females, length 12.4%–14.5% SL ($\bar{x}$= 13.6) in 25 males 149–185 mm SL, 12.2%–13.3% HL ($\bar{x}$ = 13.0) in 26 females, 149–193 mm SL. Scales absent on head, nape, pectoral fin and base, and in pectoral axil immediately posterior to fin base only. Scales present on body, abdomen to line between pectoral bases, tail and on unpaired fins extending to about 50–75% of their height, the greatest extent posteriorly. Eye ovoid, just entering dorsal profile of head. Gill slit extending ventrally to lower end of pectoral base. No opercular flap at upper end of gill slit, instead slit fused above pectoral base to body, forming characteristic "siphon-shaped fold" (Andriashev, 1955); dorsally slit vertical, or nearly so, and not continued forward, or if so in a few, for very short distance. Pectoral fin origin at body midline, insertion on abdomen; posterior margin of fin evenly rounded, ray tips exserted, more so ventrally, ventralmost 6–7 rays thickened.

Mouth inferior, upper jaw extending to middle of eye or its anterior quarter. Upper jaw longer in adult males than in females, 32.7%–43.1% HL ($\bar{x}$ = 37.4) in 25 males 149–185 mm SL, 29.1%–34.1% HL ($\bar{x}$ = 30.2) in 26 females

149–193 mm SL. Nostril tube reaching more than half way from its base to upper lip when pressed forward, almost touching lip in some. Upper lip well-delimited, adnate to snout tip. Labial lobe of lower jaw well-developed, generally hidden when mouth is closed. Oral valve not coalesced with sides of palate, and extending to rictus, but not reaching vomer. Jaw teeth conical, sharp; upper jaw with single row in both sexes, lower jaw with 2–3 irregular rows near symphysis; anteriormost teeth in adult males caniniform, about three times the size of those in females. Numbers of teeth in both jaws significantly different for the sexes of similar sizes. Premaxillary teeth 7–12 ($\bar{x} = 8.9$) in 27 males 142–188 mm SL, 10–20 ($\bar{x} = 13.1$) in 26 females 149–193 mm SL. Dentary teeth 10–16 ($\bar{x} = 13.6$) in same males, 21–29 ($\bar{x} = 24.0$) in same females. Vomerine and palatine teeth relatively few, only 7% of total sample with more than four palatine teeth, 13% with more than four vomerine teeth.

Cephalic lateralis system with three postorbital pores, arising from frontal, pterotic and lateral extrascapulars (positions one, three and four). Two pairs of anterior supraorbital (nasal) pores, one set anteromesial to small nostril tube, the other posteromesially. Usually nine suborbital pores, eight arising from ventral ramus of bone chain under eye and one from ascending ramus behind eye just ventral to first postorbital pore (8 + 1); suborbital pore variation rare, four fish with formula 7 + 0/7 + 0 and one with 8 + 1/9 + 1. Eight preoperculomandibular pores, four arising from dentary, one from anguloarticular and three from preopercle (no variation). Interorbital pore usually absent, present in only two specimens. Occipital pores two (left and right laterals). Body lateral line ventral, complete, steeply bowing on anterior portion of body in pectoral axil.

Dorsal fin origin above mid-pectoral fin, associated with vertebrae 6–8, with no supraneurals. Anal fin origin associated with ultimate or penultimate precaudal vertebrae, with 4–7 ray-bearing pterygiophores inserted anterior to haemal spine of first caudal vertebra. Pterygiophore of last dorsal ray associated with third through fifth preural vertebrae; pterygiophore of last anal ray associated with second preural vertebra, with 1–2 rays articulating with haemal spine. Caudal fin with 1–2 epural (usually two), 3–4 upper hypural and 2–4 (usually four) lower hypural rays.

Gill rakers on upper limb small, acute; on lower limb only ventralmost 6–8 acute, others more rectangular. Pseudobranch filaments long, usually 4–5. Pyloric caeca two nublike swellings, poorly delimited.

Color in alcohol dark brown or bluish, head and fins darker. Body color in life (pers. observ.) dark cobalt blue, fins black. Dorsal surface of head dark brown, cheek and opercular area dark blue. Pectoral fin with large, pale blue, iridescent blotch covering about half of fin surface, quickly fading after capture. Lining of orobranchial chamber and peritoneum black. Stomach pale (unpigmented).

This species reaches 203 mm TL. Ripening ova 2.2 mm in diameter were found in a 157 mm SL female (OS 14376). The largest ova were seen in a 188 mm SL specimen in SIO 85-51 at 3.5–3.6 mm in diameter. Stomach contents in specimens from off central California were about 80% bivalves, the rest gastropods and crustacean debris.

DISTRIBUTION. — Off central Oregon to southern California. Depth range: 1200–1830 m.

ETYMOLOGY. — From the Greek καλλιστοσ (most beautiful) in reference to the author's perception of the physical appearance of this species compared to its congeners.

REMARKS. — This species is closest to *L. rassi* Andriashev chiefly on the basis of its similar head pore patterns, fused gill opening, two pelvic fin rays, squamation and dentition. However, *L. callista* differs from *L. rassi* in sufficient characters to suggest sister-species status. These include *L. callista's* fewer vomerine and palatine teeth at comparable sizes, uncoalesced oral valve, lateral line steeply sloping in *L. callista*, gently declining in *L. rassi*, nostril tube not reaching upper lip in *L. callista*, reaching or overhanging upper lip in *L. rassi*, interorbital pore very rarely present in *L. callista*, always present in *L. rassi*, dorsal fin origin associated with vertebrae 6–8 in *L. callista*, vertebra five in *L. rassi*, generally more numerous vertebrae (126–136 in *L. callista*, 122–129 in *L. rassi*), and generally more numerous gill rakers (12–15 in *L. callista*, 11–13 in *L. rassi*).

Lycenchelys camchatica (Gilbert and Burke, 1912)

Lycodes camchaticus Gilbert and Burke, 1912:89, fig. 34 (original description. Type locality: off Avacha Bay, Kamchatka Penin., Russia). Soldatov and Lindberg, 1930:494. Rendahl, 1931:16. Popov, 1933:66. Quast and Hall, 1972:14.

Lycenchelys camchaticus: Andriashev, 1935:115. Andriashev, 1937:341–343, partim, text figs. 17, 19 only, pl. 2, fig. 26. Andriashev, 1955:354, 364–366, figs. 2, 9, 10. Andriashev, 1958:172, 174. Quast and Hall, 1972:13. Peden, 1973:117–119, fig. 1C. Fedorov, 1976:10–12. Pearcy et al., 1982:387. Toyoshima, 1985:149, 164–165, figs. 20–21, table 3.

Lycenchelys camchatica: Anderson et al., 1979:262–263. Hubbs et al., 1979:14. Pequeño, 1986:187. Anderson, 1994:117.

DIAGNOSIS. — Vertebrae 21–24 + 97–104 = 118–125; suborbital pores 7–8 + 0–1 = 7–9; postorbital pores two, opening from positions one and three; occipital and interorbital pores absent; lateral line ventral; dorsal fin origin associated with vertebrae 5–6; pectoral fin rays 12–15; scales present on nape and cheeks; total gill rakers 14–18.

COUNTS AND MEASUREMENTS. — Vertebrae 21–24 + 97–104 = 118–125; D 112–117; A 100–105; C 9–11; P 12–15; pelvic 3; vomerine teeth 2–6; palatine teeth 1–10; gill rakers 0–2 + 13–16 = 14–18; branchiostegal rays 6; pseudobranch filaments 4–5. Following measurements in percent SL: head length 13.5–16.1; head width 5.0–8.1; head depth 5.1–6.8; pectoral fin length 5.3–8.7; predorsal length 15.3–18.9; preanal length 29.9–31.9; body height 3.8–7.1; gill slit length 3.3–4.5. Following measurements in percent HL: head width 27.6–46.1; head depth 37.1–42.9; upper jaw length 32.0–46.8; pectoral fin length 37.7–60.5; snout length 22.7–35.3; eye diameter 19.2–28.1; gill slit length 23.8–29.6; interorbital width 5.2–7.9; interpupillary width 23.6–26.9; pelvic fin length 9.9–18.1; caudal fin length 8.7–11.6. Pectoral base/length ratio 36.6–43.9.

DESCRIPTION. — Based on 130 juveniles and adults; large adults rare. Head elongate, ovoid; dorsal profile gently convex or nearly flattened from snout tip to nape. Head length not longer in males than females in present sample of mostly juveniles. Scales present on nape, cheek and pectoral axil at sizes over about 100 mm SL; scales present on pectoral fin and base at sizes over about 120 mm SL; scales present on body, abdomen and unpaired fins at all sizes; scales on unpaired fins extend to their margin in large specimens. Eye ovoid, entering dorsal profile of head in juveniles, excluded in adults. Gill slit extending ventrally to lower end of pectoral base or just above it. Weak opercular flap at upper end of gill slit; slit extending forward about one-third to one-fourth eye diameter. Pectoral fin origin well below body midline, insertion on abdomen; posterior margin of fin evenly rounded, middle and ventral ray tips slightly exserted, ventralmost 4–5 rays thickened.

Mouth inferior, upper jaw extending to middle of eye, noticeably longer in largest males compared to females and juveniles of both sexes; upper jaw recessed in deep, fleshy pocket posteriorly. Nostril tube not reaching halfway from its base to upper lip when pressed forward. Upper lip poorly delimited, especially anteriorly. Labial lobe of lower jaw well-developed, not hidden when mouth is closed in some. Oral valve not coalesced with sides of palate, extending to rictus and just reaching edge of vomer. Jaw teeth conical, upper jaw with single row in both sexes, lower jaw with 3–4 irregular rows near symphysis; anteriormost teeth in adult males caniniform in lower jaw only. Numbers of jaw teeth not significantly different in present sample. Fedorov (1976) reported great individual variation in numbers of dentary teeth, but did not distinguish between the sexes. Vomerine and palatine teeth relatively few in both sexes.

Cephalic lateralis system with usually two postorbital pores, arising from frontal and pterotic (positions one and three), pores rarely doubled at one position. Two pairs of anterior supraorbital (nasal) pores, one set anteromesial to small nostril tube, the other posteromesially. Usually eight suborbital pores, seven arising from ventral ramus of bone chain under eye and one from ascending ramus behind eye just ventral to postorbital pore (8 + 0); suborbital pore variation rare, few fish with pore formulae 7 + 0 or 8 + 1. Eight preoperculomandibular pores, four arising from dentary, one from anguloarticular and three from preopercle (no variation). Interorbital pore usually absent, present in few specimens taken off Oregon. Occipital pores absent. Body lateral line ventral, steeply sloping on anterior portion of body, not traceable to tail tip even in fresh specimens.

Dorsal fin origin above mid-pectoral fin, usually associated with vertebra five, with no supraneurals. Anal fin origin associated with ultimate precaudal vertebra, with 2–4 ray-bearing pterygiophores inserted anterior to haemal spine of first caudal vertebra. Pterygiophore of last dorsal ray associated with third or fourth preural vertebrae; pterygiophore of last anal ray associated with second preural vertebra, with 1–2 (usually two) rays articulating with haemal spine. Caudal fin with two epural, 4–5 (usually four) upper hypural rays and 3–4 (usually four) lower hypural rays.

Usually single, acute gill raker on upper limb of first gill arch, ocassionally absent owing to inner membrane attachment to juncture between upper and lower limbs. All rakers slender, acute; ventralmost 5–6 more triangular (Andriashev, 1955, fig. 10). Pseudobranch filaments short. Pyloric caeca two, nublike.

Color in alcohol brown or bluish, head, fins and abdomen darker; some specimens faded to whitish-pink. Body color in life (pers. observ., specimens from California) uniformly purplish-blue; nape, cheeks and snout purple; branchiostegal membrane, lips, fins and abdomen blackish. Pectoral fin with large, bluish-green (females) or pale yellow (males), iridescent blotch covering more than half of fin surface, quickly fading after capture. Lining of orobranchial chamber and peritoneum black. Stomach pale (unpigmented). Gilbert and Burke (1912) stated the living color to be "olive-brown...with greenish gilt in varying amounts on top and sides of head and front face of pectorals, lower parts darker." In contrast to specimens described above from California, their description is of the Kamchatkan types, which must have been seen fresh by Gilbert, chief scientist of the 1906 *Albatross* cruise that captured them. Andriashev (1958) noted the sexual dichromatism of the pectoral fin blotch from ship records.

This species reaches 430 mm TL (Fedorov, 1976), but only 16 specimens over 200 mm were located. Approximately 160 specimens have been identified, several not studied or listed below. Specimens from the Bering Sea and California had eaten bivalves and gastropods in about equal amounts.

Distribution. — A eurybathic, trans-Pacific species ranging at least from Avacha Bay, Kamchatka Peninsula, Russia, across the Bering Sea slope including the Aleutian Islands, to northern Mexico in 256–2100 m. No specimens known yet between the southeast Bering Sea and Washington. Andriashev's (1937) depth of "about 200 m" at Bering Island was an approximation and seems too shallow for this species. However, SIO 74-168 (misreported as SIO 74-166 in Anderson et al., 1979) was taken at 256 m off southern California. Toyoshima's (1985:165) statement that the species occurs in the Sea of Okhotsk is presently unconfirmed, but probable.

Remarks. — This species is close to *L. crotalinus* chiefly in its similar counts of the axial skeleton and gill rakers, inner gill membrane attachment, head pore patterns, and head squamation. Indeed, it was confused with *L. crotalinus* in California waters for many years (see Anderson et al., 1979). It is mainly distinguished from *L. crotalinus* in possessing vomerine and palatine teeth, having a complete ventral lateral line, and having a lower pectoral fin ray count (12–15, usually 13–14, in *L. camchatica*, 15–18, usually 16–17, in *L. crotalinus*). Andriashev (1937) described great sexual dimorphism in the species but later discovered that the males in his collection were of another species which he named *Lycenchelys ratmanovi* (Andriashev, 1955). Fedorov's (1976:10) records of 17 pectoral fin rays and 90 caudal vertebrae for this species are in error, the latter error was typographical.

Material Examined. — Russia: USNM 74396 (holotype, male, 239 mm), SU 22366 (paratype, 243 mm) and USNM 70928 (2 paratypes, 236–241 mm); off Avacha Bay; 52°37.5'N, 158°50.0'W; *Albatross* sta. 4797; 1247 m; 20 June 1906; U. S. Fish Commission. ZIN 30012 (2; 216–232 mm); off Avacha Bay; 52°41'N, 159°13'E; *Dal'nevostochnik* sta. 3; 800–1000 m; 15 July 1932; A. P. Andriashev. ZIN 42023 (2; 180–191 mm); Shirshov Ridge; 57°53'N, 170°58'E; *Professor* sta. 327; 1050 m; 15 Sept. 1974. ZIN 40538 (1; 189 mm); So. of C. Navarin; 61°08'N, 175°45'E; *Ekvator* sta. 501; 980 m; 2 Oct. 1969. Eastern Bering Sea (Alaska): ZIN 41881 (1; 350 mm); 58°21'N, 175°11'W; *Adler* sta. 29; 630–720 m; 5 Feb. 1967. HUMZ 83128 (1; 218 mm); 54°39.1'N, 167°20.1’W; *Yakushi Maru*; 500 m; 11 June 1979; M. Yabe. UW 25162 (1; 188 mm); 54°34’N, 167°43’W; trawl 135; ca. 950–980 m; 27 Aug. 1983. HUMZ 81814 (1; 140 mm); 54°20.5’N, 167°12.5’W; *Yakushi Maru*; 800 m; 14 June 1979; M. Yabe. USNM 221091 (2; 182–202 mm); *Yakushi Maru* sta. 22; 900–930 m; 27 June 1979; D.M. Cohen. Washington: USNM 135634 (2; 116–144 mm); off Gray’s Harbor; 46°55’N, 125°11’W; *Albatross* sta. 2871; 1022 m; 23 Sept. 1888; U.S. Fish Commission. Oregon, off Columbia R. mouth: CAS 81719 (1; 114 mm); 45°47.9’N, 125°32.2’W; *Cayuse* sta. OTB-242; 2100 m; 2 Apr. 1968. Oregon, off Yaquina Bay: CAS 39568 (2; 90–136 mm); 44°40.0’N, 124°58.2’W; *Yaquina* sta. BMT-311; 950 m (not 825 m as in Anderson et al., 1979); 1940–2012 hrs.; 22 Oct. 1972. OS 14368 (2; 134–141 mm); same data as preceding. OS 14386 (2; 49–56 mm); 44°38.0’N, 124 °52.6’W; *Yaquina* sta. BMT-182; 620 m; 15 Mar. 1970. OS 14402 (2; 90–106 mm); 44°34.0’N, 124°55.8’W; *Yaquina* sta. OTB-385; 786 m; 21 Feb. 1971. OS 14401 (1; 87 mm); 44°24.1’N, 125°07.2’W; *Yaquina* sta. OTB-313; 1285 m; 2134–2220 hrs.; 19 Feb. 1970. Oregon, off Coos Bay: OS 14407 (5; 147–153 mm); 43°30.4’N, 125°10.6’W; *Cayuse* sta. OTB-530; 1550 m; 8 Aug. 1973. OS 14387 (1; 155 mm); 43°28.5’N, 124°52.4’W; *Yaquina* sta. BMT-457; 675 m; 26 Mar. 1975. OS 14385 (1; 147 mm); 43°27.9’N, 124°48.8’W; *Cayuse* sta. BMT-353; 534 m; 7 June 1974. OS 14406 (1; 103 mm); 43°27.5’N, 124°53.3’W; *Cayuse* sta. BMT-381; 690 m; 6 July 1974. OS 14405 (4; 65–88 mm); 43°23.3’N, 124°51.4’W; *Cayuse* sta. OTB-553; 635 m; 27 Oct. 1973. OS 14404 (2; 78–84 mm); 43°23.3’N, 124°51.4’W; *Yaquina* sta. OTB-557; 635 m; 28 Oct. 1973. OS 14370 (1; 109 mm); 43°21.6’N, 124°48.4’W; *Yaquina* sta. BMT-463; 630 m; 27 Mar. 1975. USNM 149788 (1; 230+ mm); 43°01.0’N, 125°12.5’W; *Albatross* sta. 3788; 1946 m; 27 Apr. 1901; U. S. Fish Commission. California, off Farallon Isl.: CAS 57930 (1); 37°26.3’N, 123°05.0’W; *D. S. Jordan* sta. 3; 705–925 m; 0500–0715 hrs.; 16 Dec. 1985; T. Iwamoto. California, Monterey Bay: CAS 31495 (1; 114 mm); 36°46.7’N, 121°59.5’W; *Artemia*; 768–915 m; 22 Sept. 1974; M. G. Bradbury and M. E. Anderson. California, off Pt. Sur: CAS 56234 (2); 36°29.9’N, 122°18.3’W; *Cayuse* sta. SLS-27 (MEA 85-8); 1400–1430 hrs. 0331–0401 hrs.; 6 Feb. 1985; W. Wakefield, M. E. Anderson. SIO 85-45 (2; 148–161 mm); same data as preceding. SIO 84-48 (4; 105–134 mm); 36°25.2’N, 122°08.6’W; *Cayuse* sta. SLS-11; 850–860 m; 2230–2300 hrs.; 10 May 1984; W. Wakefield, M. E. Anderson. CAS 56250 (2); 36°22.9’N, 122°04.7’W; *Cayuse* sta. MEA 85-12; 640–630 m; 0136–0146 hrs.; 7 Feb. 1985; W. Wakefield, M. E. Anderson. CAS 56245 (1); 36°20.5’N, 122°10.5’W; *Cayuse* sta. MEA 85-11; 800–850 m; 2127–2137 hrs.; 6 Feb. 1985; W. Wakefield, M. E. Anderson. CAS 56242 (8); 36°19.6’N, 122°14.7’W; *Cayuse* sta. MEA 85-10; 990–995 m; 1556–1616 hrs.; 6 Feb. 1985; W. Wakefield, M. E. Anderson. CAS 55406 (1; 153 mm); 36°18.6’N, 122°16.0’W; *Cayuse* sta. SLS-15; 950–1010 m; 1314–1404 hrs.; 25 July 1984; W. Wakefield, M. E. Anderson. SIO 88-130 (1; 147 mm); 36°02.4’N, 121°50.4’W; *D. S. Jordan* haul 53; 1010–1017 m; 1649–1930 hrs.; 2 Apr. 1988; G. Moser. California, off Pt. Piedras Blancas: SIO 74-168 (1; 142 mm); 35°32.4’N, 121°35.7’W; trawl in 256 m; 1–2 Apr. 1974. SIO 74-166 (48; 104–163 mm); 35°29.3’N, 121°35.7’W; trawl in 905 m; 1 Apr. 1974. California, off San Luis Obispo Bay: CAS 38304 (1; 142 mm); 35°13.4’N, 121°39.5’W; *D. S. Jordan* sta. 7; 1021 m; 2334–0354 hrs.; 6–7 Sept. 1976; W. Eschmeyer. California, Catalina Basin: SIO 84-65 (1; 141 mm); *Thomas Washington* sta. SLS-6; 1160 m; 1541–1612 hrs.; 24 Sept. 1984; W. Wakefield, R. Cowen. California, La Jolla Canyon: SIO 71-162 (1; 126 mm); 32°56.0’N, 117°31.8’W; *Alexander Agassiz* sta. M6-2; 786–790 m; 0135–0430 hrs.; 13 Aug. 1971; T. Matsui. California, Tanner Basin: SIO 71-13 (1; 167 mm); 32°52.2’N, 119°32.5’W; *Alexander Agassiz*; 1390 m; 21 Jan. 1971; T. Matsui. SIO 74-198 (3; 122–152 mm); 32°50.2’N, 119°31.7’W; *Oconostota*; ca. 1100 m; 0400 hrs.; 5 Sept. 1974; J. Siebenaller. SIO 74-197 (3); 32°43.5’N, 119°28.9’W; *Oconostota* sta. 6; 1363 m; 0100 hrs.; 5 Sept. 1974; J. Siebenaller. California, West Cortez Basin: SIO 76–174 (1; 187 mm); 32°25.3’N, 119°30.4’W; trawl in 1362 m; 7 May 1975. Mexico: South Tanner Bank: SIO 85-167 (2; 115–129 mm); 32°28.7’N, 118°48.0’W; *D. S. Jordan*, bottom trawl; 1332 m; 26 Sept. 1985; T. Matsui. Mexico: San Diego Trough: SIO 71-90 (3; 147–151 mm); 32°25.3'N, 117°28.9'W; M-4, sta. 1; 1211–1235 m; 1306–1649 hrs.; 22 June 1971 (date, depth incorrect in Anderson et al., 1979). SIO 72-55 (3); 32°25.8'N, 117°28.8'W; M-7, sta. 1; 1225–1244 m; 1228–1538 hrs.; 14 Sept. 1971. SIO 71-201 (2; 147–148 mm); 32°24.4'N, 117°29.5'W; *Alexander Agassiz* sta. M8-1; 1207–1244 m; 1325–1845 hrs.; 1 Nov. 1971.

Lycenchelys chauliodus sp. nov.
(Fig. 2)

HOLOTYPE. — LACM 45600-1 (male, 142 mm SL); Peru, off Trujillo; 07°58'S, 80°37'W; *Anton Bruun* sta. 88; 1105–1124 m; 14 Oct. 1965; R. J. Menzies.

DIAGNOSIS. — Vertebrae 24 + 96 = 120; suborbital pores 6 + 1; postorbital pores five; occipital pores absent; interorbital pore present; dorsal fin origin associated with vertebra four; pelvic fin rays two; gill slit above lower end of pectoral base; nostril tube overhanging upper lip; mouth terminal; total gill rakers 14.

COUNTS AND MEASUREMENTS. — Vertebrae 24 + 96 = 120; D 115; A 100; C 10; P 15; pelvic 2; vomerine teeth 9; palatine teeth 9/10; gill rakers 3 + 11; branchiostegal rays 6; pseudobranch filaments 3. Following measurements in percent SL: head length 15.4; head width 7.2; head depth 6.7; pectoral fin length 8.5; predorsal length 19.3; preanal length 34.5; body height 6.7; gill slit length 4.7. Following measurements in percent HL: head width 46.8; head depth 43.6; upper jaw length 42.7; pectoral fin length 55.1; snout length 22.0; eye diameter 21.1; gill slit length 30.3; interorbital width 7.3; interpupillary width 19.7; pelvic fin length 18.4; caudal fin length 9.2. Pectoral base/length ratio: 43.3.

DESCRIPTION. — Only holotype known. Head elongate, ovoid; dorsal profile declined, nearly straight from snout to nape. Scales absent on head, pectoral fin, pectoral axil and base. Scales present on body, abdomen (forward to line about one-third eye diameter posterior to pectoral bases), tail, and on unpaired fins extending to about 50%–80% of their height, the greatest extent posteriorly. Eye ovoid, just entering dorsal profile of head. Gill slit extending ventrally to opposite 13th pectoral ray, well above lower end of pectoral base. Opercular flap at upper end of gill slit weak, angular; slit extending forward about one-third eye diamter. Pectoral fin origin well below body midline, insertion on abdomen; posterior margin of fin evenly rounded, ray tips deeply exserted, more so ventrally, ventralmost six rays thickened.

Mouth terminal, upper jaw extending to just behind middle of eye. Nostril tube overhanging upper lip and extending almost to its anterior edge. Upper lip thin, poorly delimited anteriorly. Labial lobe of lower jaw weak and thin. Oral valve coalesced with sides of palate, not reaching vomer. Jaw teeth conical, sharp; upper jaw with three rows anteriorly, lower jaw with 2–3 rows anteriorly, outermost teeth in both jaws three times larger than inner teeth. Lower jaw inner membrane papillose. Vomerine and palatine teeth relatively numerous, strong, retrorse.

Cephalic lateralis system with five postorbital pores, arising from frontal, sphenotic, two from pterotic, and lateral extrascapulars. Two pairs of anterior supraorbital (nasal) pores, one set mesial to long nostril tube, the other posteromesial. Seven suborbital pores, six arising from ventral ramus of bone chain under eye and one from ascending ramus behind eye just posteroventral to first postorbital pore (6 + 1). Eight preoperculomandibular pores, four arising from dentary, one from anguloarticular and three from preopercle. Interorbital pore anterior in position, set almost on line joining anterior margins of eyes. Occipital pores absent, supratemporal commissure appears absent as well. Body lateral line undetectable (specimen faded).

Dorsal fin origin above anterior third of pectoral fin, associated with vertebra four, with no supraneurals. Anal fin origin associated with penultimate precaudal vertebra, with five ray-bearing pterygiophores inserted anterior to haemal spine of first caudal vertebra. Pterygiophore of last dorsal ray associated with fourth preural vertebra; pterygiophore of last anal ray associated with second preural vertebra, with one ray articulating with haemal spine. Caudal fin with two epural, four upper hypural and four lower hypural rays.

Gill rakers slender, acute, first one minute; lowermost five more triangular. Pseudobranch

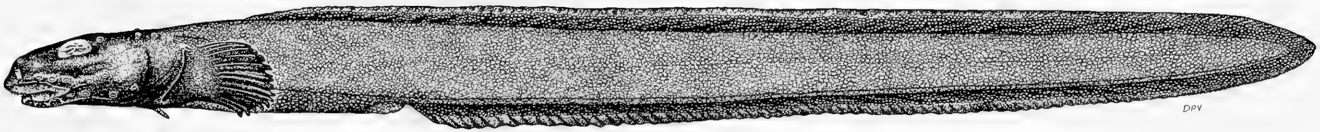

FIGURE 1. *Lycenchelys callista* sp. n., CAS 55412, holotype, 190 mm SL, off Pt. Sur, California.

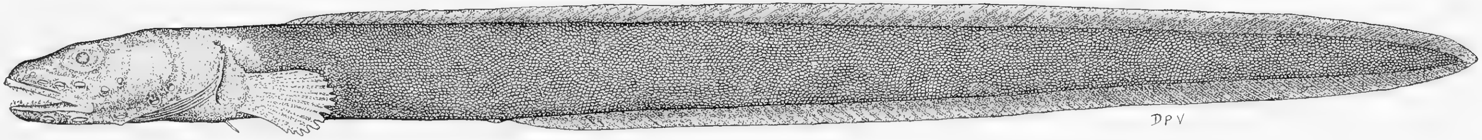

FIGURE 2. *Lycenchelys chauliodus* sp. n., LACM 45600-1, holotype, 142 mm SL, off Trujillo, Peru.

filaments short. Pyloric caeca two, nublike, but well-delimited, about one-half eye diameter in length.

Color in alcohol faded to uniform pinkish brown, jaws and fins whitish. Lining of orobranchial chamber and peritoneum dark brown, undoubtedly black in life. Stomach pale (unpigmented).

DISTRIBUTION. — Known only from off Peru in 1005–1124 m.

ETYMOLOGY. – From the Greek word χαυλιοδουσ (having prominent teeth), alluding to the large teeth in so small a specimen. Treated as a noun in apposition.

REMARKS. — The very large, ripe gonad of the relatively small holotype indicates that *L. chauliodus* may be a dwarf species.

Lycenchelys cicatrifer (Garman, 1899)
(Fig. 3)

Lycodes cicatrifer Garman, 1899:136, pl. 31, fig. 1 (original description. Type locality: Gulf of Panama). Jordan et al., 1930:475. Grey, 1956:197.

Lycenchelys cicatrifer: Andriashev, 1955:351. Parin and Makushok, 1973:175 (lapsus calami, *cicarifer*), 182. Anderson, 1982a:210. Pequeño, 1986:186. Anderson, 1994:117.

DIAGNOSIS. — Vertebrae 23–26 + 92–100 = 116–124; suborbital pores 7–8 + 0–1, usually 7 + 0; postorbital pores 3–4, usually three; occipital pores absent; interorbital pore usually absent; lateral line double (mediolateral and ventral); dorsal fin origin associated with vertebrae 5–7; total gill rakers 10–13.

COUNTS AND MEASUREMENTS. — Vertebrae 23–26 + 92–100 = 116–124; D 108–115; A 97–104; C 9–10; P 16–18; pelvic 3; vomerine teeth 4–11; palatine teeth 1–8; gill rakers 2 + 8–11 = 10–13; branchiostegal rays 6; pseudobranch filaments 3–7. Following measurements in percent SL: head length 15.1–19.2; head width 6.6–10.3; head depth 7.1–8.0; pectoral fin length 8.2–12.3; predorsal length 20.8–22.1; preanal length 33.8–36.6; body height 5.8–8.1; gill slit length 5.7–6.8. Following measurements in percent HL: head width 38.8–45.5; head depth 38.9–46.6; upper jaw length 34.9–48.8; pectoral fin length 54.3–62.3; snout length 21.5–27.8; eye diameter 20.9–30.3; gill slit length 32.7–36.9; interorbital width 5.3–6.1; interpupillary width 19.1–25.1; pelvic fin length 12.9–19.7; caudal fin length 5.8–11.3. Pectoral base/length ratio: 28.0–48.9.

DESCRIPTION. — Based on 30 known adults and juveniles; by far, most specimens are large, mature adults. Head elongate, ovoid; dorsal profile gently convex to snout area, more depressed behind eye in adult males than females. Head somewhat longer in males than in females, length 16.1%–18.0% SL ($\bar{x}$ = 17.0) in 10 males 222–280 mm SL, 15.1–17.6 ($\bar{x}$ = 16.5) in 12 females 205–278 mm SL. Scales absent on head, pectoral base and pectoral axil immediately posterior to fin base only. Scales present on nape, pectoral fin (occasionally absent), abdomen to isthmus in largest specimens, tail and on unpaired fins extending to about 50%–90% of their height, the greatest extent posteriorly. Eye ovoid, entering dorsal profile of head. Gill slit extending ventrally to lower end of pectoral base. Opercular flap at upper end of gill slit well-developed, angular; slit extending forward about half eye diameter. Pectoral fin origin well below body midline, insertion on abdomen; posterior margin of fin evenly rounded dorsally, ray tips exserted except upper most 4–5, deeply exserted ventrally, lowermost 7–8 rays thickened.

Mouth inferior, upper jaw extending to middle of eye or its posterior quarter (large males). Upper jaw longer in adult males than in females, 38.7%–48.8% HL ($\bar{x}$ = 42.1) in 10 males 222–280 mm SL, 34.9%–39.4% HL ($\bar{x}$ = 36.6) in 15 females 128–278 mm SL. Nostril tube not reaching upper lip. Upper lip well-developed, broadly adnate to snout tip. Labial lobe of lower jaw well developed. Oral valve not coalesced with sides of palate, extending almost to rictus, but not reaching vomer. Jaw teeth conical, upper jaw with 2–3 rows anteriorly, single row (males) or double (some females) posteriorly, lower jaw with 2–3 irregular tooth rows near symphysis, often rear row is of few teeth, single row posteriorly. Numbers of teeth in both jaws insignificant between the sexes. Vomerine teeth in irregular patch. Palatine teeth in single series.

Cephalic lateralis system usually with three postorbital pores, arising from frontal, pterotic and lateral extrascapulars (positions one, three and four); four individuals with pore two (sphenotic) present on at least one side. Two pairs of anterior supraorbital (nasal) pores, one set mesial to nostril tube, the other posteriorly.

Usually seven suborbital pores, all arising from ventral ramus of bone chain under eye; five individuals with eight ventrals on at least one side; one individual with eight ventrals on one side, seven on the other and one pore in the ascending ramus behind eye, resulting in the unusual formula 8 + 0/7 + 1. Eight preoperculomandibular pores, four arising from dentary, one from anguloarticular and three from preopercle (no variation). Interorbital pore absent except in one specimen in LACM 43764-1. Occipital pores absent. Body lateral line with ventral branch steeply sloping on anterior quarter of body and mediolateral branch originating about two-thirds pectoral fin length posterior to pectoral base; both running to tail tip.

Dorsal fin origin above posterior third of pectoral fin, associated with vertebrae 5–7, usually 6–7, with no supraneurals. Anal fin origin associated with ultimate or penultimate precaudal vertebrae, with 2–5, usually 4–5, ray- bearing pterygiophores inserted anterior to haemal spine of first caudal vertebra. Pterygiophore of last dorsal ray associated with third through fifth preural vertebrae; pterygiophore of last anal ray associated with second preural vertebra, with two rays articulating with haemal spine. Caudal fin with two epural, four upper hypural and 3–4, usually three, lower hypural rays.

Gill rakers short, only dorsalmost acute (both limbs); on lower limb, ventralmost rakers triangular. Pseudobranch filaments long, usually 4–5. Pyloric caeca two nublike swellings, not well-delimited in some specimens.

Color in alcohol dark brown, head and fins darker, stated to be black in fresh material (Garman, 1899). Lining of orobranchial chamber and peritoneum likewise probably black in life. Stomach pale (unpigmented).

This species reaches 282 mm SL. Most specimens examined had stomach contents: exclusively bivalves in most, with a few also having eaten gastropods and some unidentifiable crustacean.

DISTRIBUTION. — Guaymas Basin, Gulf of California, to southern Peru. Depth range: 1430–3058 m.

REMARKS. — This species is very close to *L. porifer* but is distinguished by its inferior mouth, pale stomach, position of first suborbital pore, lack of an abdominal plica, and more scaly vertical fins.

MATERIAL EXAMINED. — Mexico, Gulf of California: ZIN 48143 (2; 188–205 mm); 27°00.3'N, 111°25.3'W; *Akademik Mstislav Keldysh* sta. 1551; 2023–2026 m; 22 Nov. 1986. Panama: MCZ 28684 (holotype; ca. 230 mm); 06°17.0'N, 82°05'W; *Albatross* sta. 3360; 3058 m; 24 Feb. 1891; U.S. Fish Commission. Peru: LACM 43764-1 (20; 220–280 mm); 04°10.2'S, 81°26.5'W; *Anton Bruun* sta. 766; 1860–1815 m; 9 Sept. 1966; L. W. Knapp. USNM 135618 (1; 253 mm); 05°46'S, 81°32'W; Albatross sta. 4654; 1895 m; 12 Nov. 1904; A. Agassiz. ZIN 45775 (1; 209 mm); 05°59'S, 81°15'W; *Akademik Kurchatov* sta. 300; 1940 m; 0410–0450 hrs.; 4 Nov. 1968; N. V. Parin. ZIN uncat. (5; 128–168 mm); 14°44'S, 76°12'W; *Dmitry Mendeleyev* sta. 1654; 1495–1430 m; 2335–0120 hrs.; 19–20 Mar. 1978; N. V. Parin.

Lycenchelys crotalinus (Gilbert, 1890)

Lycodopsis crotalinus Gilbert, 1890:105 (original description. Type locality: Santa Cruz Basin, southern California).

Lycodopsis crassilabris Gilbert, 1890:106. Jordan and Evermann, 1898:2459.

Lycodopsis crotalinus: Gilbert, 1896:454, pl. 32. Jordan and Evermann, 1896:478.

Embryx crotalinus (Gilbert): Jordan and Evermann, 1898:2458. Jordan and Evermann, 1900, fig. 851. Hubbs, 1928:15. Ulrey, 1929:11. Jordan, Evermann and Clark, 1930:473. Barnhart, 1936:89, fig. 269. Schultz, 1936:195. Schultz and DeLacy, 1936:141. Taranetz, 1937:161. Andriashev, 1939:27, 51, 79. Shmidt, 1950:258. Andriashev, 1955:30. Grinols, 1965:95. Alton, 1972:590. Peden, 1973:115, 116, 119, 120. Fedorov, 1973a:24. Fedorov, 1973b:56. Fedorov, 1976:12–17. Pearcy et al., 1982:387. Eschmeyer and Herald, 1983:104. Toyoshima, 1985:178, figs. 132–133.

Embryx crassilabris (Gilbert): Jordan and Evermann, 1898:2458. Starks and Morris, 1907:240. Townsend and Nichols, 1925:15, 20, pl. 3, fig. 2. Ulrey and Greeley, 1928:44. Ulrey, 1929:11. Andriashev, 1955:30. Grinols, 1965:96. Fitch and Lavenberg, 1968:142. Peden, 1973:119.

Lyciscus crotalinus (Gilbert): Jordan and Gilbert, 1899:484. Evermann and Goldsborough, 1907:342.

Embryx parallelus Gilbert, 1915:360, pls. 9, 10. Jordan et al., 1930:474. Andriashev, 1955:30. Grinols, 1965:96. Peden, 1973:119.

Embryx crotalina (Gilbert): Bayliff, 1954:19, 77–81, pls. 4, 9. Wilimovsky, 1954:288. Wilimovsky, 1958:92. Bayliff, 1959:78. Fitch and Lavenberg, 1968:42. Miller and Lea, 1972:78–79. Quast and Hall, 1972:13. Kukowski, 1972:21. Pearcy et al., 1982:395.

Embryx parallela (Gilbert): Fitch and Lavenberg, 1968:142. Kukowski, 1972:11, 27.

Lycenchelys crotalinus: Anderson, 1988:87; 1994:65, 117.

DIAGNOSIS. — Vertebrae 22–24 + 98–109 = 121–131; suborbital pores 7–8 + 1–2 = 8–10; postorbital pores usually two, in positions one and three; occipital and interorbital pores absent; lateral line coursing to ventral position anteriorly, then rising to mediolateral position at mid-tail; dorsal fin origin associated with vertebrae 4–6; vomerine and palatine teeth absent; scales present on nape and cheeks; total gill rakers 15–18.

COUNTS AND MEASUREMENTS. — Vertebrae 22–24 + 98–109 = 121–131; D 118–125; A 103–113; C 10–11; P 15–18; pelvic 3; vomerine and palatine teeth absent; gill rakers 0–2 + 14–18 = 15–18; branchiostegal rays 6; pseudobranch filaments 5–7. Following measurements in percent SL: head length 12.7–17.9; head width 4.8– 8.2; head depth 5.5–7.5; pectoral fin length 6.6–10.1; predorsal length 16.8–20.7; preanal length 28.6–33.3; body height 5.2–7.6; gill slit length 5.4–6.3. Following measurements in percent HL: head width 33.6–66.6; head depth 38.5–50.1; upper jaw length 30.2–41.1; pectoral fin length 38.8–65.5; snout length 17.3–27.9; eye diameter 17.6–25.3; gill slit length 30.7–41.1; interorbital width 4.3–7.9; interpupillary width 21.9–29.1; pelvic fin length 9.6–20.7; caudal fin length 5.5–9.0. Pectoral base/length ratio 33.1–46.7.

DESCRIPTION. — Head elongate, ovoid; dorsal profile more dorsoventrally depressed in large specimens than in small juveniles. Head somewhat longer in large males than females of comparable sizes, length 15.3%–17.5% SL ($\bar{x}$ = 16.6) in 23 males over 320 mm SL, 14.3%–16.8% SL ($\bar{x}$ = 15.5) in 26 females over 320 mm. Head broader in males than in females owing to development of adductor mandibulae muscles (Toyoshima, 1985, fig. 33). Scales in adults and subadults present on back of head, nape, cheeks, pectoral axil, lower pectoral fin (but not on base), abdomen to pelvic base or anterior to it, body, tail, and unpaired fins to about 60%–80% of their height, the greatest extent posteriorly. Eye ovoid, entering dorsal profile of head in juveniles, but not adults. Gill slit usually extending beyond lower end of pectoral base, reaching pelvic base in some specimens, or just reaching lower end of pectoral base in others. Opercular flap at upper end of gill slit well-developed, angular; slit extending forward up to three-quarters eye diamter. Pectoral fin origin well below body midline, insertion on abdomen; posterior margin of fin wedge-shaped in adults, ray tips exserted, more so ventrally, ventralmost 7–8 rays thickened.

Mouth inferior, upper jaw extending to middle of eye or its anterior quarter; posterior end hidden in deep, fleshy pocket. Upper jaw longer in adult males than in females, 34.3%–42.1% HL ($\bar{x}$ = 38.3) in 23 males over 320 mm SL, 30.2%–35.7% HL ($\bar{x}$ = 33.1) in 26 females over 320 mm SL. Nostril tube reaching upper lip in most adults, reaching about half way from its base in small juveniles. Upper lip well-delimited, broadly adnate to snout tip. Labial lobe of lower jaw somewhat elongate, mostly hidden when mouth is closed. Oral valve usually a low fold in large specimens, not coalesced with sides of palate in all sizes, not extending to rictus and not reaching vomer. No sexual differences in numbers of jaw teeth; dentary with 4–5 irregular rows of teeth near symphysis, premaxilla with single row throughout. Palate without teeth.

Cephalic lateralis system with usually two postorbital pores, arising from frontal and pterotic (positions one and three), rarely with a third pore from position four. Two pairs of anterior supraorbital (nasal) pores, one set anterior to nostril tube, the other posteriorly. Usually eight suborbital pores, seven arising from ventral ramus of bone chain under eye and one from ascending ramus behind eye just ventral to first postorbital pore (7 + 1); rarely 8 + 1, even more rarely 8 + 2 or 7 + 2. Eight preoperculomandibular pores, four arising from dentary, one from anguloarticular and three from preopercle (no variation). Interorbital and occipital pores absent. Body lateral line pattern unique in genus: anteriorly ventral, with steep bow under pectoral fin, rising on tail to mediolateral position (Toyoshima, 1985, fig. 32).

Dorsal fin origin above mid-pectoral fin, associated with vertebrae 4–6, usually five, with no supraneurals. Anal fin origin associated with ultimate or penultimate precaudal vertebrae, with 3–5, usually 3–4, ray-bearing pterygiophores inserted anterior to haemal spine of first caudal vertebra. Pterygiophore of last dorsal ray associated with third or fourth preural vertebrae; pterygiophore of last anal ray associated with second preural vertebra, with two rays articulating with haemal spine. Caudal fin with two epural, 4–5 upper hypural and 3–4 lower hypural rays.

Usually single, acute gill raker on upper limb of first gill arch, occasionally absent owing to inner membrane attachment to juncture between upper and lower limbs. All rakers slender, acute, ventralmost 5–8 more slender than those above. Pseudobranch filaments long. Pyloric caeca two small nubs.

Fresh coloration (pers. observ.) dark, chocolate brown, snout, lips, branchiostegal membranes, opercular area and fins black or brownish black. Inner lining of anterior head pores bluish white. Pectoral fin with large, ovoid, iridescent bluish white or greenish blue blotch surrounded by narrow, black margin, blotch quickly fading after capture; inner surface of tips of lower pectoral rays whitish. Lining of orobranchial chamber and peritoneum black. Stomach pale (unpigmented).

This species reaches 468 mm TL (Toyoshima, 1985). Fedorov (1976) reported the bivalve *Yoldia* and polychaetes from stomachs of Bering Sea specimens. Bivalves, ostracods and gastropods were found in California specimens.

DISTRIBUTION. — Western Bering Sea from Commander Plateau east of Bering Island and Shirshov Ridge across the Bering Sea slope to southern California. Recorded depths range from 200–2816 m, but rare above 700 m or below 1500 m regardless of locality.

REMARKS. — This species is close to *L. camchatica* (see above). Toyoshima (1985) attempted to describe the sexual dimorphism exhibited by *L. crotalinus*, but had only two adult females, 338 and 368 mm TL. Nonetheless, his small sample did reflect the species' dimorphic head proportions. As with other species in his paper on *Lycenchelys*, Fedorov (1976) detailed morphometric variation in *L. crotalinus* but stated it all to be age-related, failing to see the sexual dimorphism. Other shortcomings in Fedorov's work are an incorrect pectoral fin ray count of 14 and a statement that the oral valve is absent. The species name has been treated as adjectival, but it is derived from "krotalon", Greek for rattle, which has been used as a generic name for New World rattlesnakes (as *Crotalus*). The name is here interpreted as a diminuitive noun in apposition, i.e., "little rattlesnake."

MATERIAL EXAMINED. — Approximately 250 specimens have been identified. The following 62 were used for descriptive purposes. Russia, Commander Islands: ZIN 39306 (2); 55°30'N, 165°30'E; *Adler* sta. 11; 200–305 m; 8 Mar. 1963. Russia, Shirshov Ridge: ZIN 42664 (14); 59°22'N, 170°50'E; *Professor* sta. 318; 1000 m; 12 Sept. 1974; V. Fedorov. Russia, Koryak coast: ZIN 40530 (1, 220 mm); 61°06'N, 176°04'E; *Ekvator* sta. 502; 1220 m; 2 Oct. 1969. British Columbia, off Queen Charlotte Islands: NMC 72-62 (1); 53°00.8'N, 132°55.8'W; 1317 m; 18 Sept. 1971. Oregon: UW 17571 (2; 280–335 mm); 46°06.0'N, 125°05.0'W; 1463 m; 30 May 1964; R. B. Grinols. UW 18191 (3; 325–365 mm); 46°00.0'N, 124°00.0'W; 732 m; 5 Sept. 1964; R. B. Grinols. OS 14373 (1; 69 mm); 44°42.0'N, 124°58.5'W; *Cayuse* sta. OTB-53; 799 m; 14 Jan. 1965. OS 14372 (4, 151–311 mm); 44°40.0'N, 124°58.2'W; *Yaquina* sta. BMT-311; 950 m; 1940–2012 hrs.; 22 Oct. 1972. CAS 81720 (1; 170 mm); 44°37.6'N, 125°39.9'W; *Yaquina* sta. BMT-185; 2816 m; 1517–1717 hrs.; 16 Mar. 1970. OS 14403 (1; 90 mm); 44°34.0'N, 124°55.8'W; *Yaquina* sta. OTB-385; 786 m; 21 Feb. 1971. OS 14371 (3; 322–385 mm); 44°24.7'N, 125°07.0'W; *Yaquina* sta. OTB-313; 1285 m; 2134–2220 hrs.; 19 Feb. 1970. UW 21537 (1; 347 mm); 44°09.5'N, 125°01.3'W; *Halfmoon Bay* sta. 37; 951 m; 16 Sept. 1984. OS 12742 (1; 337 mm); 42°54'N, 125°02'W; *Jaguar*; 1006 m; 6 Mar. 1990; D. Markle. California, off Cape Mendocino: HSU 29000–10 (18 orig.; 137–428 mm); 40°10.1'N, 124°58.0'W; *Pacific Raider*; 961 m; 26 Jan. 1973. California, Monterey Bay: USNM 75818 (holotype of *Embryx parallelus*, 388 mm male); 36°46.2'N, 122°04.5'W; *Albatross* sta. 4514; 743–721 m; 23 May 1904; U. S. Fish Commission. California, off Pt. Sur:

SIO 84-48 (2; 204–235 mm); 36°25.2'N, 122°08.6'W; *Cayuse* sta. SLS-11; 850–860 m; 2230–2300 hrs.; 10 May 1984; W. Wakefield and M. E. Anderson. California, Santa Cruz Basin: USNM 44279 (holotype of *Lycodopsis crotalinus*, 318 mm male); 33°49.8'N, 119°24.5'W; *Albatross* sta. 2980; 1103 m; 12 Feb. 1889; U. S. Fish Commission. California: Catalina Basin: USNM 44280 (holotype of *Lycodopsis crassilabris*, 295 mm male); 33°08.8'N, 118°40.0'W; *Albatross* sta. 2839; 757 m; 8 May 1888; U.S. Fish Commission. California, Tanner Basin: SIO 71–141 (4; 182–286 mm); 32°51.0'N, 119°32.0'W; 1390 m; 13 July 1971. SIO 89-107 (1; 255 mm); trawl in 1400 m; 5 July 1989; R. Kaufman.

Lycenchelys folletti sp. nov.
(Fig. 4)

HOLOTYPE. — SIO 68-83 (female, 148 mm); Gulf of California, Guaymas Basin; 27°40.0'N, 111°22.6'W; *Thomas Washington* sta. MV 68-I-50; 931–953 m; 0908–1220 hrs.; 16 Jan. 1968; C. L. Hubbs and party.

PARATYPES. — SIO 68-83 (four females, two males and one indeterminate, 90–156 mm); same collection as holotype.

ADDITIONAL MATERIAL. — CAS 57833 (indet., 138 mm); Mexico, south of Cabo Corrientes; 19°43.5'N, 105°35.5'W; *Te Vega* sta. 19–17; 660–800 m; 1025–1305 hrs.; 10 July 1968; M. G. Bradbury. Trawl damaged.

DIAGNOSIS. — Vertebrae 21–22 + 80–88 = 102–109; suborbital pores 7 + 1; postorbital pores three; occipital and interorbital pores absent; dorsal fin origin associated with vertebrae 3–4; vomerine and palatine teeth absent; total gill rakers 14–15.

COUNTS AND MEASUREMENTS. — Values for holotype first, followed by range of other specimens in parentheses: vertebrae 21 + 88 = 109 (21–22 + 80–86 = 102–108); D 104 (97–102); A 92 (83–90); C 11 (10–11); P 15 (14–15); pelvic 3 (3); vomerine and palatine teeth absent; gill rakers 1 + 14 (1 + 13–14); branchiostegal rays 6 (6); pseudobranch filaments 3 (3–4). Following measurements in percent SL: head length 19.7 (18.9–20.2); head width 7.2 (6.9–9.0); head depth 8.7 (8.2–9.7); pectoral fin length 7.6 (8.3–9.1); predorsal length 21.8 (21.6–24.2); preanal length 37.0 (34.1–37.0); body height 5.9 (6.0–6.8); gill slit length 6.6 (6.1–7.9). Following measurements in percent HL: head width 36.3 (36.4–47.0); head depth 44.2 (43.5–48.0); upper jaw length 33.9 (31.2–38.6); pectoral fin length 38.4 (44.1–44.8); snout length 24.3 (25.9–26.0); eye diameter 17.6 (15.9–16.6); gill slit length 33.6 (32.4–38.9); interorbital width 4.3 (6.6–7.4); interpupillary width 15.8 (16.5–18.0); pelvic fin length 13.7 (13.3–13.5); caudal fin length 6.9 (not present). Pectoral base/length ratio: 51.8 (38.7–42.7).

DESCRIPTION. — Based on nine known specimens, all juveniles: five females, two males and two of indeterminate sex. All were damaged in some way, the types appear to have dehydrated somewhat before preservation. Head elongate, ovoid or nearly triangular; dorsal profile evenly declined from behind eye to steeply sloping snout tip; nape rather hunched in the more desiccated specimens. Scales absent on head, nape, pectoral fin, base and its axil, and dorsal and anal fins except posteriorly. Scales present on body, abdomen to mid-pectoral region in largest specimen, tail and on unpaired fins in their posterior eighth, extending to about 25% of their height; no scales on unpaired fins in smallest specimens. Eye ovoid, just entering dorsal profile of head. Gill slit extending ventrally to just above lower end of pectoral base. Opercular flap at upper end of gill slit well-developed; slit extending forward about one-half eye diameter or more; flap distorted (folded forward) in present material. Pectoral fin origin well below body midline, insertion on abdomen; posterior margin of fin evenly rounded, ray tips slightly exserted, more so ventrally; ventralmost 6–7 rays thickened.

Mouth inferior, upper jaw extending to middle of eye or its posterior quarter. Nostril tube not reaching half way from its base to upper lip when pressed forward. Upper lip poorly delimited. Labial lobe of lower jaw poorly developed, a mere flap with ventral margin parallel with ventral margin of jaw. Oral valve coalesced with sides of palate and not reaching vomer. Jaw teeth conical, sharp; upper jaw with single row, lower jaw with two rows near symphysis blending into single, posterior row. No vomerine or palatine teeth.

Cephalic lateralis system with three postorbital pores, arising from frontal, pterotic and

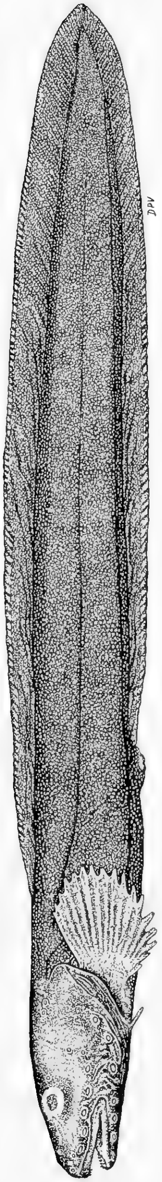

FIGURE 3. *Lycenchelys cicatrifer* (Garman, 1899), LACM 43764-1, 274 mm SL, off Peru.

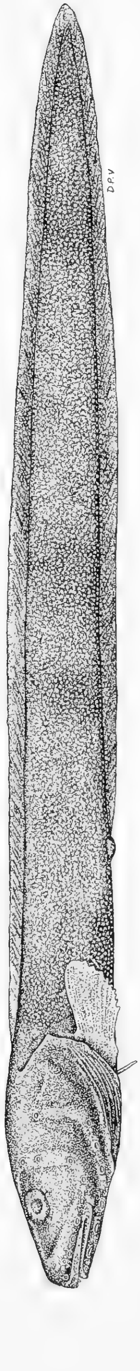

FIGURE 4. *Lycenchelys folletti* sp. n., SIO 68–83, holotype, 148 mm SL, Gulf of California.

lateral extrascapulars (positions one, three and four). Two pairs of anterior supraorbital (nasal) pores, one set anteromesial to small nostril tube, the other set posteromesially. Eight suborbital pores, seven arising from ventral ramus of bone chain under eye and one from ascending ramus behind eye just ventral to first postorbital pores (7 + 1). Eight preoperculomandibular pores, four arising from dentary, one from anguloarticular and three from preopercle. Interorbital and occipital pores absent. Body lateral line undetectable in these faded specimens. Dorsal fin origin above pectoral base, associated with vertebrae 3–4, with no supraneurals. Anal fin origin associated with ultimate precaudal vertebra, with 3–4 ray-bearing pterygiophores inserted anterior to haemal spine of first caudal vertebra. Pterygiophore of last dorsal ray associated with fourth preural vertebra; pterygiophore of last anal ray associated with second preural vertebra, with 1–2 rays articulating with haemal spine. Caudal fin with two epural, 4–5 upper hypural and four lower hypural rays.

Upper gill rakers on lower limb short, with squared-off tips; single upper limb raker and lowermost blunt, pyramidal. Pseudobranch filaments short, usually four. Pyloric caeca two small nubs.

Body color in alcohol faded to uniform dark brown, fins pale. Lining of orobranchial chamber and peritoneum dark brown, probably black in life. Stomach and intestines pale (unpigmented).

Juveniles only, the largest 158 mm TL. Small gastropods were found in the stomachs of a few specimens.

DISTRIBUTION. — Gulf of California to central Mexico. Depth range: 660–953 m.

ETYMOLOGY. – Named in honor of Mr. Wilbur Irving ("Bill") Follett (1901–1992), late Curator in the Department of Ichthyology, California Academy of Sciences, friend, inspiration and benefactor, in recognition of his many contributions (1927–1990) to ichthyology, zoological nomenclature and archaeology.

REMARKS. — *Lycenchelys folletti* shares some characters with two other eastern Pacific congeners without vomerine and palatine teeth, but is easily distinguished from both. Notable differences from *L. hadrogeneia* include the lack of interorbital and occipital pores in *L. folletti*, its three (vs. four) postorbital pores, its more numerous gill rakers (14–15 vs. 11–13), fewer pectoral rays (14–15 vs. 17) and fewer vertebrae (102–109 vs. 110–112), although there is probably overlap in the last character. *Lycenchelys crotalinus* possesses more gill rakers (15–18), more pectoral fin rays (usually 16–18), more vertebrae (121–131) and has scales on the cheeks. An additional requirement to the diagnosis of this species is observation on the course of the body lateral line.

Lycenchelys hadrogeneia sp. n.
(Fig. 5)

HOLOTYPE. — CAS 55589 (male, 180 mm); Ecuador, off Gulf of Guayaquil; 02°25'S, 81°10'W; *Te Vega* sta. 19-148; 700–1000 m; 0850–1210 hrs.; 1 Sept. 1968; M. G. Bradbury.

PARATYPES. — CAS 81540 (4; 86, 162, 166 and 174 mm); same collection as holotype.

DIAGNOSIS. — Vertebrae 21–23 + 87–90 = 110–112; suborbital pores 7 + 1–2; postorbital pores four; occipital pores two; interorbital pore present; lateral line mediolateral (?); dorsal fin origin associated with vertebrae 3–4; vomerine and palatine teeth absent; chin tip with fleshy lobe, mandibular symphysis length 15.3–17.7 HL; total gill rakers 11–13.

COUNTS AND MEASUREMENTS. — Values for holotype first, followed by range of paratypes in parentheses: vertebrae 21 + 89 = 110 (22–23 + 87–90 = 110–112); D 105 (105–106); A 92 (92–93); C 11 (10–11); P 17 (17); pelvic 3 (3); vomerine and palatine teeth absent (absent); gill rakers 2 + 10 (1–2 + 9–11 = 11–13); branchiostegal rays 6 (6); pseudobranch filaments 4 (5). Following measurements in percent SL: head length 18.2 (15.1–16.4); head width 10.3 (6.2–8.9); head depth 8.5 (7.8–8.0); pectoral fin length 9.1 (9.3–12.2); predorsal length 19.0 (16.2–17.1); preanal length 33.0 (31.6–34.0); body height 7.4 (5.9–7.8); gill slit length 7.7 (4.8–6.8). Following measurements in percent HL: head width 56.6 (40.8–54.2); head depth 46.8 (48.6–51.5); upper jaw length 60.6 (32.7–41.0); pectoral fin length 49.9 (56.3–80.3); snout length 23.6 (23.1–29.2); eye diameter 18.4 (21.0–24.6); gill slit length 42.2 (31.5–41.6); interorbital width 7.2 (7.0–7.7); interpupillary width 24.2 (22.3–25.9); pelvic fin length 15.3 (17.8–23.1); caudal fin length 6.1 (10.5–

15.4). Pectoral base/length ratio: 50.9 (33.5–49.4).

DESCRIPTION. — Only type series known: a small juvenile male, an adult male, and three young adult females. Head short, ovoid; dorsal profile gently convex, snout steeply sloping anteriorly. Head longer in adult male (18.2% SL) than in females (16.4%–16.9% SL), typical of genus. Head broader in adult male (10.3% SL) than in females (7.6%–8.9% SL). Scales absent on head, nape, abdomen, pectoral fin and base and in pectoral axil. Scales present on body, tail, and on unpaired fins extending to about 30%–70% of their height in adults, but absent in juvenile male. Eye ovoid, not entering dorsal profile of head. Gill slit extending ventrally to level just above pelvic fin base. Opercular flap at upper end of gill slit well-developed, angular; slit extending forward about one-half eye diameter, or slightly less. Pectoral fin origin well below body midline, insertion on abdomen; posterior margin of fin evenly rounded, middle and lower rays exserted, more so ventrally; ventralmost 7–8 rays thickened.

Mouth subterminal, upper jaw extending to middle of eye (females), just before it (juvenile male), or well beyond it (adult male; Fig. 5). Upper jaw length 32.7% HL in juvenile, 38.1%–41.0% HL in females and 60.6% HL in adult male. Nostril tube small, reaching from about one-third to one-half the distance from its base to upper lip when pressed forward. Upper lip well-delimited. Labial lobe of lower jaw well-developed, mostly hidden when mouth is closed, outer margin of lobe parallel with edge of jaw. Chin with characteristic fleshy lobe, producing thick mandibular symphysis, as in *Lycenchelys aratrirostris* (Andriashev and Permitin, 1968, fig. 2; Anderson, 1988, fig. 31; Anderson, 1990, fig. 3). Oral valve not coalesced with sides of palate, and extending to rictus, but not reaching vomer. Jaw teeth conical, sharp; upper jaw with single row of teeth in juvenile, 2–3 irregular rows in others; lower jaw the same except in adult male, which has four rows of teeth anteriorly. Vomerine and palatine teeth absent.

Cephalic lateralis system with four postorbital pores, arising from frontal, sphenotic, pterotic and lateral extrascapulars (positions 1–4). Two pairs of anterior supraorbital (nasal) pores, one set anteromesial to small nostril tube, the other posteromesially. Eight suborbital pores, seven arising from ventral ramus of bone chain under eye and one from ascending ramus behind eye just ventral to first postorbital pore (7 + 1); suborbital pore variation observed in juvenile male, which had 7 + 1 on right side and 7 + 2 on left. Eight preoperculomandibular pores, four arising from dentary, one from anguloarticular and three from preopercle. Anterior interorbital pore present. Occipital pores two (left and right laterals). Body lateral line difficult to observe in these faded specimens, neuromasts of mediolateral branch seen in three specimens on body, none on tail; no trace of ventral branch.

Dorsal fin origin just posterior to vertical through pectoral fin base, associated with vertebrae 3–4, with no supraneurals. Anal fin origin associated with ultimate precaudal vertebra, with 2–3 ray-bearing pterygiophores inserted anterior to haemal spine of first caudal vertebra. Pterygiophores of last dorsal ray associated with fourth preural vertebra; pterygiophore of last anal ray associated with second preural vertebra, with two rays articulating with haemal spine. Caudal fin with two epural, 4–5 upper hypural and four lower hypural rays.

Gill rakers on upper limb small, acute; on lower limb bluntly triangular in juvenile male, longer and more acute, especially ventrally, in others. Pseudobranch filaments long, slender. Pyloric caeca two small nubs.

Color in alcohol faded to pale pinkish gray. Fins and areas on head and body dark brown; eye blue. Lining of orobranchial chamber and peritoneum dark brown, probably black in life. Stomach pale (unpigmented).

Largest specimen measured 182 mm TL.

DISTRIBUTION.—Known only from off Ecuador in 700–1000 m.

ETYMOLOGY. – From the Greek αδροσ (strong) and γενειον (chin) alluding to the prominent, fleshy chin lobe.

REMARKS. — This species appears close to *Lycenchelys aratrirostris* from the Antarctic chiefly on the basis of its relatively few vertebrae and thick, fleshy mandibular symphysis. It differs from *L. aratrirostris* primarily in its head pore pattern, lack of vomerine and palatine teeth, and (apparently) ventral lateral line.

Lycenchelys hippopotamus Shmidt, 1950

Lycenchelys hippopotamus: Shmidt, 1935:35 (nomen nudum). Taranetz, 1937:161 (nomen nudum).

Lycenchelys hippopotamus Shmidt, 1950:106, fig. 4, pl. IX (original description. Type locality: Sea of Okhotsk). Andriashev, 1955:354, 361, figs. 2, 7, 8. Fedorov, 1976:8. Toyoshima, 1983:267, 332, text fig. Toyoshima, 1985:169, figs. 24, 25. Anderson, 1994:65, 117.

DIAGNOSIS. — Vertebrae 23–25 + 107–114 = 132–137; suborbital pores 7–9 + 0–1 = 8–10; postorbital pores 3–4; occipital pores 1–2; interorbital pores 1–2; lateral line ventral; dorsal fin origin associated with vertebrae 4–5; first suborbital pore at snout tip directly below nostril tube; rostral fold well-developed; total gill rakers 12–17.

COUNTS AND MEASUREMENTS. — Vertebrae 23–25 + 107–114 = 132–137; D 125–132; A 113–120; C 9–11; P 13–16; pelvic 3; vomerine teeth 4–6; palatine teeth 2–7; gill rakers 1–3 + 11–14= 12–17; branchiostegal rays 6; pseudobranch filaments 3–4. Following measurements in percent SL: head length 12.2–14.7; head width 3.9–5.1; head depth 4.8–5.2; pectoral fin length 7.4–9.1; predorsal length 14.1–15.9; preanal length 27.0–29.8; body height 3.6–6.2; gill slit length 4.0–4.9. Following measurements in percent HL: head width 31.4–40.8; head depth 35.4–40.8; upper jaw length 27.0–38.5; pectoral fin length 52.4–69.1; snout length 22.8–27.4; eye diameter 18.8–26.0; gill slit length 29.8–36.8; interorbital width 4.9–7.1; interpupillary width 16.2–22.6; pelvic fin length 18.8–27.7; caudal fin length 4.9–18.1. Pectoral base/length ratio 27.5–37.7.

DESCRIPTION. — Based on 18 known specimens, only six of which are considered adults, none mature. Head elongate, ovoid; dorsal profile gently convex or dorsoventrally depressed behind eye; snout steeply sloping. Snout tip with thick, fleshy lobe overhanging upper lip (rostral fold), which may be variously wrinkled and distorted in preservative. Head lengths of adults not detectably different owing to small sample size. Scales absent on head, nape, pectoral fin and base, and in pectoral axil. Few, isolated scales on inner and outer surfaces of pectoral fin in larger specimens. Scales present on body, abdomen to isthmus, tail and on unpaired fins, extending to about 50%–70% of their height posteriorly in large specimens. Eye ovoid, entering dorsal profile of head. Gill slit extending ventrally to lower end of pectoral fin base. Opercular flap at upper end of gill slit well-developed; slit extending forward one-half or more eye diameter. Pectoral fin origin at body midline, insertion on abdomen; posterior margin of fin evenly rounded; ventral ray tips greatly exserted; ventralmost 7–8 rays thickened; rays 13–14 except in one specimen (ZIN 40536), which has 16.

Mouth inferior, upper jaw extending to front of eye or its anterior quarter. Upper jaw apparently longer in adult males (length 34.7%–38.5% HL in two) than in adult females (30.4%–36.2% HL in four). Nostril tube small, not reaching half way from its base to upper lip when pressed forward. Upper lip well-delimited, anteriorly hidden by rostral fold. Labial lobe of lower jaw weak, posterior end of outer margin nearly parallel with ventral margin of jaw. Oral valve not coalesced with sides of palate, extending nearly to rictus, and not reaching vomer. Jaw teeth conical, sharp; upper jaw with single row except in adult females, which may have an inner row consisting of few teeth, lower jaw with 2–4 irregular rows near symphysis; anteriormost teeth in adult males greatly enlarged fangs, up to 10 times as large as inner teeth. Vomerine and palatine teeth relatively few; palatine teeth in single series.

Cephalic lateralis system with 3–4, usually three, postorbital pores, arising from frontal, pterotic and lateral extrascapulars (positions 1, 3, 4); when four pores present, two arising from pterotic, never one from sphenotic. Two pairs of anterior supraorbital (nasal) pores, one set anteromesial to small nostril tube, the other posteromesially. Usually nine suborbital pores, eight arising from ventral ramus of bone chain under eye and one from ascending ramus behind eye just ventral to first postorbital pore (8 + 1); suborbital variation as follows: three fish with pores 7 + 1/ 7 + 1, one with pores 8 + 1/9 + 1 and one with pores 8 + 1/8 + 0; first suborbital pore swung forward of usual position, lying directly beneath nostril tube. Eight preoperculomandibular pores, four arising from dentary, one from anguloarticular and three from preopercle; some specimens with a doubling of anguloarticular (fifth) pore in shallow pocket to produce nine pores, but new position not created. Interorbital region with 1–2 pores along midline (when one, located either above mid-eye or on vertical through its posterior margins). Occipital pores two (left and right laterals), except in one specimen with a median pore. Body lateral line ventral, complete, gently sloping on anterior portion of body and running relatively high above anal fin base to tail tip.

Dorsal fin origin above anterior quarter of pectoral fin, associated with vertebrae 4–5, with no supraneurals. Anal fin origin associated with ultimate, penultimate or antepenultimate precaudal vertebrae, with 4–7 ray-bearing pterygiophores inserted anterior to haemal spine of first caudal vertebra. Pterygiophore of last dorsal ray associated with fourth or fifth preural vertebrae; pterygiophore of last anal ray associated with second preural vertebra, with two rays articulating with haemal spine. Caudal fin with two epural, 4–5 upper hypural and 3–4 lower hypural rays.

Gill rakers on upper limb small, acute; on lower limb, ventralmost 5–8 acute, others with blunt tips. Pseudobranch filaments long, usually four. Pyloric caeca two small nubs.

Live coloration unknown, color in alcohol purplish to brown, abdomen, fins and head darker. Lining of orobranchial chamber and peritoneum in recent material black, eye blue. Stomach pale (unpigmented).

This species reaches 223 mm TL (a ripening female with ova up to 1.8 mm in diameter). Bivalves, gastropods and ostracods were found in a few stomachs.

DISTRIBUTION. — Throughout the southern Sea of Okhotsk to the northwestern Bering Sea off Cape Navarin. Depth range: 840–1340 m. The depth of 160–170 m recorded for ZIN 46786 (below) may be in error.

REMARKS. — Originally described on the basis of three specimens, a lectotype was designated by Andriashev (1955:363, footnote). As this was inadequate with regard to the 1985 Code of Zoological Nomenclature (Recommendations 73C and 74C), the specimen's data are presented below. Andriashev gave incorrect vertebral counts for the lectotype in my view (23 + 112 = 135; printer's error puts precaudal vertebrae as "123" in original), which is here corrected to 24 + 111 = 135. The lengths of the types given by Shmidt (1950, table 18) are in error (noted by Andriashev, 1955), as is the name of the Soviet vessel that captured them in Fedorov (1976). Other errors in Fedorov (1976) include 17 pectoral fin rays for ZIN 40536 (there are 16) and 4–5 preopercular pores (there are three; Fedorov included the anguloarticular pores). Toyoshima (1985) gave erroneous vertebral counts for the three HUMZ specimens, and these are corrected to 23–24 + 113–114 = 136–137. Toyoshima, like Fedorov, also counted the anguloarticular pore as a preopercular, but miscounted these and arrived at six. Andriashev (1955) also characterized and illustrated *L. hippopotamus* with six "external gustatory organs" under the rostral fold. These are superficial neuromasts (free lateralis organs elsewhere), are tactile organs, and are present in many *Lycenchelys* species. Their occurrence and positions are not diagnostic.

MATERIAL EXAMINED. — Lectotype: ZIN 24826 (female, 208 mm); Sea of Okhotsk, east coast of Sakhalin Isl.; 53°09.5'N, 149°52.0'E; *Gagara* sta. 229; 1150 m; 7 Aug. 1932. Paralectotypes: ZIN 24826b (male, 167 mm; female, 198 mm); same collection as lectotype. Non-types, Sea of Okhotsk: ZIN 32958 (2; 174–204 mm); 54°32.2'N, 147°25.0'E; *Vityaz'* sta. 101; 840–880 m; 12 Sept. 1949. ZIN 32959 (1; 208 mm); ca. 52°N, 145°E; *Vityaz'* sta. 116; 1030 m; 17 Nov. 1949. ZIN 46787 (3; 139–172 mm); E. of Sakhalin Isl.; *Ara* sta. 29; 1150 m; 11 Nov. 1932; P. Shmidt. ZIN 46786 (1; 215 mm); 46°48.7'N, 152°01.9'E; *Shantar* sta. 196; 160–170 m (?); 2 June 1978. HUMZ 77571 (1; 195 mm); 44°25.0'N, 145°04.0'E; 1320–1340 m; 11 Oct. 1978. HUMZ 77774 (1; 201 mm); 44°22.5'N, 144°29.5'E; 1310–1340 m; 26 Sept. 1978. HUMZ 77573 (1; 221 mm); 44°20.6'N, 144°56.5'E; 1000–1010 m; 12 Oct. 1978. NW Bering Sea: ZIN 40536 (1; 100 mm); 57°30.3'N, 170°25.0'E; *Ekvator* sta. 204; 990–1000 m; 2 Aug. 1969. ZIN 42015 (3; 107–128 mm); 61°02.6'N, 175°35.0'E; *Professor* sta. 210; 1000 m; 4 Aug. 1974; V. Fedorov. ZIN 42016 (1; 131 mm); 61°22.0'N, 177°44.0'E; *Professor* sta. 221; 1000 m; 7 Aug. 1974; V. Fedorov.

Lycenchelys incisa (Garman, 1899)
(Fig. 6)

Lycodes incisus Garman, 1899:135, pl. 30, fig. 2 (original description. Type locality: off Panama).

Jordan et al., 1930:475.
Lycenchelys incisus: Andriashev, 1955:351.
Lycenchelys incisa: Anderson, 1982a:211. Anderson, 1994:117.

DIAGNOSIS. — Vertebrae 22–24 + 83–88 = 106–110; suborbital pores 7 + 2; postorbital pores 4–5; occipital pores three; interorbital pore present; lateral lines mediolateral and ventral; dorsal fin origin associated with vertebrae 3–4; total gill rakers 13–14.

COUNTS AND MEASUREMENTS. — Vertebrae 22–24 + 83–88 = 106–110; D 100–104; A 85–88; C 9–10; P 16–18; pelvic 3; vomerine teeth 2–12; palatine teeth 3–10; gill rakers 1–2 + 11=13 = 13–14; branchiostegal rays 6; pseudobranch filaments 5–6. Following measurements in percent SL: head length 15.7–21.8; head width 5.5–9.5; head depth 6.5–9.6; pectoral fin length 7.8–9.7; predorsal length 16.5–22.0; preanal length 33.3–39.5; body height 4.7–7.8; gill slit length 5.7–8.1. Following measurements in percent HL: head width 33.5–44.8; head depth 40.5–45.3; upper jaw length 32.8–54.8; pectoral fin length 38.6–58.8; snout length 21.5–26.8; eye diameter 15.5–30.4; gill slit length 34.3–40.6; interorbital width 5.7–6.8; interpupillary width 19.3–24.0; pelvic fin length 9.2–15.3; caudal fin length 4.6–8.6. Pectoral base/length ratio: 34.5–46.4.

DESCRIPTION. — Based on all known specimens: two adult males, one adult female and four juvenile females, one a post-hatchling. Head elongate, ovoid in young, more triangular in large males; dorsal profile gently convex or evenly declined from nape to snout tip. Scales absent on head, nape, pectoral fin and base, pectoral axil and dorsal fin anteriorly in smaller specimens. Scales present on body, abdomen to pelvic base in adult males, tail and on unpaired fins, extending to about 50%–75% of their height, the greatest extent posteriorly. Eye ovoid, not entering dorsal profile of head. Gill slit angular in larger specimens, more rounded in juveniles, extending ventrally to lower end of pectoral base. Opercular flap at upper end of gill slit well developed; slit extending forward about one-half eye diameter in small specimens to more than an eye diameter in largest male. Pectoral fin origin well below body midline, insertion on abdomen; posterior margin of fin evenly rounded in small specimens, more wedge-shaped in largest male; ray tips exserted, more so ventrally; ventralmost 6–8 rays thickened.

Mouth subterminal, upper jaw extending to middle of eye in young to well behind its posterior margin in largest male (Fig. 6). Upper jaw apparently longer in adult males than in adult females, 43.6%–54.8% HL in the two males, 41.6% HL in adult female (32.8%–36.9% HL in the juveniles). Nostril tube not reaching upper lip when pressed forward except in largest male. Upper lip well-delimited. Labial lobe of lower jaw well-developed, mostly hidden when mouth closed; ventral margin of lobe generally parallel with ventral margin of jaw. Oral valve not coalesced with sides of palate, and extending to rictus, but not reaching vomer. Jaw teeth conical, sharp; upper jaw with double row anteriorly in both sexes, lower jaw near symphysis with three irregular rows in juvenile females, five rows in largest male; anteriormost teeth in both sexes not especially enlarged, those of adult males about the same relative size as those of females. Vomerine and palatine teeth relatively numerous; vomerine teeth in irregular patch, palatine teeth in single row.

Cephalic lateralis system with 4–5 postorbital pores, usually four, arising from frontal, sphenotic (in one), anteriorly and posteriorly from pterotic, and lateral extrascapulars (positions 1–4 or 1–5). Two pairs of anterior supraorbital (nasal) pores, one set mesial to small nostril tube, the other posteriorly. Nine suborbital pores, seven arising from ventral ramus of bone chain under eye and two from ascending ramus (7 + 2). Garman (1899, pl. 30) illustrates one of the types with pores 7 + 3, but this cannot be confirmed as the skin disintegrated long ago. Eight preoperculomandibular pores, four arising from dentary, one from anguloarticular and three from preopercle (no variation). Single interorbital pore, located on plane passing through anterior quarter of eye. Occipital pores three, mesial and two laterals. Body lateral line with ventral branch traceable in present material only anteriorly on body, mediolateral branch commencing behind pectoral fin margin, complete.

Dorsal fin origin above anterior quarter of pectoral fin, associated with vertebrae 3–4, with no supraneurals. Anal fin origin associated with

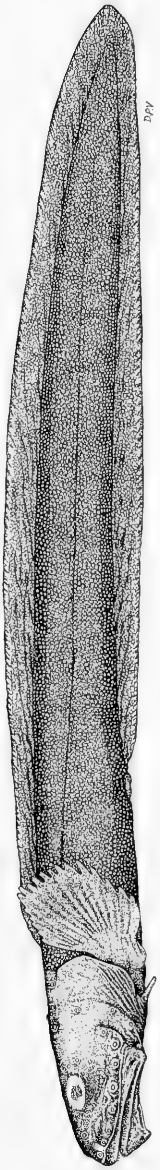

FIGURE 5. *Lycenchelys hadrogeneia* sp. n., CAS 55589, holotype, 180 mm SL, off Ecuador.

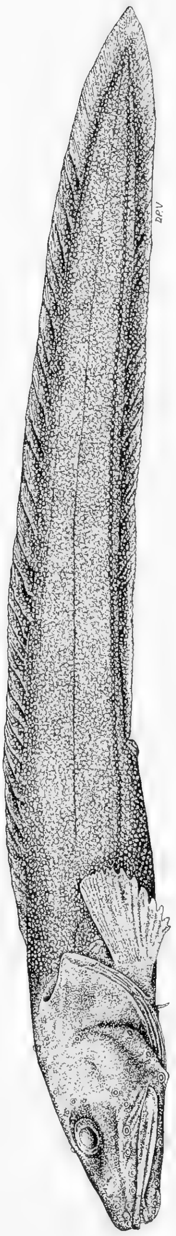

FIGURE 6. *Lycenchelys incisa* (Garman, 1899), SIO 68-105, 264 mm SL, Gulf of California.

ultimate precaudal vertebra, with three ray-bearing pterygiophores inserted anterior to haemal spine of first caudal vertebra in all. Pterygiophore of last dorsal ray associated with fourth or fifth preural vertebra; pterygiophore of last anal ray associated with second preural vertebra, with 1–2 rays articulating with haemal spine. Caudal fin with two epural, four upper hypural and 3–4 lower hypural rays.

Gill rakers on upper limb slender, acute; on lower limb, ventralmost few triangular in small specimens, more blunt-tipped in largest male. Pseudobranch filaments long, usually six. Pyloric caeca two small nubs.

Color in alcohol faded to brown or purplish, head fins and throat dark brown. Abdomen and eye blue in most-recently caught specimens. Lining of orobranchial chamber and peritoneum black or faded pale. Stomach pale (unpigmented).

This species reaches 268 mm TL. A ripening female (CAS 57836), 122 mm SL, had ova 3.2–3.8 mm in diameter. Four specimens had guts packed with ophiuroids and nothing else.

DISTRIBUTION. — Southern Gulf of California to central Chile. Depth range: 700–1475 m.

REMARKS. — Lectotype (herein designated): MCZ 28685 (female, 195 mm SL); off Penin. de Azuero, Panama; 07°06.3'N, 80°34.0'W; *Albatross* sta. 3353; 1271 m; 23 Feb. 1891. Paralectotype: MCZ 122484 (female, ca. 240 mm); same collection as lectotype. Both damaged.

MATERIAL EXAMINED. — Mexico, Gulf of California, Carmen Basin: SIO 68-105 (1; 264 mm); 25°53.7'N, 110°35.4'W; *Thomas Washington* sta. MV 68-I-76; 1321–1344 m; 1744–2115 hrs.; 22 Jan. 1968; C. L.Hubbs. Mexico, WNW of Acapulco: CAS 57836 (1; 122 mm); 17°24'N, 101°31'W; *Te Vega* sta. 19-19; 940–1000 m; 1150–1250 hrs.; 12 July 1968; M. G. Bradbury. Panama: type specimens, see above. Ecuador, off Gulf of Guayaquil; CAS 55591 (1; 141 mm); 02°25'S, 81°10'W; *Te Vega* sta. 19-148; 700–1000 m; 0850–1210 hrs.; 1 Sept. 1968; M. G. Bradbury. Peru, S. of Pta. Negra: CAS 60112 (1; 245 mm); 06°26'S, 81°05'W; 1025–1086 m; 23 Jan. 1972; E. del Solar. Chile, off Pta. Topocalma: MCZ 49373 (1; 49 mm); 34°06'S, 72°26'W; *Anton Bruun* sta. AB13-61; 1400–1475 m; 2103–2337 hrs.; 3 Feb. 1966.

Lycenchelys jordani (Evermann and Goldsborough, 1907)
(Fig. 7)

Lycodes jordani Evermann and Goldsborough, 1907:343, fig. 120 (original description. Type locality: off southern Oregon; paratype: southeastern Alaska). Jordan et al., 1930:474. Schultz, 1936:195; Schultz and DeLacy, 1936:142.

Lycenchelys jordani: Taranets, 1937:161; Andriashev, 1937:343. Shmidt, 1950:106; Bayliff, 1954:71–74, table 27. Andriashev, 1955:349, 351, 359. Grey, 1956:197. Bayliff, 1959:78. Grinols, 1965:96–97. Fitch and Lavenberg, 1968:142. Alton, 1972:590. Quast and Hall, 1972:13. Hart, 1973:238, text fig. Peden, 1973:118–119, fig. 1, table 1. Hubbs et al., 1979:14; Pearcy et al., 1982:387. Pequeño, 1986:187. Anderson, 1994:117.

DIAGNOSIS. — Vertebrae 24–26 + 102–110 = 128–135; suborbital pores 7–8 + 0–1 = 7–8; postorbital pores three; occipital and interorbital pores absent; lateral lines mediolateral and ventral, complete; dorsal fin origin associated with vertebrae 6–8; stomach and duodenum black; mouth terminal; total gill rakers 11–15.

COUNTS AND MEASUREMENTS. — Vertebrae 24–26 + 102–110 = 128–135; D 119–124; A 106–114; C 8–10; P 16–19; pelvic 3; vomerine teeth 2–12; palatine teeth 3–12; gill rakers 2–3 + 9–12 = 11–15; branchiostegal rays 6; pseudobranch filaments 4–7. Following measurements in percent SL: head length 14.1–17.3; head width 4.8–8.1; head depth 5.1–7.3; pectoral fin length 6.9–10.2; predorsal length 18.7–23.4; preanal length 30.4–34.7; body height 5.4–7.8; gill slit length 4.6–5.9. Following measurements in percent HL: head width 33.1–51.9; head depth 34.2–45.3; upper jaw length 32.1–46.5; pectoral fin length 48.2–68.3; snout length 18.3–29.4; eye diameter 19.6–28.7; gill slit length 26.5–39.0; interorbital width 5.0–7.5; interpupillary width 20.0–28.2; pelvic fin length 13.7–26.3; caudal fin length 4.5–12.5. Pectoral base/length ratio 30.4–44.8.

DESCRIPTION. — Based on 53 known adults and juveniles. Head elongate, ovoid; dorsal profile gently convex or more dorsoventrally depressed from snout to nape. Some individuals with angular nape. Head longer in adult males than in females. Head length 14.8%–17.3% SL ($\bar{x}$ = 15.8) in 16 males 247–375 mm SL, 14.1%–15.2% SL ($\bar{x}$ = 14.7) in 13 females 263–383 mm SL. Scales absent on head, nape, pectoral fin and base (few, scattered scales may be present on base of largest males) and pectoral axil. Scales present on body, abdomen to between pectoral bases or, in largest adults, a narrow band of scales reaching pelvic base, tail and unpaired fins extending to about 30%–90% of their height, the greatest extent posteriorly in largest specimens. Eye ovoid, not entering dorsal profile of head. Gill slit extending ventrally to just above pelvic base. Opercular flap at upper end of gill slit well-developed; slit extending forward about one-third (juveniles) to one-half (adults) eye diameter. Pectoral fin origin just below body midline, insertion on abdomen; posterior margin of fin evenly rounded, middle and lower ray tips exserted, more so ventrally; ventralmost 8–10 rays thickened.

Mouth terminal, upper jaw extending to middle of eye or its anterior quarter. Upper jaw longer in adult males than in females, 36.3%–46.5% HL ($\bar{x}$ = 43.0) in 16 males 247–375 mm SL, 32.1%–38.4% HL ($\bar{x}$ = 35.3) in 13 females 263–383 mm SL. Nostril tube small, not reaching half way from its base to upper lip when pressed forward, 2.7%–3.5% HL. Upper lip well-delimited, especially in juveniles, broadly adnate to snout. Labial lobe of lower jaw well-developed, gently rounded. Oral valve coalesced with sides of palate, not extending to rictus or anterior edge of vomer and better developed in adults than in juveniles. Jaw teeth conical, sharp; upper jaw with 2–3 rows anteriorly (all sizes), lower jaw with 3–5 irregular rows near symphysis. Numbers of jaw teeth not different between the sexes; great individual variation. Vomerine and palatine teeth retrorse, in single row on palatine bones.

Cephalic lateralis system with three postorbital pores, arising from frontal, pterotic and lateral extrascapulars (positions one, three and four). Two pairs of anterior supraorbital (nasal) pores, one set anteromesial to nostril tube, the other posteromesially. Usually seven suborbital pores arising from ventral ramus of bone chain under eye and none from ascending ramus (7 + 0); suborbital pore variation rare, two specimens with pattern 7 + 0 on one side of head, 7 + 1 on the other, and one with 7 + 0/8 + 0. Eight preoperculomandibular pores, four arising from dentary, one from anguloarticular and three from preopercle (no variation). Interorbital and occipital pores absent. Body lateral line double, with mediolateral branch originating about one-third pectoral fin length posterior to pectoral margin, and ventral branch originating just above gill slit, steeply sloping down anterior portion of body and coursing above anal fin base to tail tip.

Dorsal fin origin above posterior quarter of pectoral fin, associated with vertebrae 6–8, usually 7–8, with no supraneurals. Anal fin origin associated with ultimate or penultimate precaudal vertebrae, with 3–7 ray-bearing pterygiophores inserted anterior to haemal spine of first caudal vertebra. Pterygiophore of last dorsal ray associated with second through fifth, usually fourth or fifth, preural vertebrae; pterygiophore of last anal ray associated with second preural vertebra, with two (rarely one) rays articulating with haemal spine. Caudal fin with two epural, 3–4 upper hypural and 3–4 lower hypural rays.

Gill rakers on upper limb small, more acute in adults; on lower limb, blunt, triangular, changing little in shape with growth. Pseudobranch filaments long, usually 5–6. Pyloric caeca two small nubs.

Color uniformly dark chocolate brown, head and fins darker. Small juveniles with blue abdomen and black head and fins. Lining of orobranchial chamber black. Eye blue. Stomach and duodenum (especially latter) black; posterior portion of fundus becoming paler in large adults, as melanophores disperse.

This species reaches 389 mm TL. Bivalves and ophiuroids were found in several stomachs.

DISTRIBUTION. — Southeastern Alaska off Sitka Sound to off Cabo Colnett, Baja California Norte, Mexico. Depth range: 1500–2570 m.

REMARKS. — See remarks section on *L. micropora* (below) for comments on relationships. The Puget Sound record of Jordan et al. (1930) is considered erroneous (see Schultz, 1936; Schultz and DeLacy, 1936; Bayliff, 1959). Schutlz and DeLacy (1936) give the locality of the holotype as northern California (an error perpetuated by Andriashev, 1955:359), however, a more accurate plotting puts it off Cape Blanco, or Bandon, Oregon.

MATERIAL EXAMINED. — Alaska, off Sitka Sound: SU 20014 (paratype; 208 mm); Cape Edgecumbe S 84°, E 21 miles; *Albatross* sta.

4267; 1686 m; 1731 hrs.; 31 July 1903; U. S. Fish Commission. British Columbia: NMC 68-1783 (1; 320 mm); 50°54.5'N, 130°06.0'W; *G. B. Reed*; 2103–2196 m; 11 Sept. 1964. Oregon: UW 19082 (3; 247–283 mm); 45°51.0'N, 125°06.0'W; *John N. Cobb*; 1536 m; 16 June 1966; R. B. Grinols. UW 17700 (8; 263 + seven badly damaged); 45°50.0'N, 125°11.0'W; *John N. Cobb*; 1646 m; 29 May 1964; R. B. Grinols. USNM 57828 (holotype; 328 mm); 43°01.0'N, 125°12.5'W; *Albatross* sta. 3788; 1946 m; 27 Apr. 1901; U. S. Fish Commission. California, off Farallon Islands: RUSI 37099 (1; 337 mm); 37°38.9'N, 123°23.7'W; *Wecoma* sta. 11; 2570–2470 m; 0744–0840 hrs.; 29 July 1991; G. M. Cailliet. RUSI 37100 (4; 315–383 mm); 37°38.4'N, 123°21.5'W; *Wecoma* sta. 12; 2375–2300 m; 1220–1310 hrs.; 29 July 1991; G. M. Cailliet. CAS 81727 and RUSI 44303 (19; 289–375 mm); 37°26.2'N, 123°18.6'W; *Golden Fleece* sta 3A-1; 1683–1674 m; 1620–1650 hrs.; 20 Sept. 1991; G. M. Cailliet. SIO 60-475 (9; 110–365 mm); otter trawl, ca. 1830 m; 10 Nov. 1960; Atomic Energy Commission. California, off Pt. Sur: CAS 78979 (1; 110 mm); 36°15.1'N, 122°25.5'W; *Cayuse* sta. SLS-16; 1580–1622 m; 0837–0907 hrs.; 26 July 1984; W. Wakefield and M. E. Anderson. California, San Clemente Basin: SIO 74-200 (1; 222 mm); 32°26.4'N, 117°54.0'W; *Oconostota* sta. 9; 1646 m; 0900 hrs.; 5 Sept. 1974; J. Siebenaller. SIO 89-108 (2; 222–243 mm); 32°36.1'N, 118°10.2'W; *R. G. Sproul*; 1500–1940 m; 12–13 Sept. 1989; R. S. Kaufman. California, East Cortez Basin: CAS 56192 (1; 254 mm); 32°15.9'N, 118°41.2'W; *Atlantis II* sta. MEA 85-6; 1678–1617 m; 2000–2100 hrs.; 20 Jan. 1985; M. E. Anderson, J. A. Seigel, R. S. Carney. Mexico, Baja California Norte: SIO 61-168 (2; 205–251 mm); 30°52'N, 116°53'W; otter trawl sta. P-274-61; 1948–1957 m; 2205–0245 hrs.; 28–29 Apr. 1961; R. Parker.

Lycenchelys lonchoura sp. n.
(Fig. 8)

HOLOTYPE. — CAS 58150 (female, 355 mm); Peru, NW of Pt. Coles; 17°08.5'S, 72°07.4'W; commercial trawler; 860 m; 0914 hrs.; 21 Jan. 1972; E. del Solar.

DIAGNOSIS. — Vertebrae 24 + 83 = 107; suborbital pores 7 + 1; postorbital pores three; occipital and interorbital pores absent; lateral line ventral, complete; dorsal fin origin associated with vertebra two; caudal fin length 4.3% SL, 24.0% HL; mouth terminal; pyloric caeca absent; total gill rakers 13.

COUNTS AND MEASUREMENTS. — Vertebrae 24 + 83 = 107; D 103; A 86; C 10; P 18; pelvic 3; vomerine teeth 4; palatine teeth 6/7; gill rakers 3 + 10; branchiostegal rays 6; pseudobranch filaments 6. Following measurements in percent SL: head length 17.7; head width 8.9; head depth 9.8; pectoral fin length 8.0; predorsal length 18.1; preanal length 38.1; body height 9.3; gill slit length 9.2. Following measurements in percent HL: head width 50.2; head depth 55.3; upper jaw length 42.0; pectoral fin length 45.5; snout length 22.8; eye diameter 17.1; gill slit length 52.3; interorbital width 8.8; interpupillary width 22.5; pelvic fin length 8.3/11.2; caudal fin length 23.9. Pectoral base/length ratio: 59.0.

DESCRIPTION. — Only holotype known. Head elongate, ovoid; dorsal profile gently declined from nape to steeper snout tip. Scales absent on head, nape, pectoral axil and anteriorly on dorsal and anal fins. Scales present and deeply imbedded on body, abdomen to pelvic base, tail, pectoral base and fin proximally and unpaired fins to about half their height or less posteriorly. Eye round, entering dorsal profile of head. Gill slit extending ventrally to pelvic base. Opercular flap at upper end of gill slit well-developed, rounded; slit extending forward about two eye diameters. Pectoral fin origin well below body midline, insertion on abdomen; posterior margin of fin wedge-shaped, ray tips exserted, more so ventrally; ventralmost seven rays thickened.

Mouth terminal, upper jaw extending to vertical through posterior margin of eye. Nostril tube reaching upper lip when pressed forward. Upper lip well-delimited. Labial lobe of lower jaw not well-developed, narrow and mostly hidden when mouth is closed; ventral margin of lobe parallel with ventral margin of jaw. Oral valve not coalesced with sides of palate, almost extending to rictus, and just reaching vomer. Jaw teeth small, conical, sharp; both jaws with three irregular rows of teeth anteriorly, narrowing into single row posteriorly. Vomerine teeth four, in small patch; palatine teeth in single series.

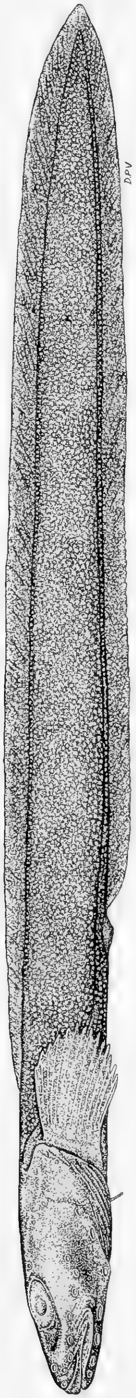

FIGURE 7. *Lycenchelys jordani* (Evermann and Goldsborough, 1907), CAS 56192, 254 mm SL, off southern California.

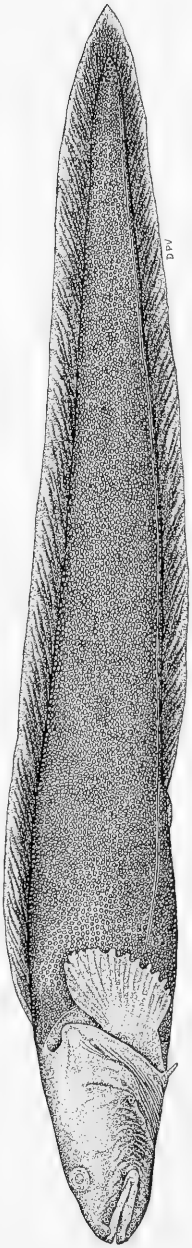

FIGURE 8. *Lycenchelys lonchoura* sp. n., CAS 58150, holotype, 355 mm SL, off Peru.

Cephalic lateralis system with three postorbital pores, arising from frontal, pterotic and lateral extrascapulars (positions one, three and four). Two pairs of anterior supraorbital (nasal) pores, one set anteromesial to nostril tube, the other posteriorly. Eight suborbital pores, seven arising from ventral ramus of bone chain under eye and one from ascending ramus behind eye just below first postorbital pore (7 + 1). Eight preoperculomandibular pores, four arising from dentary, one from anguloarticular and three from preopercle. Interorbital and occipital pores absent. Body lateral line ventral, complete, steeply sloping on anterior portion of body.

Dorsal fin origin above pectoral base, associated with vertebra two, with no supraneurals; predorsal length only slightly more than head length. Anal fin origin associated with ultimate precaudal vertebra (24), with four ray-bearing pterygiophores inserted anterior to haemal spine of first caudal vertebra. Pterygiophore of last dorsal ray associated with fourth preural vertebra; pterygiophore of last anal ray associated with second preural vertebra, with one ray articulating with haemal spine. Caudal fin with one epural, four upper hypural and five lower hypural rays.

Tips of gill rakers roughly squared-off, with small, fleshy lateral projection; first and last gill rakers somewhat acute, without projection. Pseudobranch filaments long, slender. Pyloric caeca absent.

Color in alcohol uniformly dark brown, head darker, fins pale. Eyes blue. Lining of orobranchial chamber dark brown, probably black in life. Stomach and intestines pale (unpigmented).

Single specimen, 370 mm TL, a ripe female with ova averaging 6.2 mm in diameter.

DISTRIBUTION. — Known only off Peru in 860 m.

ETYMOLOGY. – From the Greek λονχη (spearhead, lance) and ουρα (tail) referring to the shape and great length of the caudal fin.

Lycenchelys micropora Andriashev, 1955
(Fig. 9)

Lycenchelys microporus Andriashev, 1955:367, figs. 2, 11, 12 (original description. Type locality: Bering Sea abyss). Andriashev, 1958:178. Quast and Hall, 1972:13. Toyoshima, 1985:152.
Lycenchelys "B" sp. n. Pearcy et al., 1982:387.
Lycenchelys micropora: Anderson, 1994:117.

DIAGNOSIS. — Vertebrae 27–30 + 96–106 = 124–135; suborbital pores 7 + 0; postorbital pores 2–3; interorbital and occipital pores absent; lateral lines ventral and mediolateral, complete; dorsal fin origin associated with vertebrae 5–7; nostril tube length 7.8%–11.6% HL; palatine teeth present or absent; total gill rakers 10–14.

COUNTS AND MEASUREMENTS. — Vertebrae 27–30 + 94–106 = 123–135; D 115–127; A 99–109; C 8–9; P 15–18; pelvic 3; vomerine teeth 1–16; palatine teeth 0–10; gill rakers 2–3 + 8–11 = 10–14; branchiostegal rays 6–7; pseudobranch filaments 0–4. Following measurements in percent SL: head length 12.8–15.6; head width 4.8–8.7; head depth 5.1–7.5; pectoral fin length 7.1–10.0; predorsal length 15.7–19.9; preanal length 27.9–37.9; body height 4.1–7.4; gill slit length 3.7–5.8. Following measurements in percent HL: head width 35.2–57.7; head depth 37.6–52.7; upper jaw length 29.5–47.8; pectoral fin length 52.0–73.0; snout length 25.7–34.8; eye diameter 14.1–22.6; gill slit length 26.5–39.9; interorbital width 4.7–10.6; interpupillary width 18.4–26.2; pelvic fin length 11.3–23.8; caudal fin length 2.5–14.9. Pectoral base/length ratio: 31.4–50.9.

DESCRIPTION. — Forty adult and juvenile specimens are known of this species. Head elongate, ovoid, deeper in adults than in juveniles; dorsal profile more dorsoventrally depressed in juveniles than in adults. Head not longer in males than in females. Scales absent on head, nape, pectoral base, axil, and fin. Scales present on body, abdomen to a line between pectoral bases, tail and on unpaired fins extending to about 50%–80% of their height, the greatest extent posteriorly. Eye round, not entering dorsal profile of head. Gill slit extending ventrally to just below lower end of pectoral base. Slight, angular opercular flap at upper end of gill slit; slit extending forward about one-quarter to one-third eye diameter. Pectoral fin origin below body midline, more so in thicker-bodied adults than in the more slender juveniles; pectoral insertion on abdomen; posterior margin of fin evenly rounded, ray tips exserted, more so ventrally, ventralmost 8–9 rays thickened. Eastern Pacific specimens usually with

15–16 pectoral rays; holotype with 18 rays.

Mouth inferior, upper jaw extending to vertical through anterior margin of eye or its anterior quarter. Upper jaw longer in adult males than in females, 38.1%–47.8% HL ($\bar{x}$ = 40.5) in 10 males, 33.5%–38.6% HL ($\bar{x}$ = 35.6) in six females. Nostril tube elongate, reaching anterior edge of upper lip, or extending beyond it (but subject to considerable shrinkage in alcohol). Upper lip poorly delimited, broadly adnate to snout anteriorly. Labial lobe of lower jaw weak, not evident when mouth is closed. Oral valve coalesced with sides of palate, but just reaching anterior edge of vomer in some. Jaw teeth conical, sharp, retrorse; upper jaw with double row anteriorly only in largest specimens (inner row consisting of few teeth in these); lower jaw with 2–3 irregular rows near symphysis, again only in largest specimens. Numbers of jaw teeth not significantly different in present sample. Vomerine and palatine teeth relatively few in smaller fish; 62.5% of present sample lacking palatine teeth; several large females with palatine teeth in two irregular rows (including holotype); vomerine teeth continually added with growth, one 267 mm female with 16 teeth.

Cephalic lateralis system with 2–3 postorbital pores (76.9% of sample with two), arising from frontal and pterotic, or both plus lateral extrascapulars (positions 1, 3 or 1, 3, 4); one anomalous specimen with pores 1, 3 on one side of head, pores 1, 3, and a doubling at position 4 on the other. Two pairs of anterior supraorbital (nasal) pores, one set mesial to nostril tube, the other posteromesially. Seven suborbital pores arising from ventral ramus of bone chain and none from ascending ramus (7 + 0); one anomalous specimen with 7 + 0 on one side of head, 8 + 0 on the other. Eight preoperculomandibular pores, four arising from dentary, one from anguloarticular and three from preopercle (no variation). Interorbital and occipital pores absent, except one specimen with tiny, anterior interorbital pore. Body lateral line double, complete; mediolateral branch commencing at or just behind posterior margin of pectoral fin when appressed, ventral branch commencing above upper end of gill slit, coursing down abdomen without bowing, then running just above anal fin base; both branches extending to tail tip; original illustration of holotype not showing mediolateral branch (Andriashev, 1955, figs. 2, 11).

Dorsal fin origin above mid-pectoral fin, associated with vertebrae 5–6, except one specimen with vertebra seven, with no supraneurals. Anal fin origin associated with ultimate or penultimate precaudal vertebrae, with 4–8, usually 4–5, ray-bearing pterygiophores inserted anterior to haemal spine of first caudal vertebra. Pterygiophore of last dorsal ray associated with third or fourth preural vertebrae; pterygiophore of last anal ray associated with second preural vertebra, with 1–2 rays articulating with haemal spine. Caudal fin with two epural, 3–4 upper hypural and three lower hypural rays.

Gill rakers on upper limb small, on lower limb blunt and triangular in juveniles, becoming longer and more acute in adults. Pseudobranch filaments small, absent in two specimens (in one of these, one tiny filament present on left side). Pyloric caeca two small nubs. Branchiostegal rays six, except one specimen (CAS 81705) with seven: five articulating with ceratohyal and two with epihyal.

Color of fresh specimens uniformly dark brown; head, pectoral fins and margins of unpaired fins darker ("bluish-black" according to Andriashev, 1955). Eye blue. Lining of orobranchial chamber and peritoneum black. Stomach pale (unpigmented).

This species reaches 349 mm TL (holotype). Ripe females had ova 3.0–4.8 mm in diameter; in CAS 81704, 215 mm SL, the entire compliment was just 17 eggs.

DISTRIBUTION. — Bering Sea to off central Mexico. Depth range: 2377–3512 m.

REMARKS. — *Lycenchelys micropora* is close to *L. jordani* (above) on the basis of many characters, but differs chiefly in its more numerous precaudal vertebrae (27–30 vs. 24–26), longer nostril tube (length 7.8%–11.6% HL vs. 2.7%–3.5% HL), and fewer pectoral fin rays (usually 15–16 vs. usually 17–18). *Lycenchelys micropora* also occurs at greater depths than *L. jordani* (2377–3512 m vs. 1536–2570 m). The two southernmost specimens, SIO 58-420, are identified on the basis of their vertebral, gill raker and fin ray counts, dorsal fin insertion, long nostril tube and great capture depth. Both are skinned, broken and generally badly trawl damaged.

MATERIAL EXAMINED. — Aleutian Basin,

Bering Sea: ZIN 32963 (holotype, female, 342 mm SL); *Vityaz'* sta. 541; 3120 m; 26 Aug. 1950. Oregon, Cascadia Abyssal Plain: CAS 81705 (1; 239 mm); 45°57.6'N, 125°51.2'W; *Cayuse* sta. BMT-251; 2377 m; 1626–1826 hrs.; 27 Sept. 1970. CAS 56431 (1; 70 mm); 45°56.0'N, 127°37.1'W; *Yaquina* sta. BMT-323; 2763 m; 1157–1340 hrs.; 13 Mar. 1973. CAS 81707 (1; 267 mm); 45°48.2'N, 126°28.2'W; *Yaquina* sta. BMT-158; 2651 m; 0125–0325 hrs.; 17 Jan. 1970. CAS 81700 (1; 170); 45°27.8'N, 126°17.4'W; *Yaquina* sta. BMT-157; 2606 m; 1510–1714 hrs.; 17 Jan. 1970. CAS 81692 (2; 116–125 mm); 45°18.0'N, 125°47.2'W; *Yaquina* sta. BMT-191; 2597 m; 1854–2055 hrs.; 18 Mar. 1970. OS 14380 (1; 196 mm); 45°18.0'N, 126°26.4'W; *Yaquina* sta. BMT-266; 2710 m; 1600–1800 hrs.; 18 Feb. 1971. CAS 81697 (1; 152 mm); 45°14.5'N, 125°47.4'W; *Yaquina* sta. BMT-190; 2597 m; 1142–1342 hrs.; 18 Mar. 1970. CAS 81712 (1; 235 mm); 45°10.8'N, 126°43.0'W; *Yaquina* sta. BMT-160; 2784 m; 1815–2030 hrs.; 18 Jan. 1970. CAS 81709 (3; 145–213 mm); 45°09.3'N, 125°38.3'W; *Yaquina* sta. BMT-93; 2669 m; 2320–0125 hrs.; 15–16 July 1969. OS 14378 (1; 220 mm); 45°01.6'N, 127°31.0'W; *Cayuse* sta. BMT-336; 2850 m; 5 Nov. 1973. LACM 45999-1 (3; 195–217 mm); 44°58.8'N, 125°34.0'W; *Yaquina* sta. BMT-94; 2688 m; 1046–1220 hrs.; 16 July 1969. CAS 81702 (1; 156 mm); 44°58.5'N, 125°44.3'W; *Yaquina* sta. BMT-188; 2792 m; 1750–1950 hrs.; 17 Mar. 1970. CAS 81701 (1; 243 mm); 44°56.1'N, 125°39.8'W; *Yaquina* sta. BMT-187; 2770 m; 1100–1300 hrs.; 17 Mar. 1970. CAS 81698 (1; 202 mm); 44°46.7'N, 125°41.8'W; *Cayuse* sta. BMT-252; 2800 m; 0350–0550 hrs.; 30 Sept. 1970. CAS 81703 (1; 206 mm); 44°41.7'N, 125°33.5'W; *Yaquina* sta. BMT-120; 2825 m; 1002–1130 hrs.; 6 Oct. 1969. CAS 81694 (1; 220 mm); 44°44.1'N, 127°21.2'W; *Yaquina* sta. BMT-407; 3041 m; 1 Aug. 1974. OS 14374 (2; 209–211 mm); 44°36.9'N, 125°35.0'W; *Cayuse* sta. OTB-155; 2800 m; 1325–1532 hrs.; 10 Jan. 1967. CAS 81695 (1; 210 mm); 44°05.3'N, 125°23.6'W; *Yaquina* sta. BMT-288; 2940 m; 2053–2300 hrs.; 14 June 1972. CAS 81699 (1; 197 mm); 44°05.0'N, 125°24.0'W; *Yaquina* sta. BMT-291; 2926 m; 2027–2200 hrs.; 15 June 1972. CAS 81696 (3; 120–197 mm); 44°04.9'N, 125°24.5'W; *Yaquina* sta. BMT-290; 2938 m; 1330–1500 hrs.; 15 June 1972. CAS 81704 (1; 215 mm); 44°04.2'N, 125°24.1'W; *Yaquina* sta. BMT-289; 2926 m; 0615–0745 hrs.; 15 June 1972. OS 14375 (4; 103–215 mm); 43°43.2'N, 125°29.6'W; *Yaquina* sta. BMT-293; 3000 m; 0622–0755 hrs.; 17 June 1972. California, off Farallon Isl.: CAS 81708 (1; 259 mm); 37°39.1'N, 123°27.4'W; *Wecoma* sta. 9; 2840–2775 m; 2120–2241 hrs.; 28 July 1991; G. Cailliet. CAS 81716 (1; 321 mm); 37°39.0'N, 123°27.7'W; *Wecoma* sta. 6; 2865–2760 m; 0316–0409 hrs.; 28 July 1991; G. Cailliet. CAS 81717 (1; 298 mm); 37°38.5'N, 123°29.8'W; *Wecoma* sta. 1; 3010–2975 m; 0141–0204 hrs.; 27 July 1991; G. Cailliet. CAS 81714 (male, 318 mm); California, off Farallon Isls.; 37°37.5'N, 123°30.0'W; *Wecoma* sta. 16; beam trawl; 2900 m; 1350–1435 hrs.; 30 July 1991; G. M. Cailliet. Mexico, Gulf of Tehuantepec: SIO 58-420 (2; 168+, 173 mm); 14°28'N, 93°09'W; dredge; 3512 m; 2110–0400 hrs.; 18–19 Nov. 1958; R. Wisner and R. Parker.

Lycenchelys monstrosa Anderson, 1982

Lycenchelys monstrosa Anderson, 1982a:208, figs. 1–2 (original description. Type locality: Gulf of Panama). Anderson, 1994:65, 117.

DIAGNOSIS.— Vertebrae 26–30 + 96–105 = 124–132; D 111–118; A 98–108; C 9–10; P 15–17; pelvic 0–2; vomerine teeth 1–5; palatine teeth 0–2; gill rakers 2–4 + 8–11 = 11–15; branchiostegal rays 6; pseudobranch filaments 0–3, minute; pyloric caeca 0–2; dorsal fin origin associated with vertebrae 6–12, with 1–7 supraneurals; head 13.7%–15.3% SL (not 5.0%–6.2% SL as reported by Anderson, 1982); pectoral fin 8.6%–10.4% SL; predorsal length 20.2%–25.5% SL; body height 4.8%–6.3% SL; upper jaw 26.5%–36.6% HL; pelvic length (N = 2; all others lack pelvic fins) 11.6%–17.4% HL; preoperculomandibular pores nine; first postorbital pore only (doubled on one side, one specimen); suborbital pores 7–9; occipital and interorbital pores absent; body lateral line with mediolateral and ventral branches, complete.

DISTRIBUTION. — Central Baja California to Gulf of Panama. Depth range: 3193–4188 m.

MATERIAL EXAMINED. — See Anderson

(1982). Baja California record is a range and depth extension: SIO 61-176 (1; 204 mm); 27°20.0'N, 115°23.1'W; beam trawl; 4161–4188 m; 1635–0040 hrs.; 6–7 May 1961; R. Parker.

Lycenchelys pearcyi sp. n.
(Fig. 10)

Lycenchelys "C" sp. n. Pearcy et al., 1982:387.

HOLOTYPE. — CAS 81715 (male, 382 mm SL); Oregon, Cascadia Abyssal Plain; 45°17.0'N, 126°38.8'W; *Yaquina* sta. BMT-159; 2753 m; 1330–1530 hrs.; 18 Jan. 1970.

PARATYPES. — Oregon, Cascadia Abyssal Plain: OS 14379 (1; 188+ mm); 45°38.2'N, 126°47.9'W; *Yaquina* sta. BMT-262; 2721 m; 17 Feb. 1971. CAS 81706 (1; 268 mm); 45°20.6'N, 126°35.7'W; *Yaquina* sta. BMT-264; 2750 m; 0130–0330 hrs.; 17 Feb. 1971. OS 14187 (1); 44°58.2'N, 126°38.9'W; *Yaquina* sta. BMT-267; 2795 m; 0035–0501 hrs.; 18 Feb. 1971. CAS 81710 (1; 293 mm); 44°37.5'N, 127°31.5'W; *Yaquina* sta. BMT-282; 2816 m; 19 May 1971. CAS 81718 (1; 350 mm); 44°36.9'N, 125°35.0'W; *Cayuse* sta. OTB-155; 2800 m; 1325–1532 hrs.; 10 Jan. 1967. CAS 81711 (2; 122–293 mm); 44°04.9'N, 125°24.5'W; *Yaquina* sta. BMT-290; 2938 m; 1330–1500 hrs.; 15 June 1972. CAS 81693 (1; 71 mm); 44°04.2'N, 125°24.1'W; *Yaquina* sta. BMT-289; 2926 m; 0615–0745 hrs.; 15 June 1972. OS 14377 (1; 184 mm); 43°43.2'N, 125°29.6'W; *Yaquina* sta. BMT-293; 3000 m; 0622–0755 hrs.; 17 June 1972. CAS 81713 (1; 329 mm); 43°16.0'N, 125°50.5'W; *Cayuse* sta. OTB-76; 3051 m; 1310–1505 hrs.; 27 July 1965. Mexico, off Cabo Falso, Baja California Sur: SIO 62-366 (1; 275 mm); 22°35.6'N, 110°06.5'W; dredge sta. VSS-17; 2663–2707 m; 0840–1400 hrs.; 26 Mar. 1959; R. Parker.

DIAGNOSIS. — Vertebrae 27–30 + 100–104 = 128–134; preoperculomandibular pores usually nine; suborbital pores 8–11, usually nine; postorbital pores 1–2; occipital pores absent; interorbital pore absent, except in holotype; lateral line ventral; dorsal fin origin associated with vertebrae 6–7, with 1–3 supraneurals; pelvic fin rays two; pyloric caeca absent; total gill rakers 13–15.

COUNTS AND MEASUREMENTS. — Values for holotype first, followed by range of paratypes in parentheses: vertebrae 29 + 101 = 130 (27–30 + 100–104 = 128–134); D 118 (118–124); A 106 (104–109); C 8 (9–11); P 16 (16–17); pelvic 2 (2); vomerine teeth 17 (3–12); palatine teeth 5/9 (2–5); gill rakers 2 + 12 (2–3 + 11–12 = 13–15); branchiostegal rays 6 (6); pseudobranch filaments 3 (3–5). Following measurements in percent SL: head length 18.4 (14.9–17.7); head width 6.9 (4.7–7.9); head depth 7.0 (4.8–7.2); pectoral fin length 7.2 (6.8–9.5); predorsal length 20.5 (17.6–21.9); preanal length 38.1 (34.4–37.1); body height 5.6 (3.6–7.7); gill slit length 5.6 (3.9–6.3). Following measurements in percent HL: head width 37.8 (31.1–50.5); head depth 38.2 (30.3–45.8); upper jaw length 42.6 (29.7–38.5); pectoral fin length 39.2 (39.4–59.5); snout length 33.3 (29.6–37.4); eye diameter 12.7 (12.1–19.8); gill slit length 30.6 (25.9–35.3); interorbital width 6.0 (5.3–7.7); interpupillary width 14.4 (14.1–18.8); pelvic fin length 8.1 (10.2–22.4); caudal fin length 4.3 (3.3–18.9). Pectoral base/length ratio: 54.6 (35.3–58.2).

DESCRIPTION. — Based on all 11 specimens of both sexes. Adults or subadults are three males and four females. Head elongate, dorsoventrally depressed, almost triangular; dorsal profile gently declined anterior to nape, snout tip steeply sloping, more so in juveniles than adults. Head lengths of males and females not different in present, small sample. Scales absent on head, nape to line connecting upper end of gill slits, pectoral fin and base, and in pectoral axil. Scales present in adults on body, abdomen to line connecting pectoral bases, tail and unpaired fins extending to about 60%–80% of their height; scales absent on fins of two smallest specimens. Eye somewhat ovoid in small specimens, entering dorsal profile of head, rounded in adults and excluded from profile. Gill slit extending ventrally to opposite lower end of pectoral base, which is closer to pelvic base in adults than in juveniles. Opercular flap at upper end of gill slit well-developed, angular; slit extending forward from about half an eye diameter in largest (holotype). Pectoral fin origin well below body midline, insertion on abdomen; posterior margin of fin wedge-shaped, only ventral ray tips exserted; ventralmost 5–6 rays thickened. Ventral abdominal plica pres-

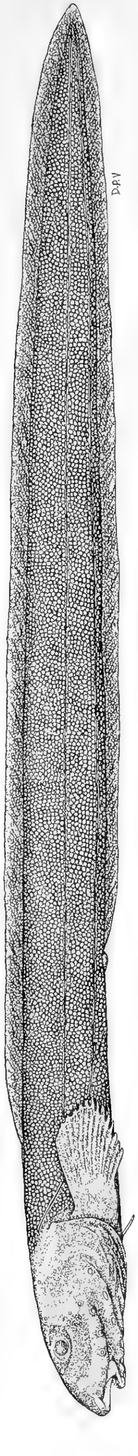

FIGURE 9. *Lycenchelys micropora* Andriashev, 1955, CAS 81708, 259 mm SL, off Farallon Isl., California.

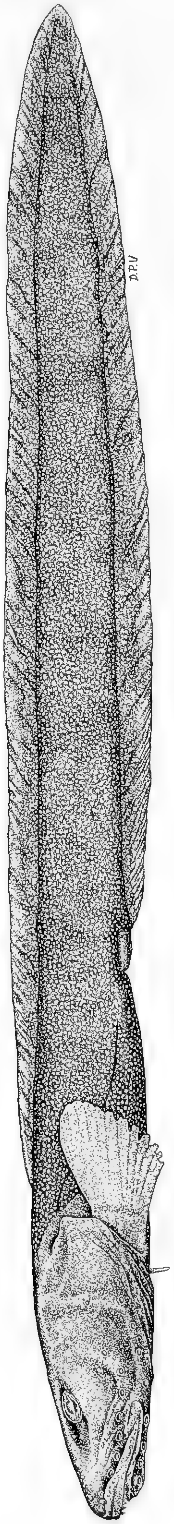

FIGURE 10. *Lycenchelys pearcyi* sp. n., CAS 81715, holotype, 382 mm SL, off Oregon.

ent, but not evident in larger, faded specimens (including holotype); plica white in better preserved, small specimens.

Mouth inferior, upper jaw extending to anterior margin of eye (smallest specimen) or its middle (holotype). Upper jaw apparently longer in adult males than in females, 37.4%–42.6% SL in three males, 32.8%–37.4% SL in four females. Nostril tube small, just reaching upper lip when pressed forward. Upper lip poorly delimited anteriorly in larger specimens, as snout tip becomes flaccid with growth. Labial lobe of lower jaw moderately well-developed, hidden when mouth is closed, but more fleshy in adults than in juveniles. Oral valve coalesced with sides of palate and not reaching vomer. Jaw teeth conical, sharp; upper jaw with single row in small specimens, three rows in holotype; lower jaw with single row in small specimens, four rows in holotype. Vomerine teeth in patch or row in small specimens, in large, ovoid patch of 17 teeth in holotype; palatine teeth in two short rows in holotype, single row in others.

Cephalic lateralis system with 1–2 postorbital pores, arising from frontal only (usually), or frontal and lateral extrascapulars (one specimen, one side; positions 1 and 4 in this). First postorbital pore doubled in three specimens. Two pairs of anterior supraorbital (nasal) pores, one set anteromesial to small nostril tube, the other set posteromesially; holotype with a third pore on left side set at posterior base of nostril. Usually nine suborbital pores, eight arising from ventral ramus of bone chain under eye, and one from ascending ramus behind eye (8 + 1); suborbital pore variation great, one fish with pattern 9 + 2/8 +1, one with 8 + 1/8 +0, one with 8 + 2/8 + 2 and one with 8 + 0/8 + 0. Nine preoperculomandibular pores, four arising from dentary, one from anguloarticular and four from preopercle; in one specimen, lowermost preopercular pore (no. 6) of the left side is doubled, producing 10 pores; in same specimen on right side pores two and three are nearly completely joined, with just a detached fleshy septum separating them. Conjoined pores five and six similarly occur in three other specimens, but these are counted as separate pores. Interorbital and occipital pores absent, except holotype with one interorbital pore set before anterior margin of eyes. Body lateral line ventral, traceable in present faded material only anteriorly on body.

Dorsal fin origin above anterior quarter of pectoral fin, associated with vertebrae 6–7, with 1–3 supraneurals. Anal fin origin associated with ultimate or penultimate precaudal vertebrae, with 4–6 ray-bearing pterygiophores inserted anterior to haemal spine of first caudal vertebra. Pterygiophore of last dorsal ray associated with third or fourth preural vertebrae; pterygiophore of last anal ray associated with second preural vertebra, with two rays articulating with haemal spine. Caudal fin with two epural, 3–5 upper hypural and 2–4 lower hypural rays.

Gill rakers on upper limb small, acute at all sizes; on lower limb acute, triangular in juveniles, ventralmost blunter in adults; tips never squared-off. Pseudobranch filaments long, shape greatly distorted in most specimens. Pyloric caeca absent.

Color in alcohol faded to pinkish brown or dark brown, head and fins darker. Lining of orobranchial chamber and peritoneum dark brown, probably black in life. Stomach pale; duodenum with dense array of melanophores, rest of intestine pale.

This species reaches 385 mm TL. A 293 mm female had 53 ripe ova measuring 4.7–5.8 mm in diameter.

DISTRIBUTION. — Off northern Oregon to southern tip of Baja California, Mexico. Depth range: 2663–3051 m.

ETYMOLOGY. – Named in honor of William G. Pearcy, professor of oceanography at Oregon State University, Corvallis, in recognition of his many contributions to the biology of North Pacific fishes.

REMARKS. — Of the Pacific species of *Lycenchelys* with nine preoperculomandibular pores, *L. pearcyi* appears closest to *L. plicifera* in also sharing the ventral, white plica (naked skin fold). It differs chiefly from *L. plicifera* in its more numerous suborbital pores (8–11 [usually nine] vs. 7–8), more pseudobranch filaments (3–5 vs. 1–2), more numerous vertebrae (128–134 vs. 122–126, although overlap probably occurs), more anteriorly placed dorsal fin (predorsal length 17.6%–21.9% SL vs. 22.3%–27.0% SL and fin origin associated with vertebrae 6–7 vs. 9–11), fewer free dorsal pterygiophores (supraneurals; 0–3 vs. 5–6) and absence of pyloric caeca.

Lycenchelys pentactina sp. n.
(Fig. 11)

HOLOTYPE. — ZIN 48392 (male, 150 mm); Peru, off Pta. Santa Maria; 14°44'S, 76°12'W; *Dmitry Mendeleyev* sta. 1654; 1495–1430 m; 2335–0120 hrs.; 19–20 Mar. 1978; N. V. Parin.

DIAGNOSIS. — Vertebrae 25 + 95 = 120; suborbital pores 6 + 1; postorbital pores five, one arising from sphenotic; occipital pores absent; interorbital pore present; lateral line ventral, complete; dorsal fin origin associated with vertebra four; branchiostegal rays five; total gill rakers 12.

COUNTS AND MEASUREMENTS. — Vertebrae 25 + 95 = 120; D 114; A 100; C 9; P 15; pelvic 3; vomerine teeth 9; palatine teeth 10/9; gill rakers 2 + 10; branchiostegal rays 5; pseudobranch filaments 3. Following measurements in percent SL: head length 15.9; head width 6.6; head depth 6.3; pectoral fin length 8.8; predorsal length 17.8; preanal length 34.5; body height 5.9; gill slit length 3.8. Following measurements in percent HL: head width 41.6; head depth 39.5; upper jaw length 39.5; pectoral fin length 55.5; snout length 24.8; eye diameter 24.0; gill slit length 24.2; interorbital width 6.3; interpupillary width 18.9; pelvic fin length 10.5; caudal fin length 12.6. Pectoral base/length ratio 35.6.

DESCRIPTION. — Only holotype known. Head elongate, ovoid; profile dorsoventrally depressed, snout tip steeply sloping. Scales absent on head, nape, pectoral fin, base and axil, and on unpaired fins anteriorly. Scales sparse on abdomen, especially anteriorly, not reaching line connecting pectoral bases. Scales also present on body, tail and unpaired fins posteriorly, extending to about 50%–60% of their height. Eye rounded, spectacle thick, excluded from dorsal profile of head. Gill slit extending ventrally to just above lower end of pectoral base —to opposite pectoral ray 13. Opercular flap at upper end of gill slit well-developed, edge rounded; slit extending forward about 80% eye diameter. Pectoral fin origin well below body midline, insertion on abdomen; posterior margin of fin wedge-shaped, middle and ventral ray tips exserted, more so ventrally; lowermost rays not appreciably thickened.

Mouth subterminal, upper jaw extending to just beyond middle of eye; posterior end of maxilla deeply imbedded in fleshy pocket. Nostril tube extending well beyond upper lip when pressed forward. Upper lip well-delimited. Labial lobe of lower jaw well-developed, ventral margin of lobe evenly rounded. Oral valve coalesced with sides of palate and not reaching vomer. Jaw teeth conical, sharp; upper jaw with double row anteriorly, lower jaw with three rows anteriorly. Vomerine and palatine teeth relatively large, recurved; some vomerine teeth caniniform.

Cephalic lateralis system with five postorbital pores, arising from frontal, sphenotic, pterotic (two) and lateral extrascapulars (positions 1–5). Two pairs of anterior supraorbital (nasal) pores, one set mesial to nostril tube, the other posteromesially. Seven suborbital pores, six arising from ventral ramus of bone chain under eye and one from ascending ramus behind eye just ventral to first postorbital pore (6 + 1). Eight preoperculomandibular pores, four arising from dentary, one from anguloarticular and three from preopercle. Interorbital pore single, set just anterior to line through center of pupils. Occipital pores absent. Body lateral line ventral, complete, difficult to trace in this faded specimen, but not steeply sloping on body.

Dorsal fin origin above anterior quarter of pectoral fin, associated with vertebra four, with no supraneurals. Anal fin origin associated with ultimate precaudal vertebra, with four ray-bearing pterygiophores inserted anterior to haemal spine of first caudal vertebra. Pterygiophore of last dorsal ray associated with fourth preural vertebra; pterygiophore of last anal ray associated with second preural vertebra, with two rays articulating with haemal spine. Caudal fin with two epural, four upper hypural and three lower hypural rays.

Gill rakers on upper limb small, slender, acute; on lower limb all rakers triangular, but longer dorsally. Pseudobranch filaments long. Pyloric caeca two nubs, but somewhat slender and longer than usual for this genus.

Color in alcohol faded to pinkish brown, fins brownish, transparent. Lining of orobranchial chamber and peritoneum dark brown, probably black in life. Stomach and intestines pale (unpigmented).

The single specimen measures 153 mm TL.

DISTRIBUTION. — Known only from off Peru in 1430–1495 m.

Etymology. – From the Greek πεντε (five) and ακτισ (ray, rod) alluding to the species' five branchiostegal rays.

Remarks. — The specimen's small size, transparent pectoral fin without appreciably thickened lower rays, gill rakers on the lower limb not well-differentiated in shape, and sparse abdominal and unpaired fin squamation indicate a juvenile state of maturity. However, the specimen has a rather large gonad that extends anteriorly in the coelom about 40% of its length. This paradox is probably best considered as precocious sexual development, which has also been observed in the eelpout genus *Gymnelus* (see Anderson, 1982b).

Lycenchelys pequenoi sp. n.
(Fig. 12)

Holotype. — LACM 44132-1 (female, 190 mm); Peru, W. of Lobos de Tierra; 06°26'S, 80°05'W; beam trawl sta. SNP1-26; 1025 m; 23 Jan. 1974; J. M. Engle, J. Coyer, Peruvian fisheries program.

Paratypes. — CAS 60243 (1; 153 mm); Peru, off Mollendo; 17°05.0'S, 72°16.9'W; Agassiz dredge; 1000 m; 0647 hrs.; 27 May 1972; E. del Solar. SIO 72-184 (2; 129, 150 mm); Chile, off Arica; 18°40.5'S, 70°36.0'W; otter trawl sta. MV72-II-27; 768–968 m; 1630–1730 hrs.; 7 May 1972; R. L. Wisner.

Diagnosis. — Vertebrae 23–25 + 96–98 = 119–122; suborbital pores 7 + 1; postorbital pores four; occipital and interorbital pores absent; lateral line ventral, complete; dorsal fin origin associated with vertebra four; pelvic fin rays two; palatine teeth absent; total gill rakers 10–11.

Counts and Measurements. — Values for holotype first, followed by range of paratypes in parentheses: vertebrae 25 + 96 = 121 (23–24 + 96–98 = 119–122); D 114 (113–116); A 99 (99–101); C 10 (9–10); P 16 (14–16); pelvic 2 (2); vomerine teeth 1 (0–1); palatine teeth absent (absent); gill rakers 3 + 8 (2–3 + 8 = 10–11); branchiostegal rays 6 (6); pseudobranch filaments 5 (4–5). Following measurements in percent SL: head length 15.0 (13.4–15.9); head width 5.6 (5.5–6.1); head depth 6.5 (6.0–6.7); pectoral fin length 7.3 (8.2–8.8); predorsal length 16.8 (16.6–17.6); preanal length 34.7 (31.7–34.1); body height 7.0 (5.4–6.1); gill slit length 6.3 (5.0–5.2). Following measurements in percent HL: head width 37.2 (37.4–41.0); head depth 43.5 (41.4–44.9); upper jaw length 36.1 (37.0–43.3); pectoral fin length 48.4 (51.7–64.6); snout length 26.0 (23.6–29.2); eye diameter 28.1 (23.9–30.3); gill slit length 41.8 (32.0–38.8); interorbital width 6.7 (5.9–6.9); interpupillary width 24.9 (23.9–27.0); pelvic fin length 14.4 (11.2–20.7); caudal fin length 10.5 (9.9–12.6). Pectoral base/length ratio: 52.9 (38.1–42.9).

Description. — Two males and two females, all juveniles, known. Head ovoid; dorsal profile steeply sloping in front of eye in holotype, paratypes with more gradual taper. Scales absent on head, nape, pectoral fin, base and axil, and dorsal fin anteriorly. Scales present on body, abdomen (to just posterior to pectoral base), tail and unpaired fins (extending to about 50%–60% of their height posteriorly in holotype). Eye round in two smaller specimens, more ovoid in larger two, just entering dorsal profile of head. Gill slit extending ventrally to below pectoral base and in advance of pelvic base except in 129 mm SL specimen, in which lower end of slit is opposite pectoral ray 12. Opercular flap at upper end of gill slit angular; slit extending forward less than one-half eye diameter. Pectoral fin origin just below body midline, insertion on abdomen; posterior margin of fin evenly rounded, ray tips exserted, more so ventrally; ventralmost 7–8 rays thickened.

Mouth subterminal, upper jaw extending to middle of eye (150 mm SL male) or just before it (three others). Nostril tube small, not reaching half way from its base to upper lip when pressed forward. Upper lip well-delimited, fleshy in larger specimens. Labial lobe of lower jaw well-developed except in smallest specimen, enlarged and fleshy in holotype. Oral valve not coalesced with sides of palate, and extending to rictus, but not reaching vomer. Jaw teeth conical, sharp; upper jaw with single row in paratypes, double row anteriorly in holotype; lower jaw with two rows near symphysis in paratypes, 3–4 irregular rows in holotype. Vomer with single tooth in three specimens, none in 150 mm SL specimen (SIO 72–184); palatine teeth absent in all.

Cephalic lateralis system with four postorbital pores, arising from frontal, sphenotic,

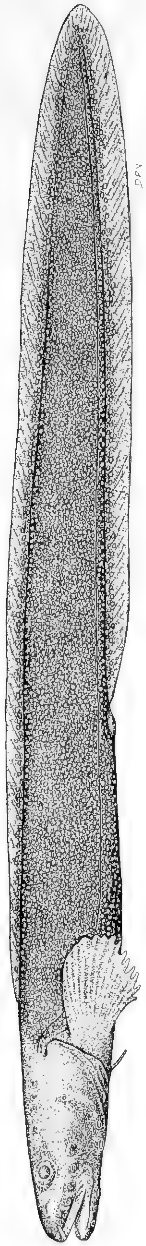

FIGURE 11. *Lycenchelys pentactina* sp. n., ZIN 48392, holotype, 150 mm SL, off Peru.

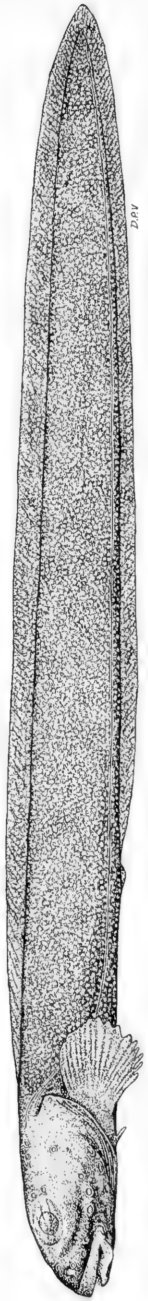

FIGURE 12. *Lycenchelys pequenoi* sp. n., LACM 44132-1, holotype, 190 mm SL, off Peru.

pterotic and lateral extrascapulars (positions 1–4). Two pairs of anterior supraorbital (nasal) pores, one set anteromesial to small nostril tube, the other posteromesially. Eight suborbital pores, seven arising from ventral ramus of bone chain under eye and one from ascending ramus behind eye just below first postorbital pore (7 + 1). Eight preoperculomandibular pores, four arising from dentary, one from anguloarticular and three from preopercle (no variation). Interorbital and occipital pores absent. Body lateral line ventral, complete, steeply sloping on anterior portion of body.

Dorsal fin origin above pectoral base or slightly behind, associated with vertebra four, with no supraneurals. Anal fin origin associated with ultimate precaudal vertebra, with 3–5 ray-bearing pterygiophores inserted anterior to haemal spine of first caudal vertebra. Pterygiophore of last dorsal ray associated with fourth or fifth preural vertebrae; pterygiophore of last anal ray associated with second preural vertebra, with 1–2 rays articulating with haemal spine. Caudal fin with two epural, four upper hypural and 3–4 lower hypural rays.

Gill rakers on upper limb short, acute; on lower limb longer dorsally, triangular and blunter than those on upper limb, but not much differentiated in shape from one another. Pseudobranch filaments long and slender. Pyloric caeca two small nubs.

Color of paratypes in alcohol faded to pinkish gray; holotype dark brown, head and fins darker, eye blue. Lining of orobranchial chamber and peritoneum dark brown, probably black in life. Stomach pale (unpigmented), duodenum black.

Holotype, largest specimen, measures 193 mm TL.

DISTRIBUTION. — Peru and northern Chile. Depth range: 768–1025 m.

ETYMOLOGY. – Named in honor of Dr. Germán Pequeño Reyes, Instituto de Zoologia, Universidad Austral de Chile, Valdivia, in recognition of his many contributions to the ichthyology of the southern hemisphere.

Lycenchelys peruana sp. n.
(Fig. 13)

HOLOTYPE. — LACM 45998-1 (male, 103 mm); Peru, off Trujillo; 07°59'S, 80°37'W; *Anton Bruun* sta. 90; 991–1015 m; 14 Oct. 1965; R. J. Menzies.

PARATYPE. — LACM 44134-1 (female, 102 mm); Peru, between Lobos de Tierra and Lobos de Afuera; 06°42.0'S, 80°47.1'W; beam trawl sta. SNP1-23; 1090–1100 m; 0957–1031 hrs.; 22 Jan. 1974; J. M. Engle, J. Coyer, Peruvian fisheries program.

DIAGNOSIS. — Vertebrae 24 + 99–100 = 123–124; suborbital pores 8 + 1; postorbital pores three; occipital pores two; interorbital pore absent; lateral line ventral; dorsal fin origin associated with vertebrae 5–6; pelvic fin rays two; total gill rakers 11 (+).

COUNTS AND MEASUREMENTS. — Values for holotype first, followed by paratype values in parentheses: vertebrae 24 + 99 = 123 (24 + 100 = 124); D 116 (117); A 102 (102); C 10 (10); P 15 (14); pelvic 2 (2); vomerine teeth 4 (3); palatine teeth 2/1 (1/0); gill rakers 2 + 9 (2 + 9); branchiostegal rays 6 (6); pseudobranch filaments 3 (3). Following measurements in percent SL: head length 11.8 (12.0); head width 4.7 (4.7); head depth 4.6 (4.5); pectoral fin length 8.3 (8.4); predorsal length 16.0 (16.5) preanal length 28.5 (28.8); body height 4.4 (4.4); gill slit length 4.4 (4.3). Following measurements in percent HL: head width 39.3 (39.3); head depth 38.5 (37.7); upper jaw length 36.5 (34.4); pectoral fin length 69.7 (70.5); snout length 25.0 (25.4); eye diameter 28.7 (26.2); gill slit length 36.9 (36.1); interorbital width 9.8 (9.8); interpupillary width 25.4 (25.4); pelvic fin length 27.5 (26.2); caudal fin length 16.4 (8.2). Pectoral base/length ratio: 25.3 (27.9).

DESCRIPTION. — Known from two early juveniles, one male (holotype) and one female (paratype). Head elongate, ovoid, nape depressed; dorsal profile evenly declined to steeply sloping snout tip. Scales absent on head, nape, pectoral fin, base, axil and unpaired fins. Scales present on body, abdomen to just posterior to pectoral bases, and tail. Eye ovoid, entering dorsal profile of head. Gill slit extending ventrally to just above lower end of pectoral base—to opposite pectoral ray 11 or 12. Opercular flap at upper end of gill slit angular; slit extending forward about one-third eye diameter. Pectoral fin origin well below body midline, insertion on abdomen; posterior margin of fin wedge-shaped, ventral rays exserted, not appreciably thickened.

Mouth inferior, upper jaw extending to middle of eye (male) or just before (female). Nostril tube minute, not reaching half way from its base to upper lip when pressed forward. Upper lip thin, not well-delimited. Labial lobe of lower jaw poorly developed, ventral margin of lobe parallel to ventral margin of jaw. Oral valve coalesced with sides of palate and not reaching vomer. Jaw teeth conical, sharper in female than in male; upper jaw with single row in both specimens, lower jaw with double row near symphysis; jaw teeth of male enlarged, caniniform, largest four times the size of largest teeth in female. Teeth on palate of male also caniniform; no right palatine teeth in female.

Cephalic lateralis system with three postorbital pores, arising from frontal, pterotic and lateral extrascapulars (positions one, three and four). Two pairs of anterior supraorbital (nasal) pores, one set anteromesial to small nostril tube, the other posteromesially. Nine suborbital pores, eight arising from ventral ramus of bone chain under eye and one from ascending ramus behind eye just ventral to first postorbital pore (8 + 1); pore 8 in paratype doubled on left side, with one small pore anterior to main pore at this position. Eight preoperculomandibular pores, four arising from dentary, one from anguloarticular and three from preopercle. Interorbital pore absent. Occipital pores two (left and right laterals). Body lateral line ventral, complete, gently declined down abdomen, but irregularly curving.

Dorsal fin origin above anterior third of pectoral fin, associated with vertebrae 5–6, with no supraneurals. Anal fin origin associated with ultimate or penultimate precaudal vertebrae, with 5–6 ray-bearing pterygiophores inserted anterior to haemal spine of first caudal vertebra. Pterygiophore of last dorsal ray associated with fifth preural vertebra; pterygiophore of last anal ray associated with second preural vertebra, with two rays articulating with haemal spine. Caudal fin with two epural, four upper hypural and four lower hypural rays.

Gill rakers on upper limb small, slender, acute; on lower limb ventralmost rakers short, triangular, others slightly longer and with blunter tips. Pseudobranch filaments long, slender. Pyloric caeca two small nubs.

Color in alcohol greatly faded—in paratype, areas of head and fins dark brown, eye blue. Lining of orobranchial chamber mesially and peritoneum dark brown, probably black in life. Stomach and intestines pale (unpigmented).

Holotype, largest specimen, measures 105 mm TL.

DISTRIBUTION. — Known only off Peru in 991–1100 m.

ETYMOLOGY. – Named after the species' provenance.

Lycenchelys plicifera Andriashev, 1955

Lycenchelys pliciferus Andriashev, 1955:372, figs. 2, 15, 16 (original description. Type locality: Bering Sea). Quast and Hall, 1972:13. Fedorov, 1976:4–5. Toyoshima, 1985:148, 155.

Lycenchelys birsteini Andriashev, 1958:178, fig. 4. Quast and Hall, 1972:13. Fedorov, 1976:4–5.

Lycenchelys bersteini (lapsus calami): Toyoshima, 1985:131, 146, 148, 155.

Lycenchelys plicifera: Anderson, 1982a:211. Anderson, 1994:113, 117.

DIAGNOSIS. — Vertebrae 28–30 + 92–98 = 122–126; preoperculomandibular pores nine (with eight as a result of incomplete development); suborbital pores 8 + 0–1; first postorbital pore present (sometimes doubled); occipital and interorbital pores absent; lateral line with ventral and mediolateral branches; dorsal fin origin associated with vertebrae 9–11, with 5–6 supraneurals; pelvic fin rays two; total gill rakers 13–16.

COUNTS AND MEASUREMENTS. — Vertebrae 28–30 + 92–98 = 122–126; D 110–115; A 99–102; C 9–10; P 15–16; pelvic 2; vomerine teeth 2–12; palatine teeth 3–7; gill rakers 2 + 11–14 = 13–16; branchiostegal rays 6; pseudobranch filaments 1–2. Following measurements in percent SL: head length 15.0–16.4; head width 5.9–6.2; head depth 4.7–5.1; pectoral fin length 8.5–12.1; predorsal length 22.3–27.0; preanal length 34.6–38.6; body height 4.5–4.8; gill slit length 4.7–5.4. Following measurements in percent HL: head width 36.4–41.0; head depth 29.5–34.1; upper jaw length 29.7–34.5; pectoral fin length 53.0–77.0; snout length 27.1–32.8; eye diameter 14.4–18.2; gill slit length 29.4–35.6; interorbital width 6.6–9.6; interpupillary width 16.5–18.2; pelvic fin length 19.2–23.9; caudal fin length 4.4–18.2. Pectoral base/length ratio 24.4–40.0.

DESCRIPTION. — Based on four known juveniles (only one a male). Head elongate, dorsoventrally depressed, nape with low but distinct hump (most evident in largest specimen); snout tip steeply sloping. Scales absent on head, nape, in strip before dorsal fin, pectoral fin, axil and base, and unpaired fins. Scales present on body, tail, extending forward on abdomen to just behind vertical through pectoral base. Eye ovoid, more so in larger specimens, not entering dorsal profile of head. Gill slit extending ventrally to below pectoral base, almost reaching pelvic fins. Opercular flap at upper end of gill slit well-developed, slit extending forward about one eye diameter. Pectoral fin origin at or just below body midline, insertion on abdomen; posterior margin of fin wedge-shaped, ray tips exserted, middle and ventralmost deeply so; ventralmost 6–7 rays thickened.

Mouth inferior, upper jaw extending to middle of eye or just before it in smallest specimen. Nostril tube small, not reaching upper lip when pressed forward. Upper lip well-delimited, adnate to snout tip. Labial lobe of lower jaw moderate, generally hidden when mouth closed. Oral valve coalesced with sides of palate and not reaching vomer. Jaw teeth conical, sharp, sparse in these juveniles; upper jaw with single row of teeth except in largest specimen which has short, second row anteriorly; lower jaw with two rows near symphysis in all. Vomerine teeth relatively numerous (12) in largest specimen (2–7 in others).

Cephalic lateralis system with 1–2 pores opening at position one (frontal bone); when pore doubled (on at least one side in three specimens), smaller pore one-half to one-quarter the size of main pore. Two pairs of anterior supraorbital (nasal) pores, one set anteromesial to small nostril tube, the other posteromesially. Eight suborbital pores arising from ventral ramus of bone chain under eye and none from ascending ramus except holotype with single (ninth) pore just below doubled first postorbital pore on right side; no ninth suborbital pore on left side as illustrated by Andriashev (1955, fig. 16). Eight or nine preoperculomandibular pores, four arising from dentary, 1–2 from anguloarticular, and three from preopercle; two anguloarticular pores in types of *L. pliciferus* (complete septum between them), but types of *L. birsteini* with one enlarged pore with incomplete septa set in common pocket, better developed in paratype. Interorbital and occipital pores absent. Body lateral line with mediolateral and ventral branches, the former originating about three eye diameters dorsoposterior to upper end of pectoral base, the latter originating above upper end of gill slit, steeply bowing in pectoral axil and coursing to tail tip just above anal fin base (Andriashev, 1955, fig. 15).

Dorsal fin origin externally obscured by low rudiment of fin fold; from radiograph, origin above posterior third of pectoral fin and associated with vertebrae 9–11, with 5–6 supraneurals. Anal fin origin associated with ultimate to antepenultimate precaudal vertebrae, with 3–5 ray-bearing pterygiophores inserted anterior to haemal spine of first caudal vertebra. Pterygiophore of last dorsal ray associated with third or fourth preural vertebrae; pterygiophore of last anal ray associated with second preural vertebra, with two rays articulating with haemal spine. Caudal fin with two epural, four upper hypural and 3–4 lower hypural rays.

Gill rakers on upper limb small, acute; on lower limb only ventralmost 5–7 acute, dorsalmost with blunt tips. Pseudobranch filaments short, few (only one in largest specimen). Pyloric caeca two low nubbins, poorly delimited in types of *L. pliciferus*.

Color in alcohol uniformly dark brown (types of *L. birsteini* quite faded), head and fins darker. Andriashev (1955:373) reported live coloration as monotone violet-gray, with head and paired fins bluish-black and vertical fins transparent though darker than body. Stomach, intestine, lining of orobranchial chamber and peritoneum coal black, abdomen blue, anus ringed in white, ventral plicae white (but not clear in faded holotype of *L. birsteini*).

Maximum length unknown, largest juvenile measured 190 mm TL.

DISTRIBUTION. — Aleutian Basin and adjacent Kuril-Kamchatka Trench. Depth range: 3820–4070 m.

REMARKS. — Andriashev (1955) named this species to note the white, abdominal skin fold (plica), which is conspicuous (and readily observed in the 140 mm SL paratype of *Lycenchelys birsteini*, ZIN 34669b). The ventral plica, although not always white, has also been observed in *L. callista*, *L. jordani*, *L. pearcyi*, *L. porifer*, *L. rassi*, and *L. vitiazi*. Andriashev

(1955) reported the vertebral counts of *L. plicifera* as 28–29 + 96–97. I find 28 + 96–98. Andriashev (1958) also erred in stating the types of *L. birsteini* have seven free supraneurals (interneurals); there are actually 5–6.

MATERIAL EXAMINED. — ZIN 32961 (holotype, male, 125 mm); Bering Sea, NW of Mednyi (Copper) Isl.; *Vityaz* sta. 972; 3820–3830 m; 2340–0620 hrs.; 3–4 Oct. 1951. ZIN 32961a (paratype, female, 105 mm); same collection as holotype. ZIN 34669 (holotype of *L. birsteini*, female, 188 mm); Kuril-Kamchatka Trench off Paramushiro Isl.; *Vityaz* sta. 2209; 3960–4070 m; 23–24 Jun. 1953. ZIN 34669a (paratype of *L. birsteini*, female, 141 mm); same collection as holotype.

Lycenchelys porifer (Gilbert, 1890)
(Fig. 14)

Lycodes porifer Gilbert, 1890:104 (original description. Type locality: Gulf of California).
Lycodes anguis Garman, 1899:133, pl. 30, fig. 1. Jordan et al., 1930:475.
Lycodes serpens Garman, 1899:134. Jordan et al., 1930:475.
Lycenchelys porifer: Jordan et al., 1930:476. Andriashev, 1955:351. Peden, 1973:117. Anderson, 1982a:211. Anderson, 1994:66, 117.

DIAGNOSIS. — Vertebrae 22–26 + 88–96 = 113–120; suborbital pores 6–8 + 0–1 = 6–9; postorbital pores 3–5; occipital and interorbital pores absent; lateral line mediolateral and ventral, complete; dorsal fin origin associated with vertebrae 5–7; total gill rakers 10–15.

COUNTS AND MEASUREMENTS. — Vertebrae 22–26 + 88–96 = 113–120; D 104–111; A 92–100; C 9–10; P 15–17; pelvic 3; vomerine teeth 3–15; palatine teeth 2–12; gill rakers 2–3 + 8–13 = 10–15; branchiostegal rays 6; pseudobranch filaments 4–6. Following measurements in percent SL: head length 17.2–20.2; head width 6.2–8.8; head depth 6.0–8.2; pectoral fin length 9.0–13.2; predorsal length 21.3–23.9; preanal length 33.2–37.5; body height 4.3–7.0; gill slit length 5.8–7.3. Following measurements in percent HL: head width 33.1–47.9; head depth 31.7–42.8; upper jaw length 31.3–49.0; pectoral fin length 44.9–70.5; snout length 23.5–28.4; eye diameter 15.4–24.1; gill slit length 30.9–38.6; interorbital width 4.9–8.4; interpupillary width 15.5–21.7; pelvic fin length 13.7–20.7; caudal fin length 5.6–12.8. Pectoral base/length ratio: 22.5–44.4.

DESCRIPTION. — Based on 46 known adults and juveniles. Head elongate, dorsoventrally depressed at all sizes, gently declined from nape to snout tip. Head length not detectably longer in males than in females in present sample. Scales absent on head, nape, pectoral fin and base, and in pectoral axil. Scales present on body, abdomen to line between pectoral bases (adults), tail, and on unpaired fins extending to 60%–75% of their height in larger specimens; no scales on fins in smallest juveniles. Eye ovoid, not entering dorsal profile of head. Gill slit extending ventrally to just below lower end of pectoral base. Opercular flap at upper end of gill slit well-developed, angular; slit extending forward about one-third to one-half eye diameter. Pectoral fin origin below body midline, insertion on abdomen; posterior margin of fin evenly rounded, ray tips exserted, more so ventrally; ventralmost 6–7 rays thickened.

Mouth subterminal, upper jaw extending to anterior quarter of eye (females and juveniles of both sexes) or its posterior quarter (large males); upper jaw length 41.2%–49.0% HL ($\bar{x}$ = 42.4) in 18 adult males, 31.3%–38.6% HL ($\bar{x}$ = 34.9) in 14 adult females. Nostril tube small, not reaching half way from its base to upper lip when pressed forward. Upper lip well-delimited. Labial lobe of lower jaw generally hidden when mouth closed, fleshy, but ventral margin nearly parallel with ventral margin of jaw. Oral valve not coalesced with sides of palate, and extending to, or nearly to, rictus, but not reaching vomer. Jaw teeth small, conical, sharp; upper jaw with double row in adults of both sexes, lower jaw with 2–3 irregular rows (juveniles and subadults) to six rows in largest males. Vomerine teeth relatively numerous, in two broad bands in larger specimens; teeth on palate larger in males than in females.

Cephalic lateralis system with usually three postorbital pores, arising from frontal, posterior border of pterotic and between lateral extrascapulars (positions one, three and four). In five specimens pore two (from sphenotic) present, and in one of these pore five present, arising from posterior end of second lateral extrascapular. Two pairs of anterior supraorbital (nasal) pores, one set anteromesial to small nostril tube, the other posteromesially. Usually

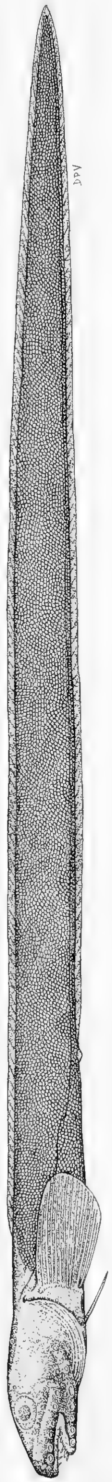

FIGURE 13. *Lycenchelys peruana* sp. n., LACM 45998-1, holotype, 103 mm SL, off Trujillo, Peru. Pectoral fin reconstructed after paratype.

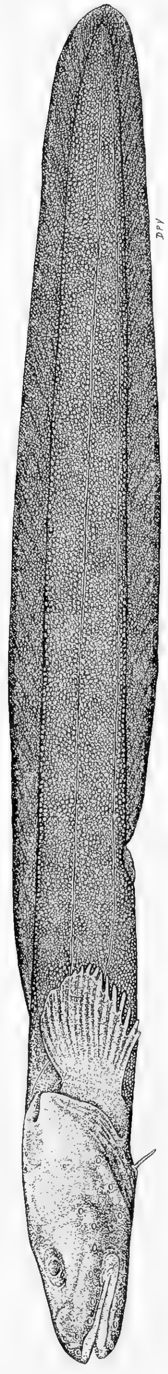

FIGURE 14. *Lycenchelys porifer* (Gilbert, 1890), SIO 68-82, 267 mm SL, Gulf of California.

seven suborbital pores, all arising from ventral ramus of bone chain under eye (7 + 0); suborbital pore variation uncommon: three specimens with pores 7 + 0 on one side, 8 + 0 on the other, one specimen with 8 + 0 pores on both sides, and one specimen with pores 7 + 0 on one side, 8 + 1 on the other. Eight preoperculomandibular pores, four arising from dentary, one from anguloarticular, and three from preopercle (no variation). Interorbital and occipital pores absent. Body lateral line double; mediolateral branch commencing just anterior to pectoral fin margin in axil, ventral branch commencing above upper end of gill slit, coursing down abdomen without steep bow, then running just above anal fin base; both branches reaching tip of tail.

Dorsal fin origin above anterior third to middle of pectoral fin, associated with vertebrae 5–7, usually six, with no supraneurals. Anal fin origin associated with ultimate, penultimate or antepenultimate precaudal vertebrae, with 2–6 ray-bearing pterygiophores inserted anterior to haemal spine of first caudal vertebra. Pterygiophore of last dorsal ray associated with fourth preural vertebra; pterygiophore of last anal ray associated with second preural vertebra, with 1–2 rays articulating with haemal spine. Caudal fin with 1–2, usually two, epural rays, 4–5 upper hypural rays and 3–4 lower hypural rays.

Gill rakers on upper limb and lowermost on lower limb short, triangular, with acute tips; uppermost rakers on lower limb longer, tips blunt. Pseudobranch filaments long, slender, usually 5–6. Pyloric caeca two small nubs.

Color in alcohol dark brown or faded to pinkish brown, head and fins darker. Most recently collected specimens with abdomen and eyes blue, anus ringed in white. Lining of orobranchial chamber and peritoneum black (or dark brown in older material). Dorsal surface of stomach and duodenum densely covered with melanophores.

This species reaches 270 mm TL. One ripening female, LACM 44736-1, 225 mm SL, had ova 2.4–2.6 mm in diameter.

Distribution. — Gulf of California and off Peru. Depth range: 1567–1875 m.

Remarks. — The paratype of *L. serpens* Garman is now completely destroyed. Lectotype designation for *Lycodes anguis* Garman given below.

Material Examined. — Gulf of California, Guaymas Basin: LACM 38031-1 (3; 110–129 mm); 27°35.2'N, 111°03.5'W; *Velero IV* sta. 14852; 1692–1738 m; 1715–0100 hrs.; 16–17 Nov. 1970. SIO 68-82 (20; 74–267 mm); 27°23.0'N, 111°19.5'N; *Thomas Washington* sta. MV 68-I-49; 1792–1875 m; 2153–0408 hrs.; 15–16 Jan. 1968; C. L. Hubbs and party. SIO 70-247 (1; 252 mm); 27°22.5'N, 111°20.9'W; *Thomas Washington* otter trawl sta.; 1810 m; 14 June 1970; R. McConnaughey. SIO 70-248 (3; 222–248 mm); 27°22.4'N, 111°20.5'W; *Thomas Washington* otter trawl sta.; 1810 m; 14 June 1970; R. McConnaughey. LACM 43736-1 (3; 178–225 mm); 27°19.5'N, 111°43.0'W; *Velero IV* sta. 11815; 1674 m; 28 Nov. 1967. SIO 70-249 (10; 128–257 mm); 27°11.5'N, 111°31.8'W; *Thomas Washington* otter trawl sta. 4; 1829–1875 m; 1505–2121 hrs.; 15 June 1970; R. McConnaughey. USNM 44384 (holotype, 258 mm); 27°09.0'N, 111°42.0'W; *Albatross* sta. 3009; 1567 m; 20 Mar. 1889; U. S. Fish Commission. MCZ 28686 (holotype of *Lycodes serpens* Garman, male, ca. 255 mm) and MCZ 117364 (paratype, indet. sex and length); 27°03.7'N, 110°53.7'W; *Albatross* sta. 3436; 1655 m; 22 Apr. 1891. MCZ 115068 (lectotype of *Lycodes anguis* Garman, herein designated, 225+ mm); 26°48'N, 110°45'W; *Albatross* sta. 3435; 1571 m; 22 Apr. 1891. MCZ 28687 (two paralectotypes of *Lycodes anguis* Garman, ca. 165–185 mm); same collection as lectotype. MCZ 28688 (one paralectotype of *Lycodes anguis* Garman, 210 mm); same data as MCZ 28686. Peru: off Trujillo: LACM 45709-1 (1; 154 mm); 08°26'S, 80°37'W; *Anton Bruun* sta. 650E; 1829 m; 2355–0923 hrs.; 8–9 June 1966; SEPBOP cr. 16.

Lycenchelys rassi Andriashev, 1955
(Fig. 15)

Lycenchelys rassi Andriashev, 1955:359, figs. 2, 5, 6 (original description. Type locality: Sea of Okhotsk). Andriashev, 1958:171, 172. Peden, 1973:115–117, fig. 1B. Fedorov, 1976:4, 5. Toyoshima, 1985:146, 147, 149, 173, 174, figs. 27C, 27D, 28, 31J.

Diagnosis. — Vertebrae 23–25 + 98–105 = 122–129; suborbital pores 7–8 + 1; postorbital pores 3–4; occipital pores two; interorbital pore present; lateral line ventral, complete; dorsal fin origin associated with vertebra five; pelvic fin rays two; total gill rakers 11–13.

COUNTS AND MEASUREMENTS. — Vertebrae 23–25 + 98–105 = 122=129; D 117(?)-125; A 105–113; C 9; P 14–16; pelvic 2; vomerine teeth 5–8; palatine teeth 6–7; gill rakers 1–2 + 9–11 = 11–13; branchiostegal rays 6; pseudobranch filaments 3–4. Following measurements in percent SL: head length 13.5–16.3; head width 5.3–7.6; head depth 5.8–8.3; pectoral fin length 6.7–8.4; predorsal length 16.2–17.7; preanal length 29.7–32.6; body height 5.5–5.9; gill slit length 4.2–5.8. Following measurements in percent HL: head width 35.9–48.9; head depth 37.3–41.9; upper jaw length 30.0–41.0; pectoral fin length 44.1–58.6; snout length 22.4–29.1; eye diameter 19.2–21.6; gill slit length 28.6–35.9; interorbital width 4.6–6.7; interpupillary width 17.0–21.8; pelvic fin length 12.9–15.1; caudal fin length 4.8–11.2. Pectoral base/length ratio: 41.7–44.3 (in three).

DESCRIPTION. — Known from five adults (both sexes) and one juvenile female. Head elongate, ovoid; dorsal profile dorsoventrally depressed, declined gently from nape to snout tip; snout tip more steeply sloping in juvenile than in adults. Scales absent on head, nape, pectoral fin, base and axil. Scales present on body, abdomen to just posterior to pectoral bases, tail and on unpaired fins to about 60%–80% of their height (even in juvenile), the greatest extent posteriorly. Eye ovoid, entering dorsal profile of head except in largest specimen (HUMZ 77747). Gill slit extending ventrally to lower end of pectoral base or beyond it to opposite pelvic base. No opercular flap at upper end of gill slit, instead, tissue joining opercle to pectoral base forming characteristic "siphon-shaped fold" (Andriashev, 1955), not continued forward. Pectoral fin origin at or just below body midline (adults) or well below it (juvenile), insertion on abdomen; posterior margin of fin evenly rounded, ray tips exserted, more so ventrally, ventralmost 6–7 rays thickened.

Mouth inferior, upper jaw extending to anterior quarter of eye (females) or from its middle to its posterior margin (males). Nostril tube reaching to or overlapping upper lip. Upper lip well-delimited. Labial lobe of lower jaw well-developed, mostly hidden when mouth is closed. Oral valve coalesced with sides of palate and not reaching vomer. Jaw teeth conical; upper jaw with double row anteriorly in adults, single row in juvenile, lower jaw of largest male with four irregular rows near symphysis; anteriormost teeth in adult males caniniform, about 4–5 times the size of those of females. Vomerine and palatine teeth relatively numerous; vomerine teeth in broad patch in large males.

Cephalic lateralis system with 3–4 postorbital pores, arising from frontal, sphenotic (absent in those with three pores), pterotic and lateral extrascapulars (positions 1–4 or one, three, four); pore three doubled (small, separate pore adjacent to main one on right side in MCZ 34074). Two pairs of anterior supraorbital (nasal) pores, one set anteromesial to nostril tube, the other posteromesially. Usually eight suborbital pores, seven arising from ventral ramus of bone chain under eye and one from ascending ramus behind eye just ventral to first postorbital pore (7 + 1); only one specimen (ZIN 35670) reflecting typical variation in this canal with pores 8 + 1. Eight preoperculomandibular pores, four arising from dentary, one from anguloarticular and three from preopercle; anguloarticular pore on right side of holotype doubled. Interorbital pore present, anterior in position (Andriashev, 1955, fig. 6; Toyoshima, 1985, fig. 27). Occipital pores two (left and right laterals). Body lateral line ventral, complete, without steep bow in pectoral axil, gently declining on abdomen to just above anal fin base.

Dorsal fin origin above anterior quarter of pectoral fin, associated with vertebra five, with no supraneurals. Anal fin origin associated with antepenultimate to ultimate precaudal vertebrae, with six ray-bearing pterygiophores (in two) inserted anterior to haemal spine of first caudal vertebra. Pterygiophore of last dorsal ray associated with fourth or fifth preural vertebrae; pterygiophore of last anal ray associated with second preural vertebra, with two rays articulating with haemal spine. Caudal fin with two epural, four upper hypural and three lower hypural rays (in two).

Gill rakers on upper limb short, acute; on lower limb ventralmost rays triangular, uppermost with blunt tips. Andriashev (1955) gives a count of eight lower gill rakers for holotype, however, there are two undeveloped raker buds at the base of the first arch, giving a count of 2 + 10 for the specimen, more in keeping with counts in other specimens. Pseudobranch filaments long, slender. Pyloric caeca two small nubs, well-delimited.

Color in alcohol (when recently preserved) with head, margins of unpaired fins and branchiostegal membranes black; opercular region and abdomen bluish black; eyes blue (Andriashev, 1955; Toyoshima, 1985). Lining of orobranchial chamber and peritoneum black. Stomach and intestines pale (unpigmented).

This species reaches 232 mm TL (Toyoshima, 1985). Specimens I examined had eaten bivalves and gastropods.

DISTRIBUTION.—Sea of Okhotsk to eastern Bering Sea. Depth range: 1040–1805 m.

REMARKS. — Toyoshima (1985, table 4) gives incorrect counts for gill rakers (0 + 9; there are 1 + 10) and preoperculomandibular pores (3 + 4; there are 8) in HUMZ 77747. He also related his *L. melanostomias* to *L. rassi* on a few characters that are uncorroborated with the present material. *Lycenchelys melanostomias* is readily distinguished from *L. rassi* on the basis of its nine preoperculomandibular pores (not eight as given by Toyoshima, 1985, table 4) vs. eight in *L. rassi*, suborbital pores 7 + 2 (not 10 total as given by Toyoshima) vs. 7 + 1 or 8 + 1 in *L. rassi*, five postorbital pores vs. 3–4 in *L. rassi*, dorsal fin origin associated with vertebra two vs. five in *L. rassi* and black stomach vs. pale stomach in *L. rassi*. See remarks section under *Lycenchelys callista* (above) for comments on the relationships of *L. rassi*.

MATERIAL EXAMINED. — Sea of Okhotsk: MCZ 34074 (1; 147 mm); 52°53'N, 144°54'E; *Rossinante*, trawl sta.; 1643 m; 10 Aug. 1932; Pacific Far-Eastern Expedition. ZIN 32962 (holotype, male, 192 mm); NE coast of Sakhalin Isl.; *Vityaz* sta. 103; 1500 m; 13 Sept. 1949; P. Shmidt. HUMZ 77747 (1; 228 mm); 44°38'N, 144°23'E; bottom trawl; 1280–1340 m; 24 Sept. 1978. Northwestern Pacific: ZIN 35670 (1; 217 mm); Kronotskii Bay, Kamchatka Penin.; *Vityaz* sta. 3304; 1230– 1040 m; 23 May 1955. Bering Sea, No. of Unalaska Isl.: USNM 47587 (2; 202–211 mm); 54°11.5'N, 167°25.0'W; *Albatross* sta. 3607; 1805 m; 18 Aug. 1895.

Lycenchelys ratmanovi Andriashev, 1955 (Fig. 16)

Lycenchelys camchaticus (non Gilbert and Burke, 1912; partim: males only): Andriashev, 1935:115. Andriashev, 1937:341–343, figs. 16, 18.

Lycenchelys ratmanovi Andriashev, 1955:355, figs. 2–4 (original description. Type locality: Avacha Bay, Kamchatka Penin., Russia). Quast and Hall, 1972:13. Fedorov, 1976:4–6. Toyoshima, 1985:166–167.

Lycenchelys longirostris Toyoshima, 1985:166, figs. 22–23.

DIAGNOSIS. — Vertebrae 21–23 + 88–93 = 110–115; suborbital pores 6–7 + 2–3 = 8–10; postorbital pores five; occipital pores 3–4; interorbital pore present; lateral line ventral, complete; dorsal fin origin associated with vertebrae 3–4; total gill rakers 8–11.

COUNTS AND MEASUREMENTS. — Vertebrae 21–23 + 88–93 = 110–115; D 105–110; A 93–97; C 9–10; P 15–18; pelvic 3; vomerine teeth 3–7; palatine teeth 4–9; gill rakers 1–2 + 7–9 = 8–11; branchiostegal rays 6; pseudobranch filaments 3–5. Following measurements in percent SL: head length 13.9–17.0; head width 4.9–8.5; head depth 5.3–7.0; pectoral fin length 7.1–8.1; predorsal length 15.2–18.5; preanal length 30.0–32.4; body height 4.6–5.9; gill slit length 4.7–6.9. Following measurements in percent HL: head width 34.9–50.8; head depth 37.7–42.1; upper jaw length 33.9–44.1; pectoral fin length 34.6–52.3; snout length 19.0–26.9; eye diameter 20.1–25.0; gill slit length 31.9–40.8; interorbital width 6.6–8.9; interpupillary width 17.4–22.0; pelvic fin length 18.4–27.8; caudal fin length 5.2–16.4. Pectoral base/length ratio: 35.2–48.0.

DESCRIPTION. — Based on 14 known specimens of both sexes, none fully mature; no small juveniles. Head elongate, ovoid; dorsal profile gently declined from nape to steeply sloping snout tip. Scales absent on head, nape, pectoral fin and base, and in pectoral axil. Scales present on body, abdomen to line between pectoral bases (or just before it in smaller specimens), tail and on unpaired fins extending to about 50%–60% of their height in large specimens, the greatest extent posteriorly; no scales on unpaired fins anteriorly in smaller specimens. Eye ovoid, not entering dorsal profile of head. Gill slit extending ventrally to just below lower end of pectoral base. Opercular flap at upper end of gill slit angular; slit extending forward about one-quarter to one-third eye diameter. Pectoral fin origin at body midline or just below it, insertion on abdomen; posterior margin of fins evenly rounded, ray tips exserted, more so posteriorly; ventralmost 5–6 rays thickened. Pectoral fin rays usually 16–17 (15 on one side in one specimen, 18 in two).

Mouth subterminal, upper jaw extending to just posterior to middle of eye (adult males; Andriashev, 1955, fig. 3) or its anterior quarter (juveniles and females; fig. 16; Toyoshima, 1985, fig. 22). Nostril tube not reaching upper lip when pressed forward. Upper lip well-delimited. Labial lobe of lower jaw well-developed, ventral margin of lobe deep, crescentic. Oral valve coalesced with sides of palate, nearly extending to rictus, but not reaching vomer. Jaw teeth conical, sharp; upper jaw with single row in juveniles, double row in both sexes in larger specimens, lower jaw with 3–4 rows near symphysis in largest, outermost enlarged. Vomerine and palatine teeth relatively numerous; vomerine teeth in 3 irregular bands in large specimens.

Cephalic lateralis system with five postorbital pores, arising from frontal, sphenotic, two from pterotic and lateral extrascapulars (positions 1–5). Two pairs of anterior supraorbital (nasal) pores, one set anteromesial to nostril tube, the other posteromesially. Usually nine suborbital pores, six arising from ventral ramus of bone chain under eye and three from ascending ramus behind eye (6 + 3); suborbital pore variation slight, three fish with pores 6 + 3/6 + 2, and two with pores 6 + 3/7 + 3. Preoperculomandibular pores 8–9, four arising from dentary, one or two from anguloarticular and three from preopercle; when two anguloarticular pores, main one doubled and septum between pores complete, but new pore position not created (counted as one pore by Fedorov, 1976). Interorbital pore present, set just behind line through anterior margin of eyes. Occipital pores usually four; two specimens with two lateral and a single median pore. Body lateral line ventral, complete, steeply bowed anteriorly in pectoral axil (Fig. 16; Andriashev, 1955, figs. 2–3).

Dorsal fin origin above anterior quarter of pectoral fin, associated with vertebrae 3–4, with no supraneurals. Anal fin origin associated with antepenultimate through ultimate precaudal vertebrae, with 4–7 ray-bearing pterygiophores inserted anterior to haemal spine of first caudal vertebra. Pterygiophore of last dorsal ray associated with third through fifth preural vertebrae; pterygiophore of last anal ray associated with second preural vertebra, with 1–2 rays articulating with haemal spine. Caudal fin with 1–2 epural, four upper hypural and 3–4 lower hypural rays.

Gill rakers on both limbs reduced: few, blunt, very short (almost vestgial; Andriashev, 1955, fig. 4); maximum of nine on lower limb. Pseudobranch filaments long, slender. Pyloric caeca two small nubs.

Color in alcohol of recently preserved material dark brown or bluish brown, head and fins darker; margin of unpaired fins with dark (black) streak. Toyoshima (1985) notes coloration of types of his *L. longirostris* after very recent preservation. Andriashev (1955) gives in vivo color notes, noting *L. ratmanovi* (males at least) has a bright greenish-blue spot on the pectoral fin (see accounts above on *L. callista, L. camchatica* and *L. crotalinus*). Lining of orobranchial chamber and peritoneum black. Abdomen and eyes blue. Stomach and intestines pale (unpigmented).

Largest specimen (immature) measured 190 mm TL (Fedorov, 1976). I found bivalves in the guts of a few specimens.

DISTRIBUTION. — Northern Kuril Islands to eastern Aleutian Islands. Depth range: 620–1120 m.

REMARKS. — This species was originally confused as the males of *Lycenchelys camchaticus* (Andriashev, 1935, 1937) but later shown to be quite distinct (Andriashev, 1955). In his original description Dr. Andriashev incorrectly gave the catalogue number ZIN 30012 for the two types (see below) and a pectoral fin ray count of 18–19 (both specimens have 18). Toyoshima (1985, table 3) made a number of errors in reporting on the two types of his *L. longirostris*, corrected here: pectoral rays of holotype 16/17, paratype 17/17; vertebrae of holotype 23 + 90, paratype 23 + 92; gill rakers of holotype 1 + 9; preopercular pores (PRP) of both three. Morphometric differences stated to separate these two specimens from *L. ratmanovi* are lessened by using snout tip to

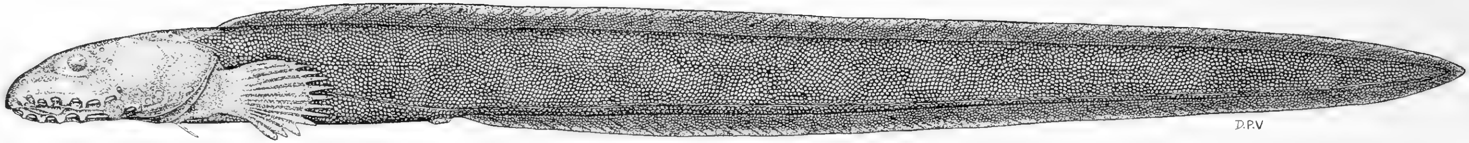

FIGURE 15. *Lycenchelys rassi* Andriashev, 1955, MCZ 34074, 147 mm SL, Sea of Okhotsk.

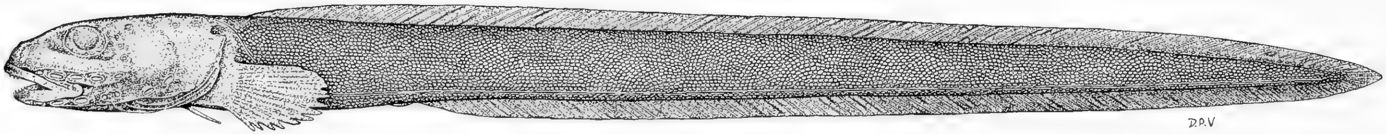

FIGURE 16. *Lycenchelys ratmanovi* Andriashev, 1955, USNM 221249, 135 mm SL, Bering Sea.

gill slit tip as a measure of head length (and not including upper lip). This especially affects snout length (hence the new name), which I re-calculated as: *L. longirostris* types, 19.3%–24.1% HL; other *L. ratmanovi*: 19.0%–26.9% HL.

MATERIAL EXAMINED. — Fedorov (1976) lists six ZIN lots not listed below and only cursorily examined by me during a 1987 visit to St. Petersburg. Northwestern Pacific: ZIN 46223 (1); off Shiashkotan Isl., Kuril Isls.; 48°38'N, 154°28'E; bottom trawl sta.; 880 m; 10 Sept. 1981; V. N. Tupokogov. ZIN 32957 (holotype, 185 mm) and 32957a (paratype, 182 mm); Avacha Bay, Kamchatka Penin.; 52°40.8'N, 151°13.0'E; *Dal'nevostochnik*, bottom dredge; 800–1000 m; 15 July 1932; Pacific Far-Eastern Expedition. ZIN 46222 (2; 170–185 mm); off Cape Olyutorsk; 59°23'N, 170°10'E; bottom trawl; 620–700 m; 15 Aug. 1982; B. A. Sheiko. ZIN 46221 (1); SW of Cape Navarin; 61°21'N, 176°24'E; bottom trawl; 1090–1120 m; 31 July 1982; B. A. Sheiko. Northeastern Pacific: HUMZ 81914 (holotype of *Lycenchelys longirostris* Toyoshima, female, 140 mm); Zhemchug Canyon; 58°33.2'N, 175°05.3'W; *Yakushi Maru* #21 bottom trawl; 895–910 m; 22 June 1979. HUMZ 83948 (paratype of *Lycenchelys longirostris* Toyoshima, male, 152 mm); vic. of Zhemchug Canyon; 58°14.4'N, 175°28.2'W; *Yakushi Maru* #21 bottom trawl; 681–818 m; 24 June 1979. USNM 221250 (1; 130 mm); Zhemchug Canyon; 58°20.4'N, 175°02.3'W; *Yakushi Maru* #21 sta. 124; 731–740 m; 24 June 1979; D. M. Cohen, T. Iwamoto, M. Yabe. USNM 221249 (1; 135 mm); W. of Pribiloff Isls.; 56°58.1'N, 173°50.8'W; *Yakushi Maru* otter trawl sta.; 720 m; 5 July 1979; D. M. Cohen and party. ZIN 40539 (1; 167 mm); off Unalaska Isl.; 54°19.4'N, 167°51.6'W; *Ekvator* sta. B-1-3-1000; 1000 m; 24 June 1969.

Lycenchelys rosea Toyoshima, 1985

Lycenchelys roseus Toyoshima, 1985:152, figs. 10–11.

DIAGNOSIS. — Vertebrae 28 + 108–109 = 136–137; suborbital pores 7 + 1; postorbital pores four; occipital pores absent; interorbital pore present; lateral line absent; dorsal fin origin associated with vertebra two; color uniformly red; total gill rakers 10–11.

COUNTS AND MEASUREMENTS. — Vertebrae 28 + 108–109 = 136–137; D 133; A 117; C 10–11; P 14–15; pelvic 3; vomerine teeth 6; palatine teeth 13–14; gill rakers 2 + 8–9; branchiostegal rays 6; pseudobranch filaments 3–4. Following measurements in percent SL: head length 11.2–13.0; head width 3.9–4.0; head depth 4.6–5.4; pectoral fin length 6.4–7.1; predorsal length 11.4–13.1; preanal length 27.0–28.1; body height 5.4–6.0; gill slit length 3.2–3.7. Following measurements in percent HL: head width 31.2–35.2; head depth 41.1–41.6; upper jaw length 33.1–33.8; pectoral fin length 54.4–56.6; snout length 16.2–23.0; eye diameter; 19.3–20.1; gill slit length 28.3–28.9; interorbital width 7.2–7.3; interpupillary width 18.4–20.6; pelvic fin length 13.0–16.9; caudal fin length 9.1–9.8. Pectoral base/length ratio 38.7–41.6.

DESCRIPTION.—Two females known. Head elongate, ovoid; dorsal profile gently convex (holotype with shallow, interorbital concavity) from snout tip to nape. Scales absent on head, nape, pectoral fin, its base, in pectoral axil and anal fin. Scales present on body, abdomen to line between pectoral bases, tail and on dorsal fin posteriorly, extending to about 60% of its height. Eye slightly ovoid, not entering dorsal profile of head. Gill slit extending ventrally to below lower margin of pectoral base. Opercular flap at upper end of gill slit well-developed, angular; slit extending forward about one eye diameter. Pectoral fin origin just below body midline, insertion on abdomen; posterior margin of fin evenly rounded, ray tips exserted slightly, ventralmost six rays thickened.

Mouth subterminal, upper jaw extending to middle of eye. Nostril tube small, not reaching half way from its base to upper lip when pressed forward. Upper lip well-delimited, narrowly adnate to snout tip. Labial lobe of lower jaw moderate, mostly hidden when mouth closed. Oral valve not coalesced with sides of palate and not reaching vomer. Jaw teeth conical, sharp; both jaws with double row anteriorly, single row posteriorly. Vomerine and palatine teeth retrorse, the latter in single row (some teeth missing, but sockets evident).

Cephalic lateralis system with four postorbital pores arising from frontal, anterior and posterior margins of pterotic and lateral extrascapulars (positions 1–4). Two pairs of anterior supraorbital (nasal) pores, one set anteromesial to nostril tube, the other posteromesially. Eight suborbital pores, seven arising from ventral ramus of bone chain under eye, and one from ascending ramus behind middle of eye just ventral to first postorbital pore (7 + 1). Eight preoperculomandibular pores, four arising from dentary, one from anguloarticular and three from preopercle. Interorbital pore in dorsal midline on line connecting anterior margins of eyes. Occipital pores absent. Body lateral line entirely absent, no remnant even on nape.

Dorsal fin origin above pectoral base, associated with second vertebra, with no supraneurals. Anal fin origin associated with antepenultimate precaudal vertebra, with eight ray-bearing pterygiophores inserted anterior to haemal spine of first caudal vertebra. Pterygiophore of last dorsal ray associated with fourth preural vertebra; pterygiophore of last anal ray associated with second preural vertebra, with two rays articulating with haemal spine. Caudal fin with two epural, 4–5 upper hypural and four lower hypural rays.

Gill rakers on upper limb small, acute (one at juncture of epibranchial and ceratobranchial); on lower limb, ventralmost 4–5 rays acute, remainder with blunt tips. Pseudobranch filaments long. Pyloric caeca two small nubbins.

Color monotone dull red. Color in alcohol after seven years preservation with reddish areas fading to brown on flanks and tail, fins orange (pectorals darker). Lining of orobranchial chamber and peritoneum dark brown to black. Stomach and intestines pale (unpigmented).

Largest specimen (adult female) measured 238 mm TL.

DISTRIBUTION. — Central Aleutian Islands. Depth range: 358–750 m.

REMARKS. — Toyoshima (1985) gave incorrect vertebral, unpaired-fin ray and gill raker counts in the original description. Re-determined counts are given above.

MATERIAL EXAMINED. — HUMZ 88487 (holotype, female, 235 mm); Aleutian Isls., off Islands of Four Mountains; 52°49.1'N, 171°01.9'W; Japanese fisheries investigations, bottom trawl; 750 m; 17 July 1980. HUMZ 89341 (paratype, female, 195 mm); Aleutian Isls., off Delarof Islands.; 51°49'N, 178°36.1'W; Japanese fisheries, trawl; 358 m; 9 Aug. 1980.

Lycenchelys scaurus (Garman, 1899)
(Fig. 17)

Lycodopsis scaurus Garman, 1899:132, pl. 32, fig. 1 (original description. Type locality: Gulf of Panama). Jordan et al., 1930:474.

Lycenchelys scaurus: Pequeño, 1986:183–188, figs. 1–2. Pequeño, 1989:48. Anderson, 1994:65, 113, 118.

DIAGNOSIS. — Vertebrae 20–22 + 75–89 = 96–110; preoperculomandibular pores nine; suborbital pores 6–8 + 2 = 8–10; postorbital pores 3–5; occipital pores usually three, rarely one, two or absent; interorbital pore absent; lateral line ventral and mediolateral, complete; dorsal fin origin associated with vertebrae 4–5; gill slit extending ventrally anterior to pelvic base; vomerine and palatine teeth absent; pectoral fin rays 18–21; total gill rakers 15–21.

COUNTS AND MEASUREMENTS. — Vertebrae 20–22 + 75–89 = 96–110; D 90–106; A 78–92; C 10–12; P 18–21; pelvic 3; vomerine and palatine teeth absent; gill rakers 1–3 + 14–18 = 15–21; branchiostegal rays 6; pseudobranch filaments 5–7. Following measurements in percent SL: head length 19.5–23.0; head width 9.1–13.5; head depth 9.4–10.9; pectoral fin length 11.7–13.3; predorsal length 22.9–25.4; preanal length 37.0–40.3; body height 7.9–10.1; gill slit length 7.8–10.9. Following measurements in percent HL: head width 41.0–59.4; head depth 42.9–48.4; upper jaw length 38.1–53.0; pectoral fin length 51.6–63.0; snout length 22.4–30.3; eye diameter 16.5–23.9; gill slit length 35.8–49.6; interorbital width 4.8–6.2; interpupillary width 20.7–26.4; pelvic fin length 13.0–18.0; caudal fin length 9.1–16.2. Pectoral base/length ratio: 42.3–51.8.

DESCRIPTION. — Based on 42 known specimens, adults and juveniles of both sexes. Head elongate, ovoid in adults, somewhat triangular in juveniles; dorsal profile gently declined from nape to snout, steeper in juveniles; snout tip steeply sloping. Head longer in adult males than in adult females, head length 20.7%–23.0% SL ($\bar{x}$ = 21.9) in 14 males 157–235 mm SL, 19.5%–21.9% SL ($\bar{x}$ = 20.3) in 14 females 159–262 mm SL. Scales absent on head, nape, pectoral fin and base, and in pectoral axil, except present in axil in largest males just posterior to pectoral base. Scales present on body, abdomen to just posterior to line through pectoral bases in largest specimens, tail and on unpaired fins extending to about 50% of their height posteriorly in juveniles; to 90% in adults; scales absent on dorsal and anal fins anteriorly in juveniles. Eye ovoid, entering dorsal profile except in largest specimens. Gill slit extending ventrally to just in front of pelvic base. Opercular flap at upper end of gill slit well-developed, angular; slit extending forward about one-quarter to one-third eye diameter. Pectoral fin rays relatively numerous (usually 19–20), pectoral origin well below body midline, insertion on abdomen; posterior margin of fin wedge-shaped, ray tips only slightly exserted ventrally; ventralmost 7–10 rays thickened.

Mouth inferior, upper jaw extending from middle of eye to its posterior margin. Upper jaw significantly longer in adult males than in females, 41.8%–53.0% HL ($\bar{x}$ = 48.1) in 12 males 165–214 mm SL, 38.1%–43.8% HL ($\bar{x}$ = 41.5) in 14 females 159–262 mm SL. Nostril tube minute, not reaching half way from its base to upper lip when pressed forward. Upper lip well-delimited. Labial lobe of lower jaw well-developed, generally hidden when mouth is closed, more so in small specimens; ventral margin of lobe deep, crescentic. Oral valve coalesced with sides of palate and not reaching vomer. Jaw teeth conical, sharp; upper jaw with single row except in large males, which have two irregular rows, lower jaw with two rows near symphysis in both sexes; no sexual differences in jaw teeth sizes or numbers. Vomerine and palatine teeth always absent.

Cephalic lateralis system with usually four postorbital pores, arising from frontal, sphenotic, pterotic and lateral extrascapulars (positions 1–4); one specimen with pores in position one, three, four, another with pores 1–5 (two from pterotic) on one side, 1–4 on the other. Two pairs of anterior supraorbital (nasal) pores, one set anteromesial to small nostril tube, the other posteromesially. Usually nine suborbital pores, seven arising from ventral ramus of bone chain under eye and two from ascending ramus behind eye (7 + 2), lowermost of these posteroventral to eye; suborbital variation rare, one fish with pores 8 + 2/7 + 2 and three with pores 6 + 2/7 + 2. Nine preoperculomandibular pores, four arising from dentary, one from anguloarticular and four from preopercle (no variation). Interorbital pores absent. Usually three occipital pores (two laterals and one median), except in four fish with no pores (but canal present), two with only median pore and two with just lateral pores. Body lateral line with ventral and mediolateral branches, both complete; ventral gently sloping anteriorly on abdomen, mediolateral originating in pectoral axil just anterior to rear margin of fin.

Dorsal fin origin above pectoral base, associated with vertebrae 4–5, usually four, with no supraneurals. Anal fin origin associated with ultimate precaudal vertebrae, with 3–5 ray-bearing pterygiophores inserted anterior to haemal spine of first caudal vertebra. Pterygiophore of last dorsal ray associated with third through fifth preural vertebrae; pterygiophore of last anal ray associated with second preural vertebra, with 0–2 rays articulating with haemal spine. Caudal fin with two epural, 4–5 upper hypural and 4–5 lower hypural rays.

Gill rakers on upper limb small, lanceolate; all on lower limb with blunt tips, but lowermost more slender; rakers on lower limb relatively numerous (usually 15 or more). Pseudobranch filaments long, usually six in number. Pyloric caeca two small nubs.

Color in alcohol faded to dark brown or pale pinkish gray, head and fins darker. Peritoneum and lining of mesial areas of orobranchial chamber dark brown (probably black in life). Stomach and intestines pale (unpigmented).

This species reaches about 305 mm TL (CAS 58149). A ripe female, 262 mm SL, had 53 ova, the largest of which measured 5.3–5.7 mm in diameter. Bivalves, gastropods and ostracods were found in several stomachs.

DISTRIBUTION. — Gulf of Panama to central Chile. Depth range: 200–1060 m.

REMARKS. — *Lycenchelys scaurus* is a relatively primitive species in retaining several important characters in their plesiomorphic state: 1) small, round head pores; 2) long gill slit; 3) high pectoral ray count; 4) high caudal ray count; 5) no sexual differences in dentition; 6) few vertebrae; 7) dorsal fin origin placed anteriorly; 8) high number of lower gill rakers; 9) high number of pseudobranch filaments. However, it possesses two derived characters that are noteworthy and diagnostic: 1) no vomerine or palatine teeth; 2) preoperculomandibular pores nine (usually found only in lower slope/abyssal species).

MATERIAL EXAMINED. — Gulf of Panama: MCZ 28689 (holotype, female, 179 mm); 07°31.5'N, 79°14.0'W; *Albatross* sta. 3384; 838 m; 8 Mar. 1891; U. S. Fish Commission. Ecuador, Gulf of Guayaquil: LACM 43731-1 (3; 227–262 mm); 03°14.7'S, 80°55.0'W; *Anton Bruun* sta. LK 66–120; 945–960 m; 10 Sept. 1966; L. W. Knapp and party. Peru: LACM 44133-1 (1, 172 mm); SE of Islas Lobos de Afuera; 07°46'S, 80°31'W; beam trawl sta. SNP1-27; 800 m; 1802–1807 hrs.; 23 Jan. 1974; J. M. Engle, J. Coyer, Peruvian fisheries program. CAS 58149 (1; 295+ mm); off Pt. Coles; 17°31.2'S, 72°00.0'W; Agassiz trawl; 1060 m; Jan. 1972; E. del Solar. Chile: MNHNC P.6424 (2; 160–199 mm); off Papudo; 32°31'S, 71°27'W; fisheries trawler; 400 m; 23 Feb. 1979. LACM W66-60-1 (22; 123–214 mm); 18 mi. W. of Valparaiso; bottom trawl; 274 m; 22–23 Dec. 1965; A. Chapman. LACM 11577- 2 (6 of 7; 162–197 mm); off Valparaiso; 200–300 m; July 1963. LACM 43718-1 (5; 150–214 mm); off Valparaiso; 33°22'S, 71°54'W; *Anton Bruun* sta. LK 66-16; 260–280 m; 1700–0000 hrs.; 31 July 1966; L. W. Knapp and party. LACM 43725-1 (1; 189 mm); same collection as preceding.

Lycenchelys volki Andriashev, 1955

Lycenchelys volki Andriashev, 1955:369, figs. 2, 13, 14 (original description. Type locality: SW Bering Sea). Quast and Hall, 1972:14. Fedorov, 1976:4, 5. Toyoshima, 1985:146–148, 152. Anderson, 1994:113, 118.

DIAGNOSIS.—Vertebrae 30 + 96 = 126; suborbital pores 8 + 0; pore opening in postorbital canal from position one (but pore abberantly doubled in type); occipital pores absent; interorbital pore in midline anterior to eyes; lateral line ventral, incomplete; dorsal fin origin associated with vertebra 11, with seven supraneurals; pelvic fin rays two; pyloric caeca absent; total gill rakers 16.

COUNTS AND MEASUREMENTS. — Vertebrae 30 + 96 = 126; D 113; A 101; C 10; P 17; pelvic 2; vomerine teeth 10; palatine teeth 8/9; gill rakers 2 + 14; branchiostegal rays 6; pseudobranch filaments 4. Following measurements in percent SL: head length 14.9; head width 7.2; head depth 5.9; pectoral fin length 9.0; predorsal length 23.9; preanal length 36.1; body height 5.5; gill slit length 5.5. Following measurements in percent HL: head width 48.2; head depth 39.7; upper jaw length 38.7; pectoral fin length 60.3; snout length 30.5; eye diameter 14.4/13.4; gill slit length 37.1; interorbital width 6.6; interpupillary width 19.7; pelvic fin length 25.1; caudal fin length 9.8. Pectoral base/length ratio 33.2.

DESCRIPTION. — Only holotype known. Head elongate, ovoid, dorsoventrally depressed; dorsal profile gently convex from snout to nape, tip of snout not steep. Scales absent on head, nape, pectoral fin, base, in pectoral axil, in rudimentary dorsal fin fold and anterior portion of vertical fins. Scales present on body, abdomen to line just posterior to pectoral base, tail and on posterior third of vertical fins extending to about 40%–50% of their height. Eye slightly ovoid, spectacle of right eye somewhat smaller than that of left; eye just excluded from dorsal profile of head. Gill slit extending ventrally well below lower end of pectoral base to line through pelvic base. Opercular flap at upper end of gill slit well-developed, rounded; slit extending forward about 1.5 eye diameters. Pectoral fin origin at body midline, insertion on abdomen; posterior margin of fin wedge-shaped, ray tips exserted, middle and ventral rays more so; ventralmost six rays thickened.

Mouth inferior, upper jaw extending to anterior margin of eye. Nostril tube small, just reaching upper lip when pressed forward. Upper lip well-developed, adnate to snout tip. Labial lobe of lower jaw moderate, mostly hidden when mouth is closed. Oral valve not coalesced with sides of palate and not reaching vomer. Jaw teeth conical, sharp; upper jaw with double row anteriorly (inner row formed of just three teeth), lower jaw with three irregular rows near symphysis. Vomerine teeth relatively numerous, in patch; palatine teeth in single row.

Cephalic lateralis system with two small pores exiting from frontal foramen (position one), an abnormal condition (pore doubling).

Two pairs of anterior supraorbital (nasal) pores, one set anteromesial to nostril tube, the other directly posteriorly. Eight suborbital pores, all arising from ventral ramus of bone chain under eye (8 + 0). Eight preoperculomandibular pores, four arising from dentary, one from anguloarticular and three from preopercle. Interorbital pore set in midline of head one-half eye diameter in front of anterior margin of eye (Andriashev, 1955, fig. 14). Occipital pores absent. Body lateral line ventral, steeply bowing on abdomen in pectoral axil, not detectable beyond region just before anus and absent on tail as well.

Dorsal fin origin above appressed posterior margin of pectoral fin, associated with vertebra 11, with seven supraneurals. Anal fin origin associated with penultimate precaudal vertebra, with four ray-bearing pterygiophores inserted anterior to haemal spine of first caudal vertebra. Pterygiophore of last dorsal and last anal rays associated with second preural vertebra, with two anal rays articulating with haemal spine. Caudal fin with two epural, four upper hypural and four lower hypural rays.

Gill rakers on upper limb short, acute; on lower limb only ventral half acute, others with blunt tips. Pseudobranch filaments moderately long. Pyloric caeca absent.

Color in alcohol dark chocolate brown, ventral surface of head, pectoral fins, lining of orobranchial chamber and peritoneum black. Length 208 mm TL.

DISTRIBUTION. — Abyssal Bering Sea in 3940 m.

MATERIAL EXAMINED. — ZIN 32964 (holotype, male, 205 mm); Aleutian Basin ca. 130 naut. mi. No. of Mednyi (Copper) Isl.; *Vityaz* sta. 618; 3940 m; 25 Sept. 1950.

Taranetzella lyoderma Andriashev, 1952
(Fig. 18)

Taranetzella lyoderma Andriashev, 1952:415–417, text fig. (original description. Type locality: W. Bering Sea). Quast and Hall, 1972:15. Pearcy et al., 1982:387. Toyoshima, 1985:144–145. Anderson, 1994:90–92, 115, 120, figs. 181–186.

DIAGNOSIS. — Vertebrae 18–20 + 70–78 = 90–97; preoperculomandibular pores nine; suborbital pores 7 + 0; postorbital pores two; occipital and interorbital pores absent; lateral line absent (or mediolateral?); dorsal fin origin associated with vertebrae 3–4; low, fleshy papillae between suborbital pores; flesh gelatinous; gill slit not reaching ventral end of pectoral base; total gill rakers 14–16.

COUNTS AND MEASUREMENTS. — Vertebrae 18–20 + 70–78 = 90–97; D 88–95; A 75–82; C 10; P 15–16; pelvic 3; vomerine teeth 3–8; palatine teeth 5–20; gill rakers 3 + 11–13; branchiostegal rays 6; pseudobranch filaments 2–4. Following measurements in percent SL: head length 16.1–19.5; head width 6.1–7.4; head depth 7.5–8.9; pectoral fin length 9.3–11.5; predorsal length 16.7–19.6; preanal length 31.6–35.2; body height 5.1–7.6; gill slit length 4.1–5.4. Following measurements in percent HL: head width 36.1–44.7; head depth 43.8–53.5; upper jaw length 35.3–44.7; pectoral fin length 53.9–62.7; snout length 20.3–27.9; eye diameter 15.3–20.5; gill slit length 23.4–30.5; interorbital width 8.4–11.5; interpupillary width 19.5–24.4; pelvic fin length 10.9–18.3; caudal fin length 11.6–25.2. Pectoral base/length ratio 35.8–42.3.

DESCRIPTION. — Based on 18 known specimens, early juveniles through adults of both sexes. Head elongate, somewhat box-shaped in large specimens, deeper than most *Lycenchelys*; no sexual dimorphism in head lengths. Scales present only on tail, extending anteriorly only to about half total length; larger specimens with more extensive squamation; smallest juvenile (61 mm SL) scaleless. Eye ovoid, not entering dorsal profile of head. Gill slit extending ventrally to midheight of pectoral base or slightly below. Opercular lobe at upper end of gill slit small, rounded; slit extending forward about one-quarter eye diameter. Pectoral fin origin below body midline; insertion on abdomen; posterior margin of fin evenly rounded, ray tips exserted, ventralmost 6–7 rays thickened.

Mouth terminal or slightly subterminal, independent of size; upper jaw extending from just before middle of eye to its posterior margin. No dimorphism in jaw lengths. Nostril tube reaching to or overlapping upper lip when pressed forward. Upper lip well-delimited, continuous across snout. Labial lobe of lower jaw weak, ventral margin parallel with jaw line, generally hidden when mouth is closed. Six low, pyramidal papillae under eye between sub-

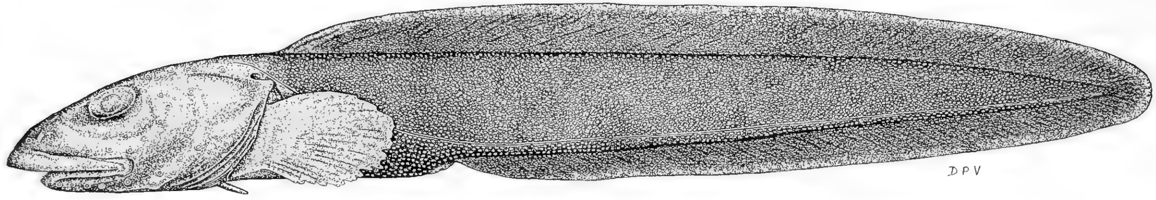

FIGURE 17. *Lycenchelys scaurus* (Garman, 1899), LACM W66-60-1, 212 mm SL, off Valparaiso, Chile.

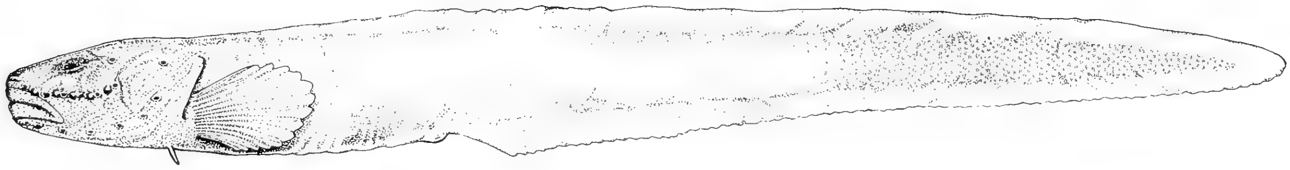

FIGURE 18. *Taranetzella lyoderma* Andriashev, 1952, CAS 82143, 158 mm SL, off Oregon.

orbital pores. Oral valve not coalesced with sides of palate, extending to rictus, and just reaching anterior edge of vomer in some smaller specimens. Jaw teeth conical, relatively few; upper jaw with single row in both sexes, lower jaw with 1–2 rows near symphysis depending on size; males with caniniform teeth anteriorly in both jaws. Vomerine teeth in patch in larger specimens; palatine teeth in two irregular rows anteriorly in these.

Cephalic lateralis system with two postorbital pores, arising from frontal and lateral extrascapular (positions one and four). Two pairs of anterior supraorbital (nasal) pores, one set directly mesial to nostril tube, the other posteromesially. Seven suborbital pores, all arising from ventral ramus of bone chain under eye (7 + 0). Nine preoperculomandibular pores, four arising from dentary, one from anguloarticular and four from preopercle. Interorbital and occipital pores absent. Body lateral line not present in material from Oregon. Weak, mediolateral line said to be present in holotype (Andriashev, 1952), but no longer evident.

Dorsal fin origin above pectoral base, associated with vertebrae 3–4 (usually three), with no supraneurals. Anal fin origin associated with ultimate or penultimate precaudal vertebrae, with 2–4 ray-bearing pterygiophores inserted anterior to haemal spine of first caudal vertebra. Pterygiophore of last dorsal ray associated with third or fourth preural vertebrae; pterygiophore of last anal ray associated with second preural vertebra, with 1–2 rays articulating with haemal spine. Caudal fin with two epural, four upper hypural and four lower hypural rays.

Gill rakers on upper limb small, acute; on lower limb, ventral half similar, upper half longer, with blunt tips. Pseudobranch filaments short, usually three. Pyloric caeca two small nubs.

Color in alcohol pinkish gray to whitish, all specimens very faded; fins without pigment. Lining of orobranchial cavity, stomach and intestines pale. Peritoneum black.

Largest specimen 165 mm TL (an unripe female).

DISTRIBUTION. — Western Bering Sea, off Oregon and northern Mexico; distribution probably continuous. Depth range: 986–3000 m.

REMARKS. — Andriashev (1952) reports a lateral line to be discernible in the holotype anteriorly on the body and to consist of pores. As the body lateral line in zoarcids consists only of superficial neuromasts, and, as other genera with gelatinous flesh lack a lateral line (e.g. *Derepodichthys, Dieidolycus, Exechodontes, Lycodapus, Melanostigma, Thermarces*; Anderson, 1994), Andriashev's observation requires verification. No trace of a lateral line (remnant neuromasts or nerves) was observed by me in the Oregon material as early as four years after the last one had been preserved (1976). Two other characters given by Andriashev to distinguish *Taranetzella* from *Lycenchelys* are erroneous: 1) the stronger dentition, and 2) the lack of an oral valve. The genus was diagnosed and described by Anderson (1994).

MATERIAL EXAMINED. — Russia: ZIN 32813 (holotype, 100 mm); Olyutorsk Bay, Kamchatka Penin.; *Vityaz* sta. 602; 986 m; 16 Sept. 1950. Washington: CAS 82140 (2; 112–147 mm); off Cape Flattery; 48°18.4'N, 127°00.8'W; *Yaquina* sta. BMT DW2; 2520 m; 2 Sept. 1971. Oregon (Cascadia Abyssal Plain): OS 15215 (1; 72 mm); 45°57.8'N, 125°44.2'W; *Yaquina* sta. BMT-195; 2048 m; 0905–1107 hrs.; 20 Mar. 1970. CAS 82141 (1; 61 mm); 45°43.8'N, 125°26.8'W; *Yaquina* sta. BMT-89; 2200 m; 1257–1400 hrs.; 14 July 1969. CAS 82142 (1; 76 mm); 45°37.5'N, 125°36.4'W; *Yaquina* sta. BMT-90; 2283 m; 2231–0100 hrs.; 14–15 July 1969. CAS 53876 (1, cleared and stained; 98 mm); 45°09.3'N, 125°38.3'W; *Yaquina* sta. BMT-93; 2669 m; 2320–0125 hrs.; 15–16 July 1969. OS 15216 (1; 133 mm); 44°58.5'N, 125°44.3'W; *Yaquina* sta. BMT-188; 2792 m; 1750–1950 hrs.; 17 Mar. 1970. CAS 82144 (2; 110–140 mm); 44°56.1'N, 125°39.8'W; *Yaquina* sta. BMT-187; 2760–2770 m; 1100–1300 hrs.; 17 Mar. 1970. CAS 38921 (1; 142 mm); 44°35.8'N, 125°34.3'W; *Yaquina* sta. BMT-97; 2862 m; 17 July 1969. CAS 82143 (formerly OS 2072) (1; 158 mm); 44°35.6'N, 125°35.2'W; *Yaquina* sta. BMT-186; 2816 m; 2230–0030 hrs.; 16–17 Mar. 1970. CAS 82145 (4; 93–160 mm); 44°05.3'N, 125°23.6'W; *Yaquina* sta. BMT-288; 2940 m; 2053–2308 hrs.; 14 June 1972. CAS 82146 (1; 69 mm); 43°44.0'N, 125°25.0'W; *Yaquina* sta. BMT-294; 3000 m; 1327–1528 hrs.; 17 June 1972. Mexico, off Guadalupe Isl.: SIO 60–48 (1; 122 mm); 29°40.2'N, 117°06.6'W; *S. F. Baird* sta. SOB-

12; 2707–2762 m; 1702–1815 hrs.; 15 Feb. 1960; R. H. Parker and C. M. Yonge.

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PHYLOGENY OF *CERATOSOMA* (NUDIBRANCHIA: CHROMORIDIDAE), WITH DESCRIPTIONS OF TWO NEW SPECIES

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ABSTRACT: Two new species of *Ceratosoma* are described. *Ceratosoma ingozi* is known only from deep water off the temperate coast of South Africa. *Ceratosoma alleni* is known from shallow reefs in the Philippine Islands. The phylogenetic relationships of the species of *Ceratosoma* are discussed. *Ceratosoma ingozi* is relatively plesiomorphic in most aspects of its morphology and appears to be most closely related to two other species known from southern Australia. *Ceratosoma alleni* is highly derived in several aspects of its morphology and appears most closely related to *C. moloch*, also from the Indo-Pacific tropics.

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INTRODUCTION

The anatomy and systematics of members of the genus *Ceratosoma* Gray have been recently reviewed (Rudman, 1988). Seven distinct species have been recognized and the systematic status of one other remains unresolved. Baba (1989) considered *C. bicolor* as an eighth distinct species, although he stated that there was a need for further study of additional specimens.

An undescribed species of *Ceratosoma* was recorded from South Africa by Gosliner (1987). Since then, an additional undescribed species has been discovered from the Philippine Islands. This paper describes these new species, their morphology and phylogenetic position.

Specimens deposited in the Department of Invertebrate Zoology and Geology of the California Academy of Sciences, San Francisco are designated by the abbreviation CASIZ. Specimens deposited in the Department of Marine Biology of the South African Museum, Cape Town are designated by the abbreviation SAM.

SPECIES DESCRIPTIONS

Ceratosoma ingozi sp. nov. (Figs. 1A, 2, 3)

Ceratosoma sp. Gosliner, 1987:85, fig. 138.

TYPE MATERIAL. — Holotype: SAM A36012, off Danger Point, Walker Bay, Cape Province, South Africa, 44 m depth, 16 April 1984, W. R. Liltved. Paratype, CASIZ 104199, one specimen, same locality and date as holotype. Paratypes, SAM A36011, four specimens, one dissected, off Danger Point, Walker Bay, Cape Province, South Africa, 26 m depth, 24 April, 1984, W. R. Liltved. Paratypes, SAM A36009, one specimen, off Danger Point, Walker

Bay, Cape Province, South Africa, 34 m depth, 11 April 1984, W. R. Liltved.

ETYMOLOGY. — *Ceratosoma ingozi* is derived from the Xhosa word for danger, *ingozi*, since this species has only been found from Danger Point.

DISTRIBUTION. — This species is known only from the vicinity of Danger Point in Walker Bay. It may be more widely distributed but has not been collected elsewhere, probably owing to the fact that it is found in deep water, near the margins of scuba diving depths.

EXTERNAL MORPHOLOGY. — The living animals (Fig. 1A) are 26–55 mm in length. The body is translucent white to pale yellow with a series of reddish purple spots scattered over the surface of the notum and sides of body and foot. The rhinophores are the same color as the body. The gills are translucent white with opaque white glands at the base of each gill.

The body is high with a distinct, continuous notal ridge along the entire notal margin. Defensive glands are found along the entire notal margin (Fig. 2A), as well. The rhinophores are perfoliate with 15–19 lamellae. The branchial plume is composed of 15–18 unipinnate and bipinnate lamellae (Fig. 2B). The reproductive opening is located on the right side of the body, about one-third of the total body length posteriorly from the anterior margin of the head.

BUCCAL ARMATURE. — The jaws consist of numerous undivided rodlets (Fig. 3A). The radula of one specimen had a formula of 66 × 180–193.1.180–193. The rachidian tooth (Fig. 3B) is vestigial, narrow and linear. The inner lateral teeth lack a distinct cusp in all teeth examined. The second to eighth lateral have a well-developed cusp with a single small denticle on the outer side of the cusp. The remaining teeth all have a well-developed cusp, but lack any denticles. The teeth from the middle portion of the half-row (Fig. 3C) are more elongate that those closer to the medial portion of the radula. The outermost teeth (Fig. 3D) are shorter and also lack denticles.

REPRODUCTIVE SYSTEM. — The reproductive organs are arranged in a triaulic arrangement (Fig. 3C) typical of doridacean nudibranchs. The ampulla is thin and elongate. It branches into a short oviduct and an elongate vas deferens. The oviduct enters the female gland mass. The distal portion of the vas deferens is prostatic, elongate and convoluted. It narrows somewhat and expands again into the muscular portion, consisting of a single fold. The proximal portion of the vas deferens opens into a short penial sac which opens adjacent to the vagina. The vagina is elongate and undulate. Near its distal end it is joined by the uterine duct, which is short and enters the female gland mass. The distal end of the vagina joins the junction of the spherical bursa copulatrix and the elongate, pyriform receptaculum seminis. The female gland mass consists of three major portions: the albumen, membrane and mucous glands. The mucous gland is the largest portion. A massive vestibular gland containing many tubules is located next to the surface of the female gland mass. It exits adjacent to the vagina and the opening of the female gland mass.

DISCUSSION. — *Ceratosoma ingozi* is most similar to *C. amoena*. Both species lack a distinct posterior glandular protuberance and lack lateral extensions or undulations of the notal margin. Although both species have purple spots, they differ markedly in other aspects of their coloration. *Ceratosoma amoena* has orange spots in addition to the purple ones and purple pigment is also present on the gills and rhinophores. Internally, there are also major differences in the buccal armature. The jaw rodlets of *C. amoena* are bifid as in *Chromodoris* while those of *C. ingozi* are undivided as in the remaining species of *Ceratosoma*. The radular morphology of *C. amoena* is more similar to that of *Chromodoris*, with well-developed rachidian and cuspidate teeth with numerous denticles. In *C. ingozi*, the rachidian teeth are reduced. The innermost lateral tooth lacks a distinct cusp and only the first several inner teeth have any trace of denticulation.

Ceratosoma alleni sp. nov.
(Figs. 1B, 4, 5)

TYPE MATERIAL. — Holotype: CASIZ 085888, 2 km E. of Lighthouse, near Dakak Resort, Dapitan, northern Mindanao, Philippines, 10 m depth, 29 March 1993, Jerry Allen. Paratype, CASIZ 104200, Kirby's Rock, Maricaban Island, Batangas Province, Luzon, Philippines, 8 m depth, 19 February 1995, Michael Miller.

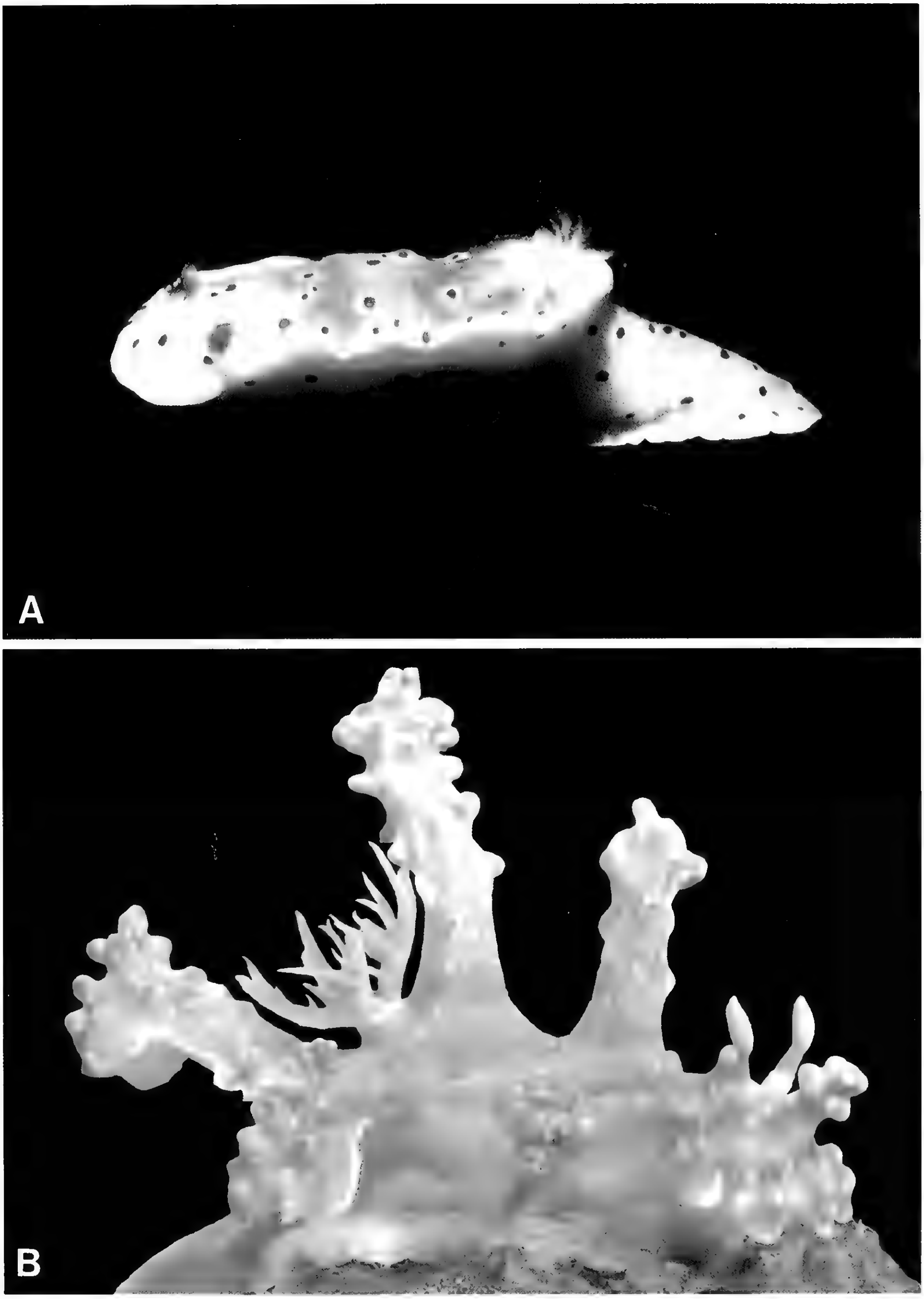

FIGURE 1. Living animals. A. *Ceratosoma ingozi* sp. nov, specimen from off Danger Point, South Africa, photo by W. R. Liltved. B. *Ceratosoma alleni*, specimen from Dakak, Mindanao, Philippines, photo by Michael Miller.

ETYMOLOGY. — *Ceratosoma alleni* is named for Jerry Allen of Tucson, Arizona, who first discovered this species on one of our joint trips to the Philippines.

DISTRIBUTION. — Thus far, this species is known only from the Mindanao and Luzon Islands in the Philippines.

EXTERNAL MORPHOLOGY. — The preserved animals are 47 and 61 mm in length. The living animals (Fig. 1B) are light brownish gray with lighter pustules over the body surface. The rhinophores are the same color as the body, but have a white apex. The gills are also brownish. The body has a rigid texture when the animal is alive.

The body shape is striking and distinctive. The head contains six pustulose, dorsoventrally flattened lobes along its anterior and lateral margins (Fig. 4A). Each of these lobes has a complex array of mantle glands on the ventral surface. Extending laterally from either side of the notum are two or three elongate, pustulose lobes with defensive glands on the ventral surface of the apical portion of the lobe (Fig. 4B). Along the median line are a series of pustulose appendages. A lobe of moderate length is present anterior to the rhinophores followed by a short lobe immediately posterior to the rhinophores. More posteriorly an elongate lobe is present followed by an even longer appendage just anterior to the gills. None of these lobes appear to contain defensive glands. Immediately posterior to the gills is an elongate, dorsoventrally flattened appendage with defensive glands. This appears to be homologous to the posterior glandular protuberance of other species of *Ceratosoma*. The rhinophores are thin and elongate with well-elevated sheaths. The rhinophores are perfoliate with 31 lamellae. The branchial plume is composed of 6–10 bipinnate lamellae. The reproductive opening is located on the right side of the body, about one-third of the total body length posteriorly from the anterior margin of the head.

BUCCAL MASS AND ARMATURE. — The buccal mass (Fig. 4C) consists of a largely muscular posterior portion and a glandular anterior one. At the junction of these two portions are three large lateral muscles on either side of the mass. A large, strap-like salivary gland is present on each side of the posterior end of the buccal mass, adjacent to the junction of the esophagus with the buccal mass.

The jaws consist of numerous elongate, undivided rodlets (Fig 5A). The radula of the paratype had a formula of 77 × 93–108.0.93–108. No trace of a rachidian tooth was observed. The inner lateral teeth (Fig. 5B) lack denticles on the inner side of the cusp, but have 1–3 rounded denticles on the outer side of the cusp. The second to seventh laterals have traces of denticular tubercles on the outer edges. The remaining teeth all have a well-developed cusp, but lack any denticles. The teeth from the middle portion of the half-row (Fig. 5C) are more elongate and curved than those closer to the medial portion of the radula. The outermost teeth (Fig. 5D) are shorter and also lack denticles.

REPRODUCTIVE SYSTEM. — The reproductive organs are arranged in a triaulic arrangement (Fig. 4D). The ampulla consists of several convolutions. It branches into a moderately short oviduct and an elongate vas deferens. The oviduct enters the female gland mass. The distal portion of the vas deferens is prostatic, elongate and convoluted. It narrows somewhat and expands again into the muscular portion, consisting of a single fold. At the point where the muscular portion loops back upon itself, the vas deferens penetrates the muscular portion of the dorsal body wall and re-emerges back into the body cavity. The proximal portion of the vas deferens opens into a moderately elongate penial sac which opens adjacent to the vagina. The vagina is elongate and convoluted. Near its distal end it is joined by the uterine duct, which is short and enters the female gland mass. The distal end of the vagina joins the junction of the spherical bursa copulatrix and the elongate, pyriform receptaculum seminis. The female gland mass consists of three major portions: the albumen, membrane and mucous glands. The mucous gland is the largest portion. A vestibular gland appears to be entirely absent.

DISCUSSION. — The external morphology of *Ceratosoma alleni* is unique among described species of *Ceratosoma*. It is the only species with prolonged lateral extensions of the notum which contain glandular arrays on the ventral surface. It is also the only species with elongate medial appendages in addition to the posterior glandular protuberance. The only other species with tuberculate pustules is *C. moloch* Rudman, 1988. This species is red in color and has de-

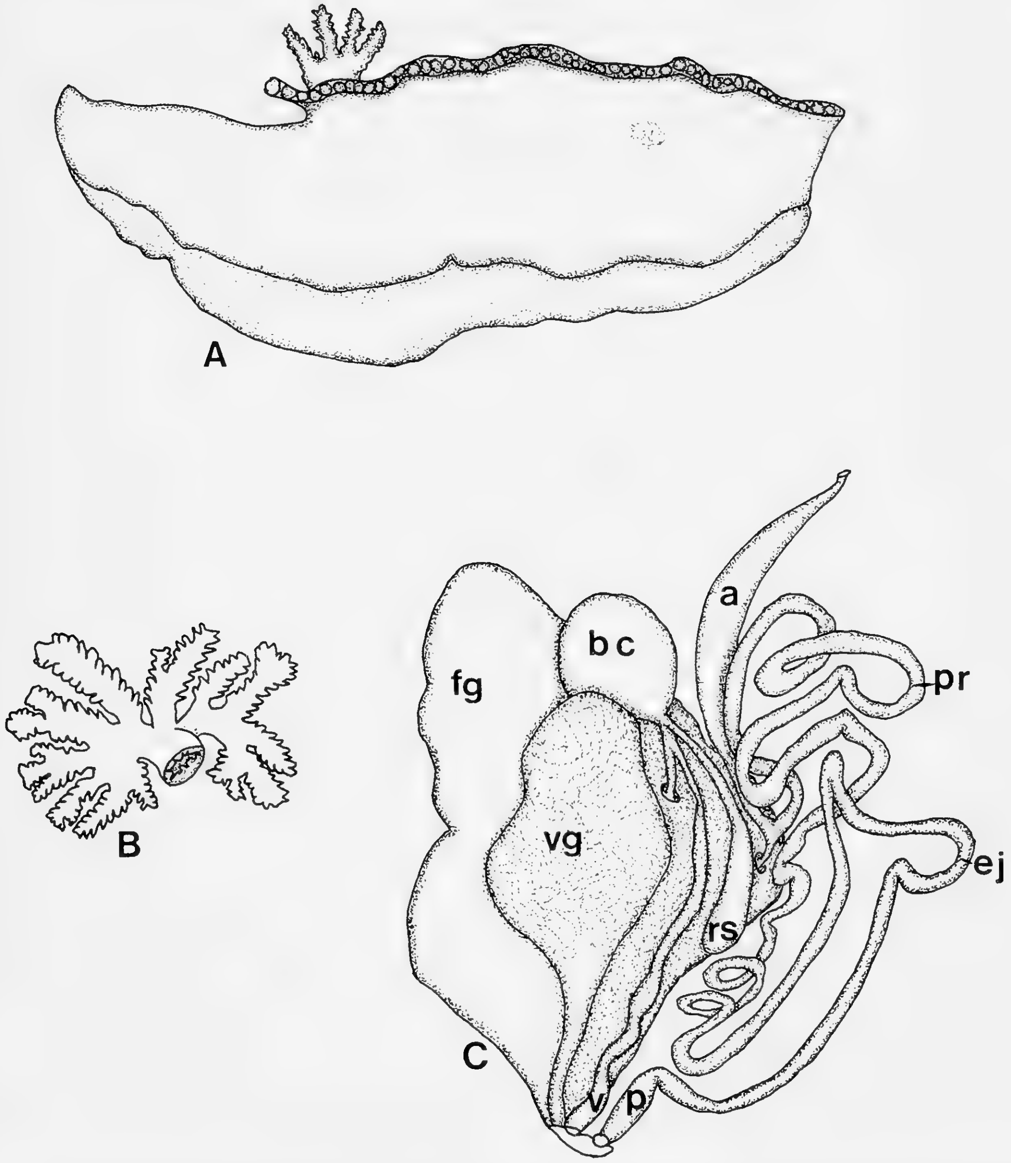

FIGURE 2. *Ceratosoma ingozi* sp. nov. A. General body shape showing distribution of mantle glands. B. Branching of gills. C. Arrangement of reproductive organs, a = ampulla; bc = bursa copulatrix; ej = ejaculatory portion of vas deferens; fg = female gland mass; p = penis; pr = prostatic portion of vas deferens; rs = receptaculum seminis; v = vagina, vg = vestibular gland.

fensive glands all over the surface of the pustules. *Ceratosoma alleni* has several denticles on the outside of the innermost teeth while a single denticle is present on the inner lateral tooth of *C. moloch*. The teeth from the middle of the half-row of *C. alleni* lack denticles while those of *C. moloch* bear 3–5 denticles. The reproductive system of *C. alleni* appears to lack a vestibular gland, while that of *C. moloch* is typical of *Ceratosoma* species with a large saccate gland.

Ceratosoma alleni closely resembles an unidentified xeniid soft coral which has been found in the same habitat. This species may

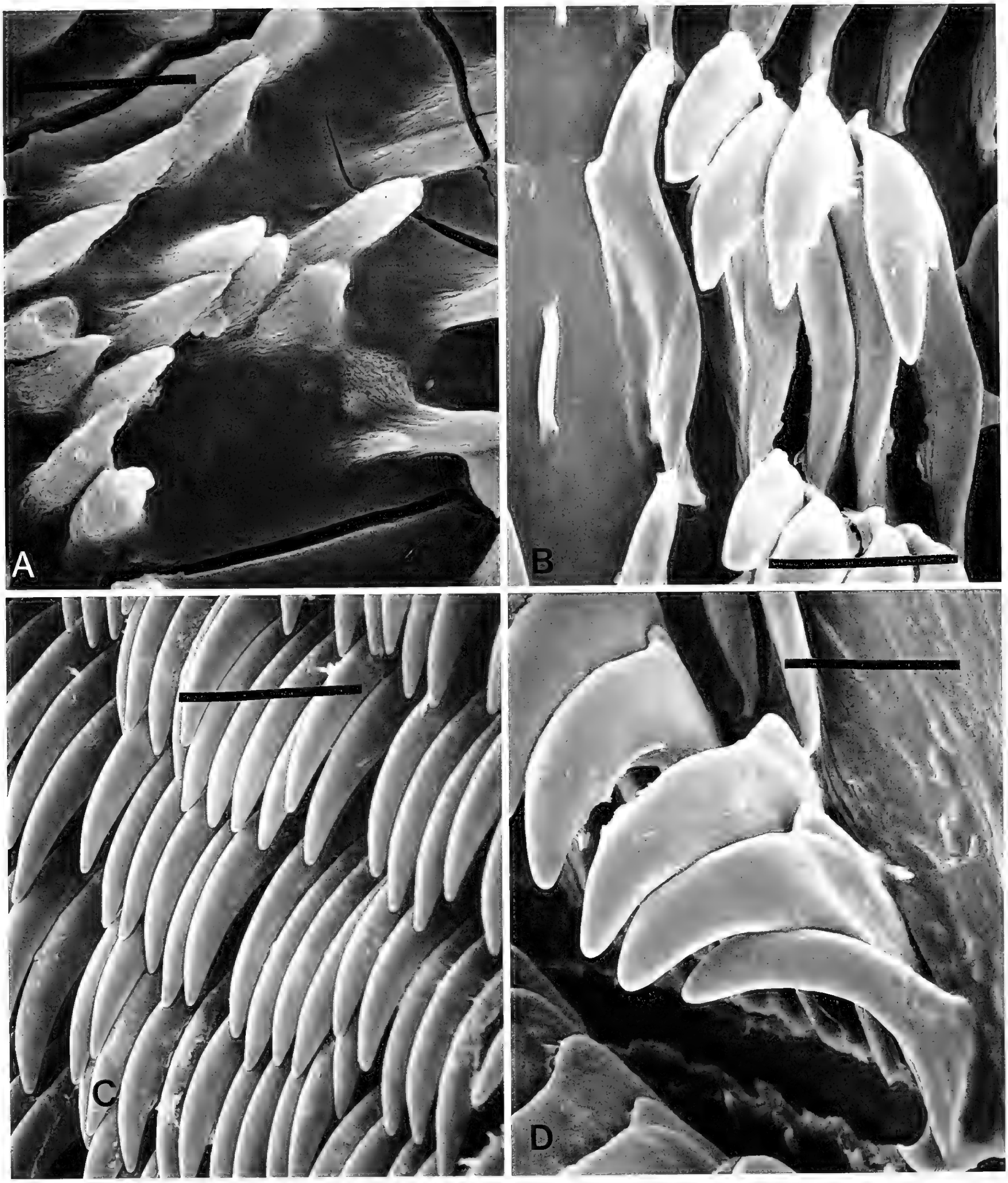

FIGURE 3. *Ceratosoma ingozi* sp. nov. Scanning electron micrographs. A. Jaw rodlets, scale = 10 µm. B. Rachidian and inner lateral teeth, scale = 43 µm. C. Teeth from central portion of half-row, scale = 100 µm. D. Outer lateral teeth, scale = 43 µm.

closely resemble the soft coral to elude visual predators. Although *C. alleni* has not been observed feeding, it is probable that it feeds upon sponges, like other chromodorids, rather than feeding upon soft corals.

PHYLOGENETIC RELATIONSHIPS

Rudman's (1988) review provides a wealth of characters for the study of phylogenetic relationships of the species of *Ceratosoma*. He

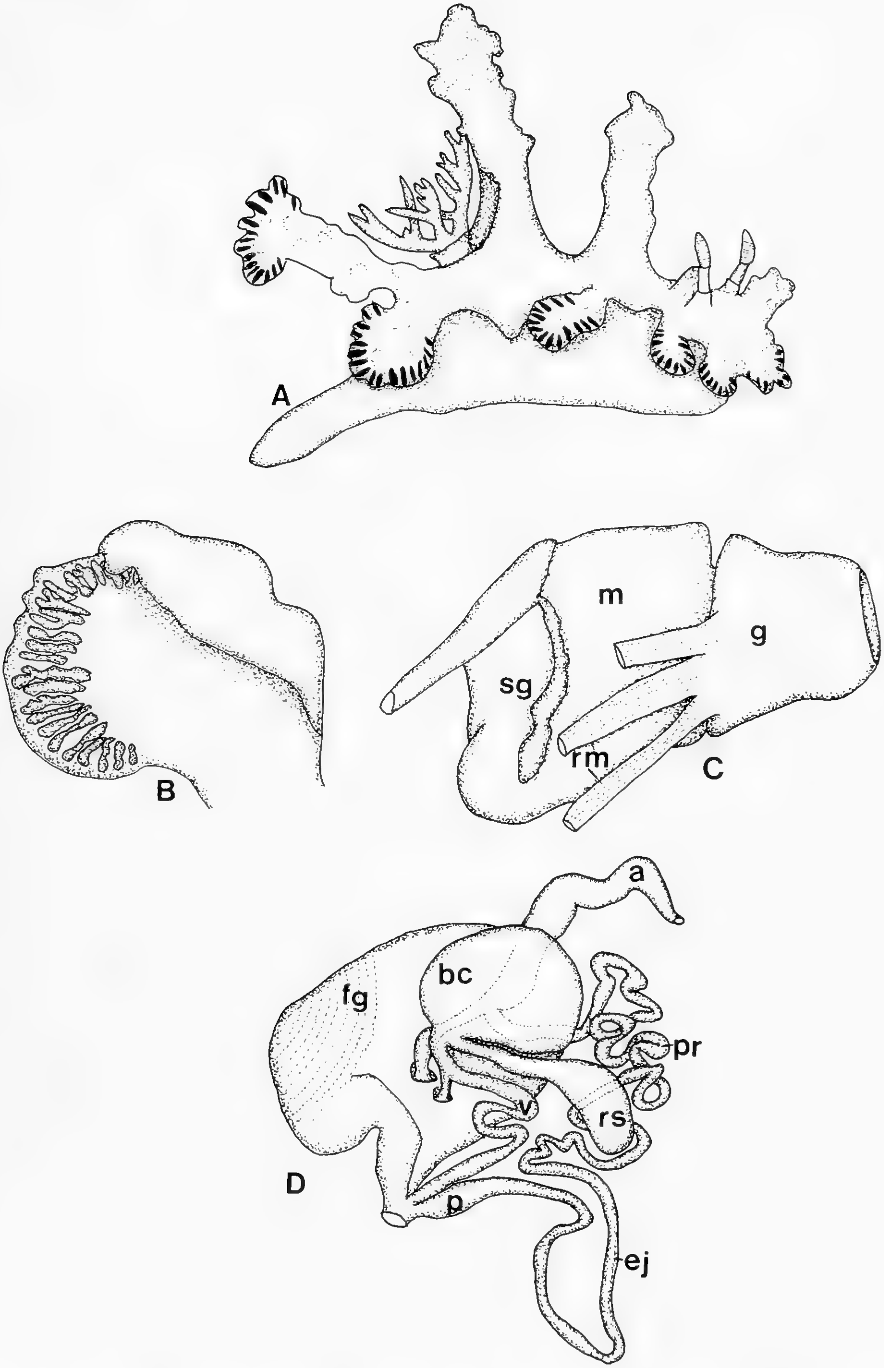

FIGURE 4. *Ceratosoma alleni* sp. nov. A. Distribution of mantle glands over body surface. B. Distribution of mantle glands on left posterior appendage. C. Buccal mass, g = glandular portion; m = muscular portion; rm = retractor muscles; sg = salivary gland. D. Reproductive system, a = ampulla; bc = bursa copulatrix; ej = ejaculatory portion of vas deferens; fg = female gland mass; p = penis; pr = prostatic portion of vas deferens; rs = receptaculum seminis; v = vagina.

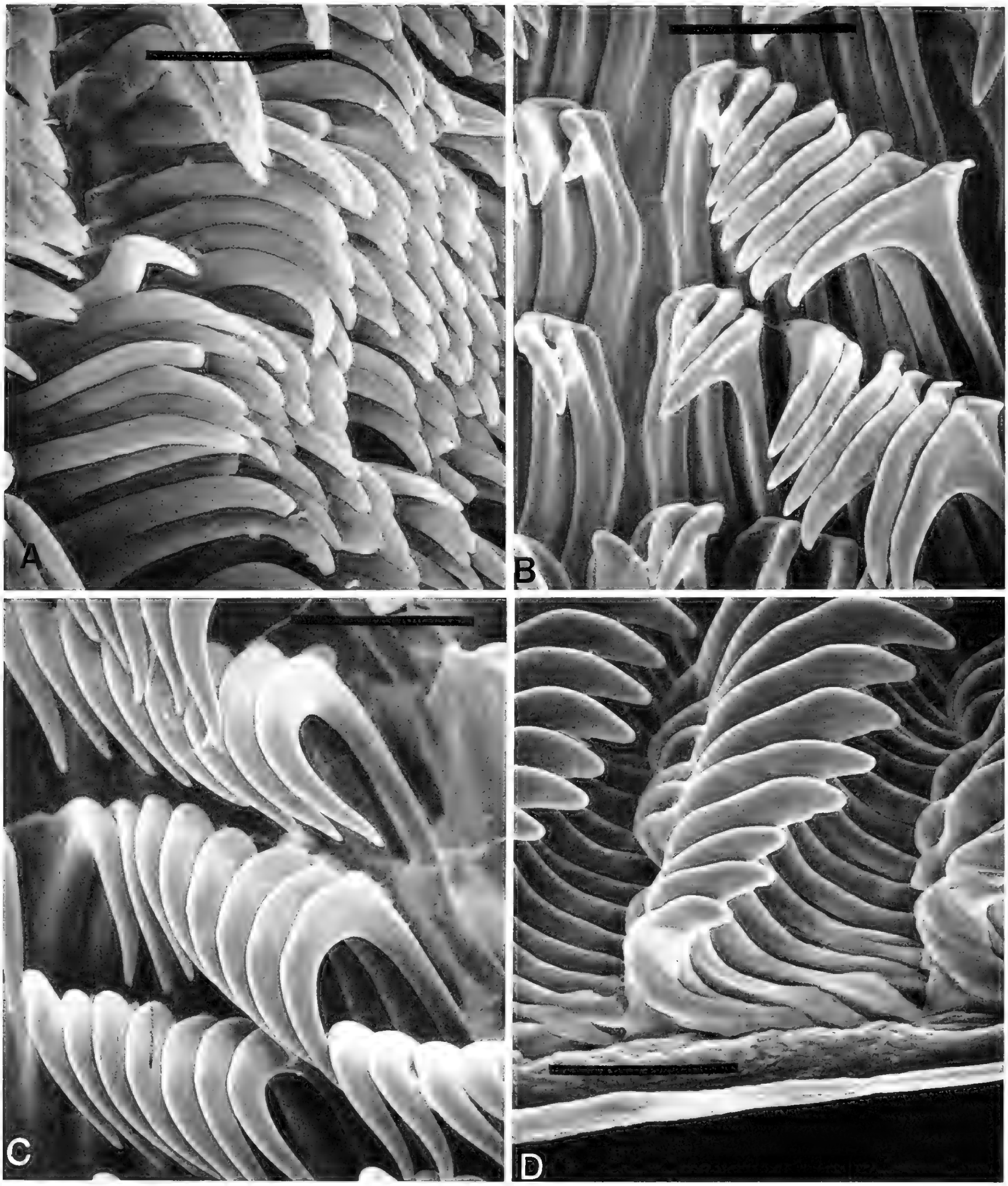

FIGURE 5. *Ceratosoma alleni* sp. nov. Scanning electron micrographs. A. Jaw rodlets, scale = 20 µm. B. Rachidian and inner lateral teeth, scale = 60 µm. C. Teeth from central portion of half-row, scale = 60 µm. D. Outer lateral teeth, scale = 43 µm.

noted that radular characters of some species of *Ceratosoma* demonstrate a more plesiomorphic condition earlier in their ontogeny while adults exhibit only the derived condition. He also discussed evolutionary trends of radular, mantle and defensive gland morphology, but did not present an explicit phylogeny of species relationships within the genus.

In order to polarize the morphological variability of species of *Ceratosoma* it is necessary to select outgroups. For this purpose, species of *Chromodoris* and *Hypselodoris* were selected, as they contain taxa with more plesiomorphic morphology and are sufficiently diverse to represent the morphological variation contained within *Ceratosoma*. Rudman (1984) has hypothesized that relationships of *Ceratosoma* to *Hypselodoris*, and considers *Hypselodoris* to be derived from a *Chromodoris* relative. The following characters (Table 1) were considered in undertaking a phylogenetic analysis:

1. Body profile. — Species of *Chromodoris* have a low body profile while all *Hypselodoris* and *Ceratosoma* have a high body profile. The condition present in *Chromodoris* is like that found in other cryptobranch dorids and is considered plesiomorphic.

2. Body firmness. — All species of *Chromodoris* and *Hypselodoris* have a soft, fleshy body; species of *Ceratosoma* have a firm and rubbery body. A more rigid body appears to be apomorphic.

3. Body texture. — Virtually all species of *Chromodoris*, *Hypselodoris* and *Ceratosoma* have a smooth body texture. *Ceratosoma moloch* and *C. alleni* have pustules over the body surface. Presence of pustules is considered the apomorphic state.

4. Notal margin. — In species of *Chromodoris*, *Hypselodoris* and most *Ceratosoma* the edge of the notum forms a continuous rim around the entire margin of the animal. In *Ceratosoma gracillimum* and *C. tenue* the mantle margin contains areas of discontinuity. A discontinuous mantle is considered apomorphic.

5. Mantle lobes. — The mantle margin of *Chromodoris*, *Hypselodoris* and some species of *Ceratosoma* is straight, without any undulations. In all species of *Ceratosoma*, except *C. amoena* and *C. ingozi*, the mantle margin contains permanent undulations or lobe-like extensions. An undulating mantle margin is considered apomorphic.

6. Posterior protuberance. — The posterior end of the mantle of *Chromodoris*, *Hypselodoris*, *Ceratosoma amoena*, *C. ingozi* and *C. palliolatum* is undifferentiated from the rest of the notal margin. In the remaining species of *Ceratosoma*, an extended lobe, containing concentrated defensive glands, is present and is considered apomorphic.

7. Mantle glands. — Mantle glands in *Chromodoris*, *Hypselodoris* and several species of *Ceratosoma* are distributed around the entire margin of the notum. In *Ceratosoma gracillimum*, *C. trilobatum* and *C. tenue*, mantle glands are present only along the margin of the head and at the apex of the posterior protuberance. In *Ceratosoma alleni*, mantle glands are present along the margin of the head, at the apex of the posterior protuberance and at the apices of the lateral mantle lobes. Both of the later arrangements are considered apomorphic. This character is treated as unordered in the analysis.

8. Gills. — The gills in species of *Chromodoris*, *Hypselodoris* and *Ceratosoma amoena* are unipinnate while those of the remaining species of *Ceratosoma* contain at least some bipinnate gills. Presence of bipinnate gills is considered apomorphic.

9. Jaw elements. — In *Chromodoris* and *Ceratosoma amoena*, the jaw rodlets are bifid. In *Hypselodoris* and adult specimens of the remaining species of *Ceratosoma*, the jaw rodlets are largely undivided. In juvenile specimens of *C. brevicaudatum*, there are more bifid rodlets that in adults. A few of the rodlets in adult specimens of *C. palliolatum* and *C. brevicaudatum* are occasionally bifid. Having mostly undivided rodlets is considered apomorphic.

10. Rachidian teeth. — In most species of *Chromodoris*, some *Hypselodoris* and some *Ceratosoma*, a distinct row of rachidian teeth is present. In some instances the rachidian teeth are prominent while in other cases they are reduced in size and are considered vestigial. In *Ceratosoma tenue* and *C. alleni* no vestige of a rachidian is apparent. The absence of rachidian teeth is considered apomorphic.

11. Outer lateral teeth. — The outer lateral teeth of *Chromodoris*, most species of *Hyp-*

TABLE 1. Character states in *Chromodoris*, *Hypselodoris* and *Ceratosoma*.

	Character															
Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Chromordoris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hypselodoris	1	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0
amoena	1	1	0	0	0	0	0	0	0	0	0	0	1	0	1	1
brevicaudatum	1	1	0	0	1	1	0	1	1	0	0	0	1	0	1	1
gracillimum	1	1	0	1	1	1	1	1	1	0	1	0	1	0	1	1
moloch	1	1	1	0	1	1	0	1	1	0	1	0	1	0	1	1
palliolatum	1	1	0	0	1	0	0	1	1	0	0	0	1	0	1	1
trilobatum	1	1	0	0	1	1	1	1	1	0	1	0	1	0	1	1
tenue	1	1	0	1	1	1	1	1	1	1	0	0	1	0	1	1
ingozi	1	1	0	0	0	0	0	1	1	0	1	0	1	0	1	1
alleni	1	1	1	0	1	1	2	1	1	1	1	0	2	0	1	1

0 = plesiomorphic condition
1, 2 = apomorphic condition

selodoris and most species of *Ceratosoma* bear small denticles. In *Ceratosoma gracillimum*, *C. moloch*, *C. trilobatum*, *C. ingozi* and *C. alleni*, all of the outer lateral teeth are smooth, without denticles. This morphology is considered apomorphic.

12. Tooth denticulation. — In species of *Chromodoris* and *Ceratosoma* the radular teeth have a single primary cusp, while in *Hypselodoris* all the teeth have a bifid cusp. The arrangement found in *Hypselodoris* is considered apomorphic.

13. Vestibular gland size. — In *Chromodoris* the vestibular gland is small and simple. In *Hypselodoris* and most species of *Ceratosoma*, the vestibular gland is greatly enlarged. In *C. alleni*, a vestibular gland appears to be entirely absent. An enlarged vestibular gland and a lack of a vestibular gland are both considered to represent apomorphic conditions. The character is treated as unordered in the analysis.

14. Vestibular gland shape. — In *Chromodoris* and *Ceratosoma*, the vestibular gland is saccate. In species of *Hypselodoris* the vestibular gland is highly ramified. The latter form is considered apomorphic.

15. Vagina. — The vaginal duct of species of *Chromodoris* and *Hypselodoris* is relatively short and thick while in *Ceratosoma* it is far more thin and elongate. A more elongate vagina is considered apomorphic.

16. Prostate. — In *Chromodoris* and *Hypselodoris*, the prostatic portion of the vas deferens is relatively short. In *Ceratosoma*, the prostatic portion consists of far more folds and convolutions and is considered apomorphic.

In order to develop phylogenetic hypotheses regarding these taxa, the above described characters were placed in a data matrix (Table 1) and analyzed by means of Phylogenetic Analysis Using Parsimony (PAUP) version 3.1.1, by David Swofford. A single most parsimonious tree was produced (Fig. 6). This tree requires 22 steps and has a consistency index of 0.818.

In the above scenario, only two characters exhibit homoplasy. The loss of denticulation of the outer lateral teeth has occurred independently in *Ceratosoma ingozi* and again in the clade containing *C. gracillimum*, *C. trilobatum*, *C. tenue*, *C. moloch* and *C. alleni*. Within that clade, a reversal to plesiomorphically denticulate outer teeth has occurred in *C. tenue*. Also, undivided jaw rodlets have originated in

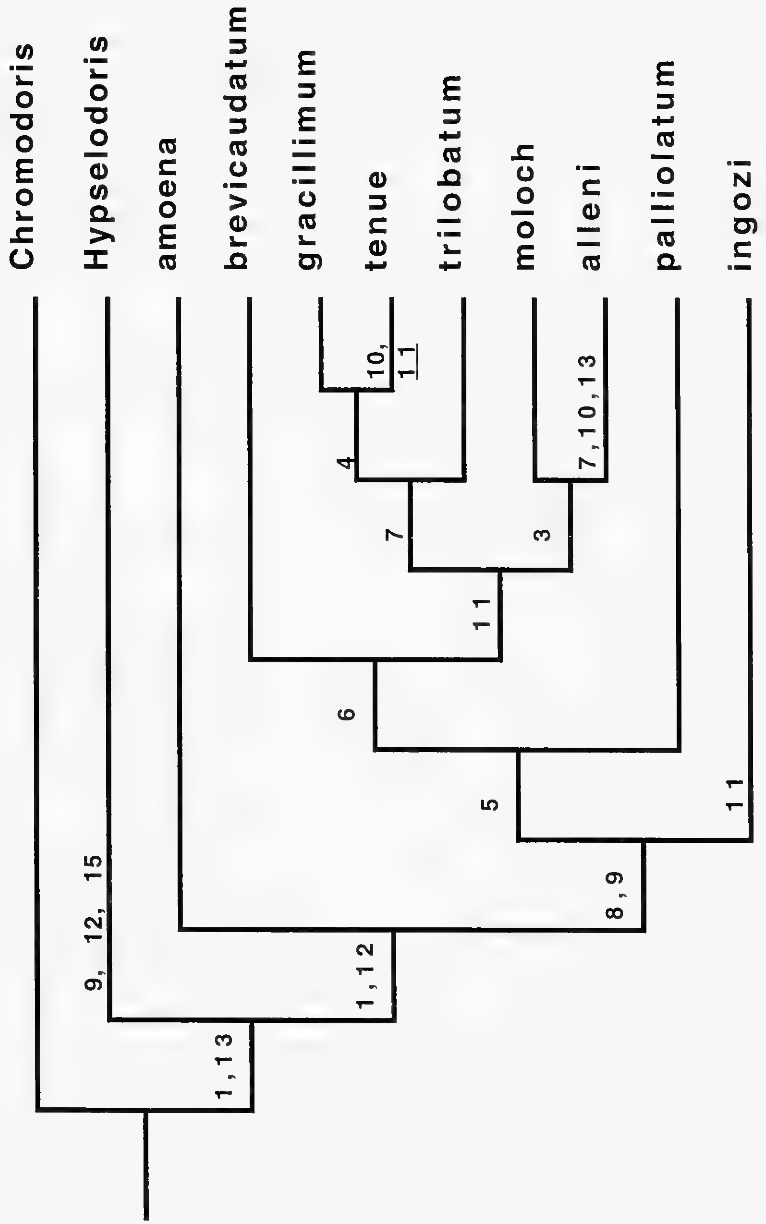

FIGURE 6. Hypothesis of phylogeny of species of *Ceratosoma*. Numbers refer to characters listed within text.

Hypselodoris and again in most species of *Ceratosoma*.

ACKNOWLEDGMENTS

I thank Jerry Allen and Mike Miller for finding the specimens of *Ceratosoma alleni* and for making their photographs of this species available for publication. Bill Liltved endured rigorous diving conditions to collect specimens of *Ceratosoma ingozi*. His continued support of research efforts on the South African molluscan fauna is greatly appreciated. Travel support for field studies in the Philippines was kindly provided through the generous support of Katharine Stewart and the Lindsay Field Research Fund of the California Academy of Sciences and United Airlines. The Photography Department of the California Academy of Sciences kindly printed the black and white photographs used in this paper.

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TYPES OF MECOPTERA, MEGALOPTERA, RAPHIDIOPTERA, AND NEUROPTERA (INSECTA) IN THE COLLECTION OF THE CALIFORNIA ACADEMY OF SCIENCES

By

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Abstract: Complete label information is presented for all primary type specimens, allotypes, and neallotypes of Mecoptera, Megaloptera, Neuroptera, and Raphidioptera housed in the California Academy of Sciences. Numbers of non-allotypic paratypes are given with the names of states or provinces of the North American species, or countries of other nations.

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INTRODUCTION

The California Academy of Sciences contains one of the major entomological type collections in the world. Although a rather young collection, it has been growing very actively since its 1915 reopening in Golden Gate Park after San Francisco's great earthquake and fire of 1906. Since that time it has become the largest collection of type specimens in the western continental North America, at present including more than 14,000 primary type specimens. In order to inform the scientific community as to what types exist in this collection, a series of catalogs has been published. Previous parts of this series include type catalogs of the Orthoptera (Rentz, 1965), Thysanoptera (Arnaud and Lee, 1973), and Diptera (Arnaud, 1979).

There are no primary types of Mecoptera and Neuropterida in this collection predating the 1906 earthquake. In fact, the first neuropteroid type in the collection was described in 1936. However, through the efforts of several contemporary neuropterists (sensu lato), the California Academy of Sciences now contains one of the ten largest collections of neuropteroid types in the world. Currently there are 9 holotypes, 4 allotypes, and 64 paratypes of Megaloptera; 7 holotypes, 3 allotypes, and 89 paratypes of Raphidioptera; 77 holotypes, 2 lectotypes, 10 allotypes, 1 neallotype, and 190 paratypes of Neuroptera; and 12 holotypes, 3 allotypes, and 33 paratypes of Mecoptera in the collection. Among those researchers actively contributing to the neuropteroid and Mecoptera type collection during the past 30 years are: Phillip A. Adams (California), Horst and Ulrike Aspöck (Austria), George W. Byers (Kansas), Elvin D. Evans (Michigan), Jason G. H. Londt (South Africa), Martin Meinander (Finland), Victor J. Monserrat (Spain), Waro Nakahara (Japan), John D. Oswald (Washington, D. C.), Norman D. Penny (California), Lionel A. Stange (Florida), and Catherine A. Tauber (New York).

Primary types (holotypes, lectotypes, neotypes, and syntypes) are defined as those type specimens which are the name-bearing specimens of the species and are used to definitely relate the name of the species to an individual with certain recognizable traits. Secondary types (allotypes, neallotypes, paratypes, etc.) are those type specimens used to delimit the phenotypic variation within a species. Although of marginal value in determining the true identity of a species, these secondary types are useful to some researchers and because we wish to maintain consistency in content within the series, these secondary types have been included. We have listed the number of paratypes, as well as country of origin, and in North America the state or province of origin. Where a paratype locality is found in a country deemed to have complex faunal relationships, such as Ecuador (Galapagos Islands) and Indonesia, we have provided more precise information. There is some confusion about the definition of neallotypes, as opposed to neoallotypes. Neallotype is herein defined as an allotype which was not part of the original type series, but subsequently designated as allotype. Until adoption of the 1985 edition of the International Code of Zoological Nomenclature (Recommendation 72A), there had been no formally accepted definition of allotype, and some workers preferred to designate allotypes from specimens other than the original paratype series, so the term neallotype was coined to separate these specimens from allotypes designated from the original type series.

Primary type specimens in the CAS collection are deposited through several different arrangements. Types from the University of California, Riverside, and Oregon State University, Corvallis, are entrusted to The Academy through a permanent deposit arrangement. The University of California, Berkeley, currently has an indefinite loan arrangement with the Academy. If not otherwise indicated, the included types are the permanent property of the California Academy of Sciences. All pinned specimens and any associated parts separated from the body have a label reading "California Academy / of Sciences / Type / No. / . . ." Also, all slides have a similar CAS type slide label attached. Where quoted label information contains a male or female symbol, we have indicated this with [MA] and [FE] letter and symbol combination. Further, where quoted label information contains ditto marks, these are indicated by ″ rather than the quote marks " used to enclose label information.

We have tried to maintain the style of previous type catalogs. The information contained on labels is transcribed as closely as possible to the original print, although not all labels contain neat, linear lines of information, and occasional placement interpretation was needed. Each line is delimited by slash marks, and each label by quotation marks and a semicolon. The journal abbreviations in the text generally conform to those used by BIOSIS, although we prefer a more abbreviated listing for Psyche (Camb.). In the Literature Cited section, journal titles have been spelled out fully. The number of paratypes indicated is exclusive of any specimen designated as allotype or neallotype.

MECOPTERA

Bittacidae

Bittacus rossi Londt.

1977, J. Entomol. Soc. South. Afr., vol. 40, no. 1, p. 94.

Holotype (male), CAS Type No. 16648; "B. CONGO: / 5 mi. S. of / Fizi, 1320 m / I-10-1958"; "E. S. Ross & / R. E. Leech / collectors"; "HOLOTYPE / Bittacus / rossi [MA] / LONDT. J. G. H."

Bittacus smithersi Londt.

1972, J. Entomol. Soc. South. Afr., vol. 35, no. 2, pp. 328–329, figs. 31, 32, 49, 62.

Paratypes, 2 (South Africa).

Boreidae

Boreus brevicaudus Byers.

1961, J. Kans. Entomol. Soc., vol. 34, no. 2, p. 74.

Holotype (male), CAS Type No. 9440; "Ore., Lane Co., / 2 mi. S. Eugene, / Spencer Butte area, / east side, Nov. 27, / 1959, David R. Smith"; "moss from / old tree"; "HOLOTYPE / Boreus / brevicaudus / George W. Byers".

Allotype (female); "Ore., Lane Co., / 3 mi. S. Eugene, / Spencer Butte, / Nov. 23, 1959 / J. D. Lattin"; "moss and / leaf litter / 1400″"; "ALLOTYPE / Boreus / brevicaudus / George W. Byers".

Remarks: Both specimens are on permanent deposit from Oregon State University. This species is currently placed in the genus *Hesperoboreus* (see Penny, 1977:184).

Boreus elegans Carpenter.
1935, Psyche, vol. 42, no. 2, p. 119.
Holotype (male), CAS Type No. 4529; "Vancouver, B. C. / XII-1930"; "H. E. Hinton / Collector"; "Type"; "Boreus elegans / Carp."

Boreus nix Carpenter.
1935, Psyche, vol. 42, no. 2, p. 114, fig. 7.
Paratype, 1 (Montana).

Boreus notoperates Cooper.
1972, Psyche, vol. 79, no. 4, pp. 270–281, figs. 1–11.
Paratypes, 2 (California).
Remarks: This species is currently placed in the genus *Hesperoboreus* (see Penny, 1977:185).

Boreus pilosus Carpenter.
1935, Psyche, vol. 42, no. 2, pp. 114–115, fig. 10.
Paratype, 1 (British Columbia).

Panorpidae

Neopanorpa globulifera Byers.
1983, Pan-Pac. Entomol. (1982), vol. 58, no. 2, pp. 92–95, figs. 1–9.
Holotype (male), CAS Type No. 15901; "LAOS Sam Thong / Xieng Khouang Prov / 90 mi NE Vientiane / 12 May 1968 / Gary L Peters"; "HOLOTYPE / Neopanorpa / globulifera / [MA] / George W. Byers".
Allotype (female)(in alcohol); same data as holotype, except dated "28 July 1968"; with additional label reading "specimen dissected; / watch for loose parts!".
Paratype, 1 (Laos).

Neopanorpa lichuanensis Cheng.
1957, Mem. Coll. Agric., Natl. Taiwan Univ., vol. 5, no. 1, p. 32, figs. 12, 13.
Holotype (female), CAS Type No. 7211; "Suisapa, 1000 M. / Lichuan Distr. / W. Hupeh, China / VIII-21-48"; "Neopanorpa lichuanensis n.sp. / By F.Y. Cheng"; "HOLOTYPE [FE]".

Neopanorpa lungtausana Cheng.
1957, Mem. Coll. Agric., Natl. Taiwan Univ., vol. 5, no. 1, pp. 32–33, figs. 14, 15.
Holotype (female), CAS Type No. 7212; "Kwangtung Prov., S. China / Lung-tau Shan. Alt. 600 M. / near Yiu Vill. above Tso- / kokwan. VI-6-47 Gressitt"; "Neopanorpa lungtausana n.sp. / By F. Y. Cheng"; "HOLOTYPE [FE]".

Neopanorpa mokansana Cheng.
1957, Mem. Coll. Agric., Natl. Taiwan Univ., vol. 5, no. 1, pp. 30–32, figs. 9–11.
Holotype (male), CAS Type No. 7213; "Mokansan China / Che Kiang Pr. / IX-19-27"; "Mrs. Dora / E. Wright / Collector"; "Neopanorpa mokansana n.sp. / By F. Y. Cheng"; "HOLOTYPE [MA]".

Neopanorpa tuberosa Byers.
1965, Pac. Insects, vol. 7, no. 4, p. 737.
Holotype (male), CAS Type No. 8903; "THAILAND: / Khao-Yai Nat. Pk. / 750 m: VII-26-62"; "E. S. Ross / D. Cavagnaro / Collectors"; "HOLOTYPE / Neopanorpa / tuberosa / [MA] / George W. Byers".
Allotype (female); same data as holotype.
Paratypes, 24 (Thailand).

Panorpa kellogi Cheng.
1957, Mem. Coll. Agric., Natl. Taiwan Univ., vol. 5, no. 1, pp. 29–30, figs. 5, 6.
Holotype (male), CAS Type No. 7214; "Foochow / China"; "C. R. Kellog [sic]/ Collector"; "Panorpa kellogi [sic] n.sp. / By F. Y. Cheng"; "HOLOTYPE [MA]".
Remarks: The original description indicated that this species was named for the collector "C. R. Kellog," a misspelling of Claude R. Kellogg. Since there was no internal evidence of the correct spelling within the article, the incorrect original spelling must be retained.

Panorpa mokansana Cheng.
1957, Mem. Coll. Agric., Natl. Taiwan Univ., vol. 5, no. 1, p. 27, figs. 1, 2.
Holotype (male), CAS Type No. 7215; "Mokansan China / Che Kiang Pr. / IX-19-27"; "Mrs. Dora / E. Wright / Collector"; "Panorpa mokansana n.sp. / By F. Y. Cheng"; "HOLOTYPE [MA]".
Remarks: The original description indicated

that the holotype was a female, but it is in fact a male.

Panorpa thompsoni Cheng.
1957, Mem. Coll. Agric., Natl. Taiwan Univ., vol. 5, no. 1, p. 29, figs. 7, 8.
Holotype (female), CAS Type No. 7216; "Tsu Shima / Lu Chu Ids. / X-5-1910"; "JC Thompson / Collector"; "Panorpa thompsoni n.sp. / By F. Y. Cheng"; "HOLOTYPE [FE]".

Panorpa wrightae Cheng.
1957, Mem. Coll. Agric., Natl. Taiwan Univ., vol. 5, no. 1, pp. 28–29, figs. 3, 4.
Holotype (female), CAS Type No. 7217; "Mokansan China / Che Kiang Pr. / Sep. 28 1927"; "Mrs. Dora / E. Wright / Collector"; "Panorpa wrighti [sic], n.sp. / By F. Y. Cheng"; "HOLOTYPE [FE]".
Remarks: Although the original description of this species bore a masculine ending (*wrighti*), the author clearly stated that the species was named for Mrs. Dora E. Wright, the collector. Thus, the name should have a feminine ending, which is given here.

Panorpodidae

Brachypanorpa sacajawea Byers.
1990, J. Kans. Entomol. Soc., vol. 63, no. 2, pp. 211–217, figs. 1–12.
Paratypes, 2 (Idaho).

MEGALOPTERA

Corydalidae

Dysmicohermes crepusculus Chandler.
1954, Pan-Pac. Entomol., vol. 30, no. 2, pp. 107–108, figs. 1, 2, 6.
Holotype (male), CAS Type No. 7197; "Pyramid R. S. / Eldorado Co. / Calif VII-20-52"; "J. W. MacSwain / Collector"; "HOLOTYPE / Dysmicohermes / crepusculus".
Allotype (female); "2 mi s.w. / Miami Ranger Sta. / Mariposa Co. / 7/25/1946"; "H. P. Chandler / No. 54 Expo. / / / 4 NE / Elv 5,000"; "ALLOTYPE / Dysmicohermes / crepusculus".
Paratypes, 2 (California).

Remarks: This species is currently placed in *Orohermes.*

Dysmicohermes ingens Chandler.
1954, Pan-Pac. Entomol., vol. 30, no. 2, pp. 105–107, figs. 3–5.
Holotype (male), CAS Type No. 7198; "Miami Ranger Sta. / Mariposa Co. Cal. / 7/27/46"; "H. P. Chandler / No. 67 Expo. / / /4 NE / Elv 5,000 SW"; "HOLOTYPE / Dysmicohermes / ingens".
Allotype (female); same data as holotype, except 2nd line of 2nd label reads "No. 61 Expo.", and holotype label is replaced by allotype label.
Paratypes, 4 (California).

Neohermes nigrinus Van Dyke.
1944, Pan-Pac. Entomol., vol. 20, no. 3, p. 110.
Holotype (male), CAS Type No. 5430; "Richardson's / Spr., Butte / Co, Calif. / V-12–44"; "Presented by / EC Van Dyke / Collector"; "Holotype Neohermes / nigrinus / Van Dyke".
Remarks: This species is currently considered a junior synonym of *Protochauliodes minimus* (Davis).

Protochauliodes aridus Maddux.
1954, Pan-Pac. Entomol., vol. 30, no. 1, pp. 70–71.
Holotype (male), CAS Type No. 7201; "Chico / R 5-10-51 / D. Maddux"; "HOLOTYPE / PROTOCHAULIODES / ARIDUS / MADDUX"; "N.sp. / HOLOTYPE / [MA] #20 / CSC #1".

Protochauliodes cascadius Evans.
1984, Pan-Pac. Entomol., vol. 60, no. 1, pp. 1–3, figs. 1–3.
Holotype (male), CAS Type No. 11404; "Ca. 8 mi W. Mill City / along Little Santiam R., / Marion Co., Ore. / VII-26-63"; "[MA] [FE] *Protochauliodes montivagus* / Sept. 1963 Chandler ?"; "HOLOTYPE [MA] / PROTOCHAULIODES / CASCADIA 1970 / Elwin D. Evans".
Allotype (female); same data as holotype, except allotype label.
Paratypes, 7 (Oregon).

Protochauliodes montivagus Chandler.
1954, Pan-Pac. Entomol., vol. 30, no. 2, p. 111, figs. 9, 10.
Holotype (male), CAS Type No. 7199; "St. Charles Hill / Sierra Co Cal. / July 7, 1923"; "Pres. by / E. H. Nast / Collector"; "HOLOTYPE / Protochauliodes / montivagus".
Paratypes, 2 (California).

Protochauliodes simplus Chandler.
1954, Pan-Pac. Entomol., vol. 30, no. 2, pp. 110–111, figs. 7, 8.
Holotype (male), CAS Type No. 7200; "Tanbark Flat / Los Angeles Co. / Calif. VII-13-50 / JD Paschke / Collector"; "HOLOTYPE / Protochauliodes / simplus".
Paratypes, 3 (California).

Sialidae

Sialis arvalis Ross.
1937, Ill. Nat. Hist. Surv. Bull., vol. 21, no. 3, p. 68.
Holotype (male), CAS Type No. 4647; "MOKEL. HILL, / CAL."; "coll. by F. E. / Blaisdell"; "Apr."; "HOLOTYPE / Sialis [MA] / arvalis / Ross".
Paratypes, 2 (California).

Sialis mohri Ross.
1937, Ill. Nat. Hist. Surv. Bull., vol. 21, no. 3, p. 74.
Paratypes, 11 (Illinois).

Sialis occidens Ross.
1937, Ill. Nat. Hist. Surv. Bull., vol. 21, no. 3, p. 69.
Holotype (male), CAS Type No. 4648; "Sequoia Natl. / Park, Calif. / Alt. 7000–9000 ft."; "Wolverton / VI-25-29"; "Pres. by / EC Van Dyke / Collector"; "HOLOTYPE / Sialis [MA] / occidens / Ross".
Allotype (female); same data as holotype, except allotype label substituted for holotype label and additional label reading "From Coll. / Calif. Acad. Sci."
Paratypes, 6 (5 California, 1 Nevada).

Sialis velata Ross.
1937, Ill. Nat. Hist. Surv. Bull., vol. 21, no. 3, p. 71.
Paratypes, 27 (Michigan).

RAPHIDIOPTERA

Inocellidae

Negha meridionalis Aspöck.
1988, Z. Arbeitsgem. Österr. Entomol., vol. 39, nos. 3/4, pp. 107–111, figs. 1–11.
Paratype, 1 (Baja California).

Raphidiidae

Agulla banksi Carpenter.
1936, Proc. Am. Acad. Arts Sci., vol. 71, no. 2, p. 120, pl. 2 (figs. 11, 12).
Paratypes, 2 (California).
Remarks: This species is currently considered a junior synonym of *Agulla modesta* Carpenter.

Agulla bractea Carpenter.
1936, Proc. Am. Acad. Arts Sci., vol. 71, no. 2, pp. 130–131, pl. 2 (fig. 16).
Paratypes, 2 (California).

Agulla directa Carpenter.
1936, Proc. Am. Acad. Arts Sci., vol. 71, no. 2, pp. 124–125, pl. 1 (fig. 3).
Holotype (male), CAS Type No. 4475; "Oroville Cal. / IV-17-1928"; "H H Keifer / Collector"; "TYPE"; "Agulla directa Carpenter / det. F. M. Carpenter"; "H. & U. Aspöck vid. 1967". Separate pin with genitalia vial, label reads "Agulla directa / Carp.".
Paratype, 1 (California).

Agulla nigrinotum Woglum and McGregor.
1964, Bull. South. Calif. Acad. Sci., vol. 63, pt. 4, pp. 201–203.
Holotype (male), CAS Type No. 9548; "Mill Potrero / Kern 7-1-63 / r. s. woglum col"; "Agulla / negrinotum [sic] / Type on HOLOTYPE"; "Agulla nigrinotum / Woglum et McGregor / Holotypus [MA] / U. Aspöck vid. 1972.".
Allotype (female); "Mill Potrero / Kern 7-1-63 / r. s. woglum col"; "ALLOTYPE"; "ALLOTYPE / Agulla / nigrinotum / Wog. & McGreg."
Paratypes, 7 (California).

Agulla occidentis Carpenter.
1936, Proc. Am. Acad. Arts Sci., vol. 71, no.

2, pp. 129–130, pl. 2 (fig. 21).

Holotype (male), CAS Type No. 4476; "Pine Crest [sic], Calif. / July Johnson"; "Type"; "Agulla occidentis Carpenter / det. F. M. Carpenter"; "Agulla herbsti / Esb.-Pet. / U. Aspöck det. 1967". Separate pin with genitalia vial, labels read "Agulla herbsti: Esb.-Pet."; "part of Holotype / Agulla / occidentis / Carpenter".

Allotype (female); "Pine Crest [sic], Calif. / Aug. 15 Johnson"; "ALLOTYPE"; "Agulla occidentis Carpenter / det. F. M. Carpenter"; "O. S. C. TYPE".

Paratypes, 3 (1 California, 2 Oregon).

Remarks: The holotype and allotype are on permanent deposit from Oregon State University.

Agulla singularis Carpenter.

1936, Proc. Am. Acad. Arts Sci., vol. 71, no. 2, p. 132, pl. 2 (fig. 23).

Holotype (male), CAS Type No. 4477; "Banning Cal / V-29-28"; "Pres by / EC Van Dyke / Collector"; "From Coll. / Calif. Acad. Sci."; "TYPE"; "Agulla singularis Carp. / det. F. M. Carpenter"; "H. & U. Aspöck vid. 1970". Separate pin with genitalia capsule, labels read "Banning, CAL. / V-29-28 / E. C. Van Dyke / collector"; "Dissection of / TYPE, Agulla / singularis / Carpenter".

Agulla unicolor Carpenter.

1936, Proc. Am. Acad. Arts Sci., vol. 71, no. 2, pp. 121–123, pl. 1 (fig. 1).

Paratypes, 60 (39 California, 8 Nevada, 10 Oregon, 3 Utah).

Raphidia arizonica Banks.

1911, Trans. Am. Entomol. Soc., vol. 37, no. 4, p. 338, pl. 11 (fig. 8).

Neallotype (female), CAS Type No. 4501; "Mono Lk / Cal. / VI-17-'17"; "Donor / C. L. Fox / Collector"; "ALLOTYPE"; "Agulla arizonica (Banks) / det. F. M. Carpenter".

Remarks: Carpenter (1936:118–119) designated the neallotype.

Raphidia (*Agulla*) *arnaudi* Aspöck.

1973, Pol. Pismo Entomol., vol. 43, no. 2, p. 234.

Holotype (male), CAS Type No. 12458; "MEX: B. Calif., Sierra / San Pedro Martir / P. H. Arnaud, Jr."; "Trail, La / Joya to La Zanja / VI-10-1953"; "medium with genitalia / water-soluble"; "Holotypus / Raphidia / (Agulla) / arnaudi / U. Aspöck 1973".

Allotype (female); same data as holotype, except that allotype label reads: "PARATYPUS / (ALLOTYPUS) [FE] / R. (Agulla) / arnaudi"; "U. Aspöck 1973".

Remarks: Abdomens of the holotype and allotype are mounted on cards attached to the respective pins.

Raphidia (*Agulla*) *barri* Aspöck.

1973, Pol. Pismo Entomol., vol. 43, no. 2, p. 238.

Holotype (male), CAS Type No. 12698; "Westgard Pass / Inyo Co. / CALIF. VI-11-69"; "beating / Pinyon Pine"; "W. F. Barr / Collector"; "Holotypus [MA] / R. (Agulla) barri / U. Aspöck 1973". Separate pin with genitalia vial; label reads "genital segments of / R (Agulla) barri / Holotypus [MA] ".

Paratypes, 6 (5 California, 1 Nevada).

Raphidia (*Aliaberaphidia*) *tenochtitlana* Aspöck and Aspöck.

1978, Z. Arbeitsgem. Österr. Entomol., vol. 30, nos. 1/2, p. 21.

Holotype (male), CAS Type No. 13336; "MEXICO: BAJA CALI- / FORNIA SUR: Sierra La / Laguna, 1770–1850 m / 30-VIII-77 / E. Fisher, R. Westcott / Calif. Acad. Sci. Coll."; "HOLOTYPUS [MA] / Raphidia (Aliaberaphidia) / tenochtitlana / Aspöck et Aspöck 1978"; "2". Separate pin with genital capsule label reads "2"; "HOLOTYPUS"; "Raphidia / tenochtitlana / [MA] / H. et U. Aspöck det 19".

Paratypes, 7 (Baja California Sur).

NEUROPTERA

Berothidae

Hemerobius hamatus Walker.

1853, List of Specimens of Neuropterous Insects in the Collection of the British Museum. Part II. (Sialidae — Nemopterides), p. 278.

Neallotype (female), CAS Type No. 5592; "Tampa Fla / May 2, '08 / Vau [sic] Duzee"; "Pres. by / E. P. Van Duzee / Collector"; "allotype"; "Lomamyia / hamata Walker / det. F. M. Carpenter".

Remarks: Carpenter (1940:265–266) designated the neallotype.

Lomamyia latipennis Carpenter.

1940, Proc. Am. Acad. Arts Sci., vol. 74, no. 7, pp. 262–263, fig. 64A–D.

Holotype (male), CAS Type No. 5590; "Phoenix Lk. / Marin Co Cal. / VII-4-1927"; "H. H. Keifer / Collector / Type"; "Lomamyia / latipennis Carp. / det. F. M. Carpenter".

Allotype (female); "Mt. Tamalpais / Marin Co. Cal. / V-23-09"; "Coll. by / E. C. Van Dyke"; "From Coll. / Calif. Acad. Sci."; "allotype"; "Lomamyia / latipennis Carp. / det. F. M. Carpenter".

Manselliberotha neuropterologorum Aspöck and Aspöck.

1988, Z. Arbeitsgem. Österr. Entomol., vol. 40, nos. 1/2, pp. 4–7, figs. 1–21.

Paratype, 1 (Namibia).

Chrysopidae

Leptochrysa prisca Adams and Penny.

1992, Pan-Pac. Entomol., vol. 68, no. 3, pp. 219–221, figs. 10–14.

Holotype (female), CAS Type No. 16743; "PERU: Dept. Amazonas / 18 km N. of Puente / Ingenio, KM 320 Alt. / 1750 m. 9-X-1964 / P.C. Hutchison & / J. K. Wright"; "Collected on / *Baccharis latifolia* / #6830"; "HOLOTYPE / Leptochrysa / prisca / Adams & Penny". Gut contents in vial of glycerin on pin; label reads "Leptochrysa / prisca / Adams - Penny / gut contents". Genitalia in vial of glycerin on pin; label reads "Leptochrysa / prisca / A & P / [MA] genitalia".

Leucochrysa serrula Adams.

1979, Folia Entomol. Mex., no. 41, pp. 97–101, figs. 1–7.

Holotype (male), CAS Type No. 15126; "3 mi. east / Carapan / Mich MEX. / VII 10 1963"; "F. D. Parker / L. A. Stange / Collectors"; "HOLOTYPE / Leucochrysa / serrula / [MA] Adams / det. P. Adams '77".

Meleoma antennensis Tauber.

1969, Univ. Calif. Publ. Entomol., vol. 58, p. 20, figs. 4, 18, pl. 2b.

Holotype (male), CAS Type No. 10005; "San Christobal, / 9 mi. E., Chiapas / MEX., VII-30-57"; "AT / light"; "J. A. Chemsak / B. J. Donnells / Collectors"; "Meleoma / antennensis Tauber / det. C. Tauber '68 / HOLOTYPE".

Remarks: The holotype is on indefinite loan from the University of California, Berkeley.

Meleoma powelli Tauber.

1969, Univ. Calif. Publ. Entomol., vol. 58, pp. 19–20, figs. 4, 17, pl. 2a.

Holotype (male), CAS Type No. 10006; "MEX: Dgo., El / Salto, 3 mi. W. / 9000' VII-23-64"; "Quercus / omissa"; "J. Powell / Collector"; "Meleoma / powelli Tauber / det. C. Tauber '68 / HOLOTYPE".

Allotype (female); "MEX: Dgo., El / Salto, 3 mi. W. / 9000′ VII-23-64"; "J. A. Chemsak & / J. Powell Black / & White lights"; "Meleoma / powelli Tauber / det. C. Tauber '68 / ALLOTYPE".

Remarks: These types are on indefinite loan from the University of California, Berkeley.

Nodita oenops Adams.

1987, Neuropt. Int., vol. 4, no. 4, pp. 290–291, figs. 2, 19–24.

Holotype (male), CAS Type No. 16027; "May 2, 1976 3 / Leon, Nica / W. Barclay "; "HOLOTYPE / Nodita [MA] / oenops / P. Adams".

Allotype (female); "4/20/86 / Leon, Nica / W. Barclay"; "ALLOTYPE / Nodita / oenops [FE] / P. Adams".

Pimachrysa albicostales Adams.

1967, Bull. Mus. Comp. Zool., Harvard Univ., vol. 135, no. 4, pp. 226–227, figs. 27, 28.

Holotype (male), CAS Type No. 9988; "MEX: B. Calif. / 22 mi. N. of / Punta Prieta / 9-XII-1958"; "H. B. Leech / Collector"; [blank label with yellow stripe]; "PIMACHRYSA / ALBICOSTALES / ADAMS / [MA] TYPE / Det. P. Adams"; "13". Genitalia on separate pin with label "13".

Pimachrysa fusca Adams.

1967, Bull. Mus. Comp. Zool., Harvard Univ., vol. 135, no. 4, p. 227, figs. 1, 7, 11–13, 21, 24.

Holotype (male), CAS Type No. 9989; "CALIF., #1 / Joshua Tree N. M., / L. Covington Flat"; "E. L. Sleeper / Collr."; "PIMACHRYSA / FUSCA / ADAMS / HOLOTYPE / Det. P. Adams"; "14". Genitalia on separate pin with label "14".

Pimachrysa nigra Adams.

1967, Bull. Mus. Comp. Zool., Harvard Univ., vol. 135, no. 4, pp. 228–229, figs. 6, 14–16, 26, 34.

Holotype (male), CAS Type No. 9990; "Gavilan / Cal. Mr. 19. 36"; "on Ceanothus / crassifolius"; "Timberlake / Coll."; "Nothochrysa / californica / Inif. det. Banks"; "PIMACHRYSA / NIGRA / ADAMS / HOLOTYPE / Det. P. Adams"; "10". Genitalia on separate pin with label "10".

Coniopterygidae

Aleuropteryx cupressi Meinander.

1974, Entomol. Scand., vol. 5, nos. 3/4, p. 218, fig. 1A–H.

Holotype (male), CAS Type No. 12352 (in alcohol); "USA. Cal. Marin Co. / 1961-05-02 emgd from / Cupressus goveniana / J. Powell"; "HOLOTYPUS / Aleuropteryx / cupressi; sp.n. [MA] / det. Meinander 1973"; "Wings slide UCA A3". Slide UCA A3 left label "USA Cal. / Marin Co / emgd 1961-05-02 / ex Cupressus goveniana / J. Powell"; right label "Aleuropteryx / cupressi [MA] / Meinander / HOLOTYPUS / det. 1973 / M Meinander".

Remarks: The holotype is on indefinite loan from the University of California, Berkeley.

Aleuropteryx longipennis Meinander.

1974, Entomol. Scand., vol. 5, nos. 3/4, pp. 218–219, fig. 2A–D.

Holotype (male), CAS Type No. 12353; "Mex: Baja Calif. / Norte, 1 mi. N. / Meling Ranch, 2100' / III-17-1972, J. Doyen / & J. Powell, at light"; "Wings slide UCA A4"; "HOLOTYPUS / Aleuropteryx [MA] / longipennis sp.n. / det. Meinander 1973". Slide UCA A4 left label "Mexico Baja Calif / Norte 1 mi N / Meling Ranch / 2100′ 1972-03-17 / J. Doyen & J. Powell"; right label "Aleuropteryx / longipennis [MA] / sp.n. / det. 1973 / M Meinander".

Remarks: The holotype is on indefinite loan from the University of California, Berkeley. The body is stored in glycerin in a genitalia capsule on pin.

Aleuropteryx maculipennis Meinander.

1972, Acta Zool. Fenn., no. 136, p. 45, fig. 13A–D.

Holotype (male), CAS Type No. 11915; "CAL.: Kern Co / 19 mi. NNE. Mojave / IV-14-1962"; "C. MacNeill, D. / Rentz & R. Brown / Collectors"; "Genitalia CAS slide 13 / Wings —″— 38"; "Aleuropteryx / maculipennis n.sp. [MA] / det. Meinander 1969". Slide 38 left label "Cal. Kern Co. / 19 mi NNE Mojave / IV-14-1962 / C. MacNeill, D. Rentz / & R. Brown coll. / Body pinned / genitalia slide 13 / CAS slide 38"; right label "Aleuropteryx / maculipennis / n.sp. [MA] / HOLOTYPUS / det. 1969 / Martin Meinander". Slide 13 left label "CAS 13 / Cal. Kern Co / 19 mi NNE Mojave / IV-14-62 / MacNeill, Rentz / Brown / body pinned"; right label "Aleuropteryx / maculipennis / n.sp. / HOLOTYPUS [MA] / det. 1966–1969 / M Meinander".

Aleuropteryx punctata Meinander.

1974, Entomol. Scand., vol. 5, nos. 3/4, p. 220, fig. 3A–H.

Holotype (male), CAS Type No. 12193 (in alcohol); "20 mi. W. Rosario, / Sin., Mex. I-30-64 / at night; E. Schlinger / black light"; "[MA] wings slide 5"; "HOLOTYPE / Aleuropteryx / punctata Mein [MA] 2 [MA][MA] / det. Meinander 1973". Slide UCR5 left label "Mexico Sin. / 20 mi W Rosario / 1964-01-30 / E. Schlinger / Slide UCR5"; right label "Aleuropteryx / punctata / Meinander [MA] / HOLOTYPE / det. 1973 / M Meinander".

Remarks: The holotype is on permanent deposit from the University of California, Riverside.

Aleuropteryx simillima Meinander.

1972, Acta Zool. Fenn., no. 136, pp. 46–47, fig. 14A–E.

Holotype (male), CAS Type No. 11916; "MEX.: Baja Calif. / Norte, San Felipe / 7-III-1963 / P. H. Arnaud, Jr."; "Genit. slide CAS 20 / wings —″— 39"; "Aleuropteryx / simillissimus n.sp. [MA] / det. Meinander 1969 / HOLOTYPUS". Slide 20 left label "CAS 20 / Mex: Baja Calif / Norte San Felipe / 7-III-1963 / P. H. Arnaud Jr / Body pinned / Wings slide 39"; right label "Aleuropteryx / simillissima / n.sp. / HOLOTYPUS [MA] / det. 1966–1969 / M Meinander". Slide 39 left label "Mexico / Baja Calif. / Norte San Felipe / 7.III.1963 / P. H. Arnaud Jr. / Body pinned / genit. slide 20 / CAS Slide 39"; right label "Aleuropteryx / simillissima / n.sp. / HOLOTYPUS / det. 1969 / Martin Meinander".

Remarks: The slide labels read "simillissima" or "simillisimus" rather than the published spelling.

Aleuropteryx unicolor Meinander.

1972, Acta Zool. Fenn., no. 136, pp. 48–49, fig. 16A–F.

Holotype (male), CAS Type No. 11917; "Boyd Desert Res. Center / 4 mi s. Palm Desert, Riv. / Co., Calif. IV-11-63"; "W. A. Steffan / Collector"; "Aleuropteryx / unicolor n.sp. [MA] / det. Meinander 1969 / wings slide 19 Body sl. 20". Slide 20 left label "Calif Boyd Desert / Res. Center / 4 mi s Palm Desert / Riv. Co. IV-11-63 / W. A. Steffan / wings slide 19 / UCal Slide 20"; right label "Aleuropteryx / unicolor n.sp. / [MA] / HOLOTYPUS / det. 1969 / M Meinander". Slide 19 with same data as slide 20, except for slide number.

Remarks: The holotype is on indefinite loan from the University of California, Berkeley.

Coniocompsa smithersi Meinander.

1972, Acta Zool. Fenn., no. 136, pp. 99–101, fig. 51A–G.

Holotype (male), CAS Type No. 11918 (in alcohol); "KENYA: 28 mi. NW. / Nairobi 6450 ft / 17-XII-1969 / M. E. Irwin & / E. S. Ross"; "genitalia / & wings / mounted on / slide"; "wings CAS slide 59, genit. 58"; "Coniocompsa / smithersi n.sp. [MA] / det. Meinander 1971 / HOLOTYPUS". Slide 58 left label "Kenya / 28 mi W [sic] Nairobi / 6450 ft. / 17-XII-1969 / M. E. Irwin & / E. S. Ross / CAS slide 58"; right label "Coniocompsa / smithersi n.sp. / [MA] / HOLOTYPUS / det. 1971 / M Meinander". Slide 59 with same data as slide 58, except for slide number.

Coniopteryx (*Coniopteryx*) *californica* Meinander.

1974, Entomol. Scand., vol. 5, nos. 3/4, pp. 225–226, fig. 9A–G.

Holotype (male), CAS Type No. 12194 (in alcohol); "Oso Flaco Lake / San Luis Obispo Co. / Cal. VIII-5-62 / E. Schlinger"; "HOLOTYPUS / Coniopteryx [MA] / californica Meinander / det. Meinander 1973".

Coniopteryx (*Scotoconiopteryx*) *chilensis* Meinander.

1990, Acta Zool. Fenn., no. 189, pp. 47–48, fig. 16A–D.

Holotype (male), CAS Type No. 16102 (in alcohol); "Chile: Chillan / Las Trancas / 1200 / 17–20-XII-83 / Luis Peña"; "Coniopteryx / chilensis Meinander [MA] / det. Meinander 1987 / HOLOTYPUS".

Coniopteryx (*Coniopteryx*) *goniocera* Meinander.

1972, Acta Zool. Fenn., no. 136, pp. 264–265, fig. 169A–F.

Holotype (male), CAS Type No. 11919 (in alcohol); "S. INDIA / 10 mi. SW. / Gudiyattam / 350 m IV-3-62"; "Collectors: / E. S. Ross / D. Q. Cavagnaro"; "genitalia / mounted on / slide"; "genit. slide CAS 29"; "[MA] placed in / general / collection"; "HOLOTYPE [MA] / Coniopteryx / goniocera n.sp. / det. Meinander 1971". Slide 29 left label "Coniopteryx / goniocera n.sp. / HOLOTYPUS [MA] / det. 1971 / M Meinander"; right label "S. India / 10 mi SW / Gudiyattam / 350 m IV.3.62 / Ross & Cavagnaro / CAS 29".

Coniopteryx (*Coniopteryx*) *mexicana* Meinander.

1974, Entomol. Scand., vol. 5, nos. 3/4, pp. 226–227, fig. 10A–E.

Holotype (male), CAS Type No. 12195 (in alcohol); "20 mi. E. Villa Union / Sin. Mexico / I-31-64 / Schlinger & Irwin / at black light"; "HOLOTYPUS / Coniopteryx / mexicana sp.n. [MA] / det. Meinander 1973".

Coniopteryx (*Coniopteryx*) *minuta* Meinander.

1972, Acta Zool. Fenn., no. 136, pp. 259–260, fig. 165A–F.

Holotype (male), CAS Type No. 11920; "Morro Bay, 8 mi E / S. L. O. Co., / Calif. V-2-62"; "Adenostoma / sp. fasciculatum"; "C. A. Toschi / Collector"; "genitalia UCal Slide 10"; "HOLOTYPUS / Coniopteryx / minuta n.sp. [MA] / det. Meinander 1971". Slide 10 left label "USA. Calif. / S. L. O. Co. / Morro Bay

/ 2.V.1962 / C. A. Toschi / UCal slide 10"; right label "Coniopteryx / minuta n.sp. [MA] / HOLOTYPE / det. 1971 / M Meinander".

Remarks: The label data "8 mi E" were not transcribed to the slide label. The holotype is on indefinite loan from the University of California, Berkeley.

Coniopteryx (*Coniopteryx*) *simplex* Meinander.

1974, Entomol. Scand., vol. 5, nos. 3/4, p. 228, fig. 11A–F.

Holotype (male), CAS Type No. 12354; "Pino Grande, SW / of Lake Edson, / El Dorado Co. / Calif. VII-8-67"; "W. J. Turner / Collector"; "HOLOTYPUS / Coniopteryx / simplex sp.n. [MA] / det. Meinander 1974".

Remarks: The holotype is on indefinite loan from the University of California, Berkeley. Body is stored in glycerin in a genitalia capsule on pin.

Conwentzia californica Meinander.

1972, Acta Zool. Fenn., no. 136, pp. 297–298, fig. 192A–E.

Holotype (male), CAS Type No. 11921; "CAL. Lee Vining / Campgd. Mono Co. / W. of Mono Lk. / 1-VII-61 / D. C. RENTZ / COLLECTOR"; "CAS slide 56"; "HOLOTYPUS / Conwentzia / californica n.sp. [MA] / det. Meinander 1970". Slide 56 left label "USA Calif / Mono Co / Lee Vining Campgd / W of Mono Lk. / 1.VII.1961 / D. C. Rentz / CAS Slide 56"; right label "Conwentzia / californica n.sp. / HOLOTYPUS [MA] / det. 1970 / M Meinander".

Helicoconis (*Helicoconis*) *californica* Meinander.

1972, Acta Zool. Fenn., no. 136, p. 119, fig. 61A–E.

Holotype (male), CAS Type No. 11922 (in alcohol); "Calif: Mono Co. / Tom's Place, 1 mi. / SW. VIII-10-1963"; "M. J. Tauber / C. A. Toschi / Collectors"; "Genit. UCal Slide 18"; "Helicoconis / californica n.sp. [MA] / det. Meinander 1969 / HOLOTYPE". Slide 18 left label "USA. Calif. Mono Co. / Tom's Place - 1 mi SW / VIII-10-1963 / M. J. Tauber / C. A. Toschi / UCal slide 18"; right label "Helicoconis / californica / n.sp. / HOLOTYPE [MA] / det. 1969 / M Meinander".

Remarks: The holotype is on indefinite loan from the University of California, Berkeley.

Helicoconis (*Helicoconis*) *similis* Meinander.

1972, Acta Zool. Fenn., no. 136, p. 124, fig. 65A–C.

Holotype (male), CAS Type No. 11923; "CANADA: B. COL. / Top of Moyie Mtn. / elev. 6868 ft. / East Kootenays / 16-VII-1959"; "H. B. Leech / Collector"; "slides CAS 16–17"; "Helicoconis / similis n.sp. / det. Meinander 1969 / HOLOTYPUS". Slide 16 left label "CAS 16 / Canada B. Col. / Top of Moyle [sic] Mtn / elev 6868 ft. / East Kootenaya [sic] / Genit. sl. 17 / Body pinned"; right label "Helicoconis / similis n.sp. [MA] / HOLOTYPUS / DET. 1969 / M Meinander". Slide 17 has same label data as slide 16, except for slide number.

Remarks: Right slide labels overlie identification labels for *Helicoconis eglini* Ohm.

Heteroconis bifurcata Meinander.

1990, Acta Zool. Fenn., no. 189, pp. 11–12, fig. 1A–E.

Holotype (male), CAS Type No. 16602 (in alcohol); "PAPUA NEW GUINEA: / Madang Province / Sapi Forest Reserve / (30 km W Madang) / 5°12′S, 145°30′E / 19 February 1987 / Norman D. Penny clr"; "Heteroconis / bifurcata Mein [MA] / det. Meinander 1987 / HOLOTYPUS"; "One pair of / wings on slide". Slide left label "Papua New Guinea / Madang Prov. / Sapi Forest Reserve / 30 km W Madang / 5°12′S 145°30′E / 19 Febr 1987 / Norman D. Penny clr"; right label "Heteroconis / bifurcata / Meinander sp.n. [MA] / HOLOTYPUS".

Heteroconis curvata Meinander.

1990, Acta Zool. Fenn., no. 189, pp. 12–14, fig. 2A–I.

Holotype (male), CAS Type No. 16603 (in alcohol); "PAPUA NEW GUINEA: / Madang Province, / Nagada Harbor / 8 km N Madang / 5°09′S 145°48′E / 8 February 1987 / Norman D. Penny"; "Heteroconis / curvata Meinander [MA] / det. Meinander 1987 / HOLOTYPUS"; "One pair of / wings on slide"; "genit. in micro- / vial". Slide left label "Papua New Guinea / Madang Province / Nagada Harbor / 8 km N Madang / 5°09′S 145°48′E / 8 Febr 1987 / N D Penny"; right label "Heteroconis / curvata

/ Meinander [MA] / HOLOTYPUS".

Heteroconis madangensis Meinander.
1990, Acta Zool. Fenn., no. 189, pp. 14–16, fig. 3A–D.
Holotype (male), CAS Type No. 16604 (in alcohol); "PAPUA NEW GUINEA: / Madang Province / Gogol River (12 km / southwest Madang) / 5°20′S 145°42′E / 25 February 1987 / Norman D. Penny"; "Heteroconis / madangensis / sp.n. [MA] / det. Meinander 1987 / HOLOTYPUS". Wing slide left label "Papua New Guinea / Madang Prov. / Gogol River / 25.II.1987 / N D Penny"; right label "Heteroconis / madangensis / sp.n. [MA] / HOLOTYPUS".

Heteroconis pennyi Meinander.
1990, Acta Zool. Fenn., no. 189, p. 18, fig. 6A–C.
Holotype (female), CAS Type No. 16605 (in alcohol); "PAPUA NEW GUINEA: / Madang Province / Sapi Forest Reserve / (30 km W Madang) / 5°12′S 145°30′E / 14 February 1987 / Norman D. Penny clr"; "Heteroconis / pennyi Meinander - [MA] / det. Meinander 1987 / HOLOTYPE"; "One pair of / wings on slide". Slide left label "Papua New Guinea / Madang Province / Nagada Harbor / 8 km N Madang / 5°09′S 145°48′E / 8 Febr 1987 N D Penny"; right label "Heteroconis / pennyi / Meinander [MA] / HOLOTYPUS".
Remarks: Erroneus locality data were transcribed to the slide label, perhaps from the holotype of *Heteroconis curvata*.

Heteroconis planifrontalis Meinander.
1969, Not. Entomol., vol. 49, no. 2, pp. 66–68, figs. 46–50.
Holotype (male), CAS Type No. 11924 (in alcohol); "Australia, N. T. / 5 mi SW. / Katherine / 75 m X-22-62"; "Collectors / E. S. Ross / D. Q. Cavagnaro"; "genitalia & / wings / mounted on / slide"; "Wings CAS slide 41 / Genitalia —″— 42"; "HOLOTYPE / Heteroconis / planifrontalis n.sp. [MA] / det Meinander 1969". Slide 42 left label "Australia N. T. / 5 mi SW / Katherine / 75 m / X-22-1962"; "body in alcohol / CAS slide 42"; right label "Heteroconis / planifrontalis / n.sp. [MA] / HOLOTYPE / det. 1969 Meinander". Slide 41 has same label data as slide 42, except for slide number.

Incasemidalis meinanderi Adams.
1973, Pan-Pac. Entomol., vol. 49, no. 3, pp. 253–254, fig. 3a-g.
Holotype (male), CAS Type No. 12011 (in alcohol); "EL CALABOZO, ILLAPEL / COQUIMBO, CHILE"; "1700 m 21/23-XI-59 / L. E. PEÑA, COL."; "Incasemidalis / meinanderi / [MA] Adams / HOLOTYPE".
Remarks: Stopper has fallen out of genitalia vial, and genitalia are probably loose in vial.

Neoconis bifurcata Meinander.
1974, Entomol. Scand., vol. 5, nos. 3/4, p. 223, fig. 7a-d.
Holotype (male), CAS Type No. 12355; "Ariz: Cochise Co. / Stewart Camp / 1 Mi. S. Portal / VIII-12/15-1971"; "J. Doyen Coll. / Ex. Malaise trap"; "HOLOTYPUS / Neoconis [MA] / bifurcata sp.n. / det. Meinander 1973".
Remarks: The holotype is on indefinite loan from the University of California, Berkeley. Body is stored in glycerin in a genitalia capsule on a pin.

Neosemidalis (*Neosemidalis*) *monstruosa* Meinander.
1972, Acta Zool. Fenn., no. 136, pp. 180–181, fig. 104A–F.
Holotype (male), CAS Type No. 11925 (in alcohol); "QUEENSLAND: Canoo- / na, 75 m. 20-XI-62 / E. S. Ross & / D. Q. Cavagnaro"; "Genit CAS Slide 46 / Wings —″— 47"; "genitalia / & wings / mounted on / slide"; "HOLOTYPE / Neosemidalis / monstruosa n.sp. / det. Meinander 1970". Slide 46 left label "Queensland / Canoona 75 m / 20-XI-62 / E. S. Ross / D. Q. Cavagnaro / wings slide 47 / Body in alcohol / CAS slide 46"; right label "Neosemidalis / monstruosa / n.sp. / HOLOTYPE / det. Meinander / 1969". Slide 47 has same label data as slide 46, except for slide number.

Neosemidalis (*Neosemidalis*) *nervalis* Meinander.
1972, Acta Zool. Fenn., no. 136, p. 181, figs. 8B, 105A–G.
Holotype (male), CAS Type No. 11926 (in alcohol); "QUEENSLAND: 17 mi. / W. Monto

500 m / 21-XI-1962 / E. S. Ross & / D. Q. Cavagnaro"; "Genit. CAS slide 48 / wings —"— 49"; "Neosemidalis / detrita McL 2 [males] / det. Meinander 1970"; "HOLOTYPE / Neosemidalis / nervalis n.sp. [MA] / det. Meinander 1970". Slide 48 left label "Queensland / 17 mi W Monto / 500 m. 21-XI-1962 / E. S. Ross / D. Q. Cavagnaro / wings slide 49 / Body in alcohol / CAS slide 48"; right label "Neosemidalis / nervalis n.sp. / HOLOTYPE [MA] / det. 1970 / M Meinander". Slide 49 has same label data as slide 48, except for slide number.

Neosemidalis (*Neosemidalis*) *serricornis* Meinander.

1972, Acta Zool. Fenn., no. 136, pp. 183–184, fig. 107A–F.

Holotype (male), CAS Type No. 11927 (in alcohol); "Australia, N. T. / Edith Falls / nr. Katherine / 110 m X-25-62 / Collectors / E. S. Ross / D. Q. Cavagnaro"; "Genitalia CAS slide 50 / Wings —"— 51"; "genitalia & / wing / mounted on / slide"; "HOLOTYPE / Neosemidalis / serricornis n.sp. [MA] / det. Meinander 1970". Slide 50 left label "Australia N. T. / Edith Falls / nr. Katherine / 110 m X-25-62 / Ross & Cavagnaro / wings slide 11 / Body in alcohol / CAS slide 50"; right label "Neosemidalis / serricornis n.sp. / HOLOTYPE [MA] / det. 1969 / M Meinander". Slide 51 has same label data as slide 50, except for slide number and cross reference genitalia slide 10.

Remarks: Slide number was changed by Meinander from 10 to 50 and 11 to 51 with body and on slides, but note as to cross reference numbers on same slides were not changed.

Pampoconis angustipennis Meinander.

1990, Acta Zool. Fenn., no. 189, pp. 30–31, fig. 10A–E.

Holotype (male), CAS Type No. 16103 (in alcohol); "Chile: Chillán / Las Trancas 1200 m / 17–20-XII-1983 / Luis Peña"; "Pampoconis / angustipennis sp.n. [MA] / det. Meinander 1987 / HOLOTYPUS"; "one pair of / wings on slide". Slide left label "Chile Chillán / Las Trancas 1200 m / 17–20-XII-1983 / Luis Peña"; right label "Pampoconis / angustipennis / Meinander [MA] / sp.n. / HOLOTYPUS".

Pampoconis punctipennis Meinander.

1973, Not. Entomol., vol. 53, no. 1, p. 25.

Lectotype (male), CAS Type No. 12012 (in alcohol); "CHILE - Santiago / Rio Colorado / X-1958 / L. E. Peña, leg."; "Rio Colorado, Santiago / CHILE X-1958"; "L. E. Pena, leg."; "Pampoconis / punctipennis / Adams / 72 / HOLOTYPE [MA]"; "Pampoconis / punctipennis / Meinander 1973 / LECTOTYPE".

Remarks: This species was originally to be described by Adams. Meinander was given an advance copy of the manuscript and used the name to compare it with a new species he was describing. Unfortunately, the original description had not yet been published (Adams, 1973), making Meinander the inadvertent author of this species. Adams (1974:324) pointed out this error and designated the lectotype.

Pampoconis uncinata Meinander.

1973, Not. Entomol., vol. 53, no. 1, p. 25.

Lectotype (male), CAS Type No. 12013 (in alcohol); "El Radal, Talca / Chile – 900 m. / 28/30-XI-57 / L. E. Pena / *Pampoconis*"; "Pampoconis / uncinatus / Adams / Holotype [MA] / and allotype / [FE]"; "Pampoconis / uncinatus [MA] / Meinander 1973 / LECTOTYPE".

Remarks: This species was originally to be described by Adams. Meinander was given an advance copy of the manuscript and used the name to compare it with a new species he was describing. Unfortunately, the original description had not yet been published (Adams, 1973), making Meinander the inadvertent author of this species. Adams (1974:324) pointed out this error and designated the lectotype.

Semidalis arnaudi Meinander.

1972, Acta Zool. Fenn., no. 136, p. 328, fig. 210A–D.

Holotype (male), CAS Type No. 11928; "MEX.: Sonora / Alamos / 27-II-1963 / P. H. Arnaud, Jr."; "slide CAS 23"; "HOLOTYPE / Semidalis / arnaudi [MA] / det. Meinander 1970". Slide 23 left label "CAS 23 / Mexico Sonora / Alamos / 27.2.1963 / P. H. Arnaud, Jr. / body pinned"; right label "Semidalis / arnaudi n.sp. / HOLOTYPE [MA] / det. 1966 / M Meinander".

Semidalis deserta Meinander.

1974, Entomol. Scand., vol. 5, nos. 3/4, pp. 230–231, fig. 12A–D.

Holotype (male), CAS Type No. 12196; "P. L. Boyd Des. Res. Center / 3.5 mi. S. Palm Desert Riv / Co. Calif. VI-24–26-1969 / Malaise; Marker #57 / Saul Frommer & B. Worley"; "UCR. ENT. MUS. / Specimen # / 19356"; "Genitalia Slide UCR 14 "; "Semidalis / deserta sp.n. [MA] / det. Meinander 1973"; "Holotypus / Semidalis / deserta / Meinander". Slide UCR 14 left label "U. S. A. Cal. Riv. Co / P.L. Boyd Des. Res. C. / 1969-06-24–26 / 19356 / S. Frommer. B. Worley / Malais [sic] / Marker #57"; right label "Semidalis / deserta sp.n. / Meinand. [MA] / HOLOTYPUS / det. 1974 / M Meinander".

Remarks: The holotype is on permanent deposit from the University of California, Riverside.

Semidalis frommeri Meinander.

1974, Entomol. Scand., vol. 5, nos. 3/4, pp. 231–232, fig. 13A–E.

Holotype (male), CAS Type No. 12197; "Deep Cyn., Riv. Co. / Cal.; VII-24-64 / M. Irwin; at light"; "UCR. ENT. MUS. / Specimen # / 9418"; "wings slide UCR 30"; "HOLOTYPUS / Semidalis / frommeri sp.n. [MA] / det. Meinander 1973". Slide UCR 30 left label "USA Cal / Riverside Co. / Deep Cyn. / 1964-07-22 / M. Irwin / Spec. # 9418"; right label "Semidalis [MA] / frommeri sp.n. / HOLOTYPUS / det. 1973: / M Meinander".

Remarks: The holotype is on permanent deposit from the University of California, Riverside.

Semidalis mexicana Meinander.

1972, Acta Zool. Fenn., no. 136, p. 334, fig. 216A–D.

Holotype (male), CAS Type No. 11929; "MEX.: Sonora / Alamos / 25-II-63 / P. H. Arnaud, Jr."; "slide CAS 19"; "HOLOTYPE / Semidalis / mexicana [MA] / det. Meinander 1970". Slide 19 left label "CAS 19 / Mexico Sonora / Alamos / 25.2.1963 / P. H. Arnaud, Jr. / body pinned"; right label "Semidalis / mexicana n.sp. / HOLOTYPE [MA] / det. 1966 / M Meinander".

Semidalis peruviensis Meinander.

1974, Not. Entomol., vol. 54, no. 4, p. 105, fig. 4J-M.

Holotype (male), CAS Type No. 12174 (in alcohol); "PERU: / Huanuco / IX-16-1954"; "E. I. Schlinger / & E. S. Ross / collectors"; "Semidalis / peruviensis sp.n. [MA] / det. Meinander 1974 / HOLOTYPUS".

Semidalis sonorana Meinander.

1975, Not. Entomol., vol. 55, no. 1, p. 32, fig. 3B, E, G.

Holotype (male), CAS Type No. 12298; "Alamos / Sonora"; "Erythroxylin / mexicanum"; "Timberlake / Coll May 13, 51"; "HOLOTYPUS / Semidalis / sonorana sp.n. [MA] / det. Meinander 1974".

Remarks: The holotype is on permanent deposit from the University of California, Riverside.

Spiloconis fijiensis Meinander.

1990, Acta Zool. Fenn., no. 189, p. 26, fig. 8A–F.

Holotype (male), CAS Type No. 16104 (in alcohol); "Fiji: 10 km east / Sigatoka, mangrove / & adjacent forest / 1 February 1987 / Norman D. Penny"; "Spiloconis / fijiensis Meinander [MA] / det. Meinander 1987 / HOLOTYPUS"; "One pair of / wings on slide". Slide left label "FIJI 10 km E / Sigatoka, mangrove / & adjacent forest / 1 Febr. 1987 / Norman D. Penny"; right label "Spiloconis / fijiensis / Meinander [MA] / HOLOTYPUS".

Dilaridae

Nallachius parkeri Penny.

1994, Pan-Pac. Entomol., vol. 70, no. 4, pp. 309–312, figs. 1–4.

Paratype, 1 (Costa Rica).

Hemerobiidae

Hemerobius elongatus Monserrat.

1990, Advances in Neuropterology, pp. 85, 87, figs. 50–55.

Paratype, 1 (Mexico).

Hemerobius nigrans Carpenter.

1940, Proc. Am. Acad. Arts Sci., vol. 74, no. 7, p. 207, fig. 7A–C.

Paratype, 1 (Wyoming).

Hemerobius ovalis Carpenter.

1940, Proc. Am. Acad. Arts Sci., vol. 74, no. 7, pp. 205–206, fig. 5A, B, pl. 1 (fig. 5).

Paratypes, 4 (1 British Columbia, 2 California, 1 Washington).

Kimminsia fumata Carpenter.

1940, Proc. Am. Acad. Arts Sci., vol. 74, no. 7, p. 225, fig. 24A–D.

Holotype (male), CAS Type No. 5588; "Longs Pk. Inn / Col. 9000 ft. / VII-13-1926"; "Pres. by / EC Van Dyke / Collector"; "Type"; "Kimminsia / fumata Carp. / det. F. M. Carpenter"; "genitalia / on slide". Slide with label "Kimminsia / fumata / CARP. / TYPE / [MA] GENITALIA / C. A. S. # 5588".

Allotype (female), CAS Type No. 5589; "Longs Pk. Inn / Col. 9000 ft. / VII-12–1926"; "Presented by / E. C. Van Dyke / Collector"; "allotype"; "Kimminsia / fumata Carp. / det. F. M. Carpenter".

Paratype, 1 (Colorado).

Kimminsia involuta Carpenter.

1940, Proc. Am. Acad. Arts Sci., vol. 74, no. 7, pp. 219–221, fig. 19A–E.

Paratypes, 2 (Colorado).

Micromus remiformis Oswald.

1987, J. N.Y. Entomol. Soc., vol. 95, no. 1, pp. 1–4, figs. 6–11.

Holotype (male), CAS Type No. 15298; "CALIF. Madera Co., / Big Creek at Boggy / Meadow 4.75 air mi / ESE. of Fish Camp, / Alt. 6400 ft. Aug. / 9, 1971 H. B. Leech"; "HOLOTYPE / Micromus / remiformis Oswald / J. D. Oswald 1985".

Notiobiella dentata Monserrat.

1990, Advances in Neuropterology, pp. 68–72, figs. 1–14.

Paratype, 1 (Indonesia, Bali).

Nusalala kruegeri Nakahara.

1965, Proc. U. S. Nat. Mus., vol. 117, no. 3509, pp. 113–115, fig. 2A–D, pl. 1 (fig. 3).

Holotype (male), CAS Type No. 9060; "Cordoba, Mex. / I-1941 / G. E. Bohart"; "Holo / Type No. / 66867 / U. S. N. M."; "Nusalala / kruegeri / [HOLOTYPE] / W. Nakahara". Wing slide "Nusalala / krügeri n.sp./ [Holotype] / W. Nakahara / Cordoba, Mexico / 1-1-1941 / G. E. Bohart". Genitalia slide "Nusalala / krügeri n.sp. / [Holotype] / W. Nakahara"; same type number label data.

Remarks: There is a USNM type label associated with this CAS holotype because the USNM gives a type number to all specimens in a type series, even if part of the material, including holotype, belongs to another institution.

Pseudomicromus fuscatus Nakahara.

1965, Proc. U. S. Nat. Mus., vol. 117, no. 3509, p. 112, pl. 1 (fig. 2).

Holotype (female), CAS Type No. 9061; "Real de Arriba / Temescaltepec / Mex. V-23-33"; "H. E. Hinton, / R. L. Usinger / Collectors"; "Holo / Type No. / 66866 / U. S. N. M."; "Pseudomicromus / fuscatus / [HOLOTYPE] / W. Nakahara". Right wing label "Pseudomicromus / fuscatus n.sp. / [Holotype] / W. Nakahara".

Remarks: There is a USNM type label associated with this CAS holotype because the USNM gives a type number to all specimens in a type series, even if part of the material, including holotype, belongs to another institution.

Sympherobius brunneus Nakahara.

1965, Proc. U. S. Nat. Mus., vol. 116, no. 3503, pp. 207–209, fig. 1a-e, pl. 1 (fig. 1).

Holotype (male), CAS Type No. 9062; "Miami Ranger Sta / Mariposa Co. Cal."; "H. P. Chandler / No. 21 Expo. / 7/5/46 NE / Elv. 5,000 SW"; "H. CHANDLER / COLLECTION"; "Sympherobius / brunneus / [Holotype] / W. Nakahara"; "Holotype". Left forewing slide "Sympherobius / brunneus n.sp. / [Holotype] / W. Nakahara". Genitalia slide with same data.

Sympherobius constrictus Oswald.

1988, J. N. Y. Entomol. Soc., vol. 96, no. 4, pp. 425–427, figs. 81–85, 90.

Holotype (male), CAS Type No. 15299; "Lobos Creek / San Francisco, / Calif. II-16-61 / J. Powell Collr."; "ex foliage / Cupressus / macrocarpa"; "HOLOTYPE / Sympherobius / constrictus Oswald".

Paratypes, 11 (California).

Remarks: The holotype is on indefinite loan from the University of California, Berkeley.

Sympherobius killingtoni Carpenter.
1940, Proc. Am. Acad. Arts Sci., vol. 74, no. 7, pp. 238–239, fig. 40A–C, pl. 2 (fig. 11).
Paratypes, 5 (1 Arizona, 2 California, 2 Texas).

Mantispidae

Nolima dine Rehn.
1939, Trans. Am. Entomol. Soc., vol. 65, no. 3, pp. 261–262, fig. 13.
Holotype (male), CAS Type No. 4927; "Peppersauce / Cn. Arizona / Aug. 16, 1924"; "J. O. Martin / Collector"; "Santa / Catalina / Mts."; "Nolima / dine / TYPE Rehn".
Allotype (female), CAS Type No. 4928; same data as holotype, except fourth label reads "Allotype / Nolima / dine Rehn / PARATYPE".
Paratype, 1 (Arizona).
Remarks: Apparently the allotype specimen was originally labeled with both allotype and paratype labels to indicate that the allotype came from the paratypic series.

Nolima kantsi Rehn.
1939, Trans. Am. Entomol. Soc., vol. 65, no. 3, pp. 260–261, figs. 11, 12, 16.
Holotype (male), CAS Type No. 4926; "Chisos Mts Tex. / Brewster Co. / July 16 1921"; "C. D. Duncan / Collector"; "Nolima / kantsi / TYPE Rehn".

Plega banksi Rehn.
1939, Trans. Am. Entomol. Soc., vol. 65, no. 3, p. 248, figs. 1, 6, 15.
Paratypes, 4 (Arizona).

Plega dactylota Rehn.
1939, Trans. Am. Entomol. Soc., vol. 65, no. 3, pp. 250–254, figs. 3, 5, 9, 17, 18, 21, 22.
Paratypes, 7 (Arizona).

Plega dactylota lipanica Rehn.
1939, Trans. Am. Entomol. Soc., vol. 65, no. 3, pp. 254–256, figs. 10, 19, 20.
Paratype, 1 (Texas).

Plega fumosa Linsley and MacSwain.
1955, Pan-Pac. Entomol., vol. 31, no. 1, pp. 16, 18–19, figs. 6–8, 10, 14.
Holotype (male), CAS Type No. 7202; "11 mi. E. Apatzingan / Michoacan, Mexico / VIII-20-1954"; "E. G. Linsley / J. W. MacSwain / R. F. Smith / Collectors"; "HOLOTYPE [MA] / Plega fumosa / Linsley & MacSwain".
Allotype (female); same data as holotype, except third label reads "ALLOTYPE [FE] / Plega fumosa / Linsley & MacSwain".
Paratype, 1 (Michoacán).

Plega melitomae Linsley and MacSwain.
1955, Pan-Pac. Entomol., vol. 31, no. 1, pp. 15–16, figs. 1–5, 9, 13.
Holotype (male), CAS Type No. 7203; "Francia, 8 m. [sic] N.E. / Cintalapa Chiapas / Mexico IV-3–53"; "R.C. Bechtel / E. I. Schlinger / Collectors"; "HOLOTYPE [MA] / Plega melitomae / Linsley & MacSwain".
Allotype (female); same data as holotype, except third label reads "ALLOTYPE [FE] / Plega melitomae / Linsley & MacSwain".
Paratype, 1 (Chiapas).

Plega yucatanae Parker and Stange.
1965, Can. Entomol., vol. 97, no. 6, pp. 606–611, figs. 2–4, 6–14.
Holotype (male), CAS Type No. 9471; "Chichen / Itza MEX. / Yucatan / IV 18 1962"; "F. D. Parker / L. A. Stange / Collectors"; "xtoloc cave"; "HOLOTYPE / Plega / [MA] yucatanae / F. Parker & / L. Stange".
Paratypes, 2 (Yucatán).

Myrmeleontidae

Brachynemurus darwini Stange.
1969, Acta Zool. Lilloana, vol. 25, no. 17, pp. 190, 192, 194–195, figs. 1–8, 15.
Holotype (male), CAS Type No. 11122; "Darwin Res. Sta. / Santa Cruz Is. / Galapagos Is. / ECU II-1-1964"; "R. Schuster / Collector"; "HOLOTYPE / Brachynemurus / darwini [MA] / L. Stange".
Paratypes, 7 (2 Abingdon Is., 1 Charles Is., 1 Duncan Is., 1 Hood Is., 1 Santa Cruz Is., 1 Santa Fe Is.).
Remarks: This species is currently placed in the genus *Galapagoleon* (see Stange, 1994:97).

Brachynemurus mimicus Stange.
1970, Univ. Calif. Publ. Entomol., vol. 55,

pp. 59–60, figs. 33, 40, 43, 47, 51, 56a, 63, 189, pl. 1, map 2.

Paratypes, 3 (Veracruz).

Remarks: This species is currently placed in the genus *Dejuna* (see Stange, 1994:85).

Brachynemurus mixtecus Stange.

1970, Univ. Calif. Publ. Entomol., vol. 55, pp. 96–97, figs. 100, 101, 104, 108, 207, map 13.

Paratype, 1 (Puebla).

Remarks: This species is currently placed in the genus *Mexoleon* (see Stange, 1994:86).

Brachynemurus nigrescens Stange.

1970, Univ. Calif. Publ. Entomol., vol. 55, pp. 135–136, figs. 138, 170, 224, map. 18.

Paratype, 1 (Arizona).

Remarks: This species is currently placed in the genus *Scotoleon* (see Stange, 1994:87).

Brachynemurus parkeri Stange.

1970, Univ. Calif. Publ. Entomol., vol. 55, pp. 69–70, figs. 53, 55, 56c, 58, 62, 192, map 4.

Paratype, 1 (Puebla).

Remarks: This species is currently placed in the genus *Atricholeon* (see Stange, 1994:82).

Brachynemurus persimilis Stange.

1970, Univ. Calif. Publ. Entomol., vol. 55, pp. 60–61, figs. 30, 42, 44, 48, 59, 60, 188, map 1.

Paratypes, 2 (Oaxaca).

Remarks: This species is currently placed in the genus *Dejuna* (see Stange, 1994:85).

Brachynemurus setosus Stange.

1970, Univ. Calif. Publ. Entomol., vol. 55, pp. 61, 63, figs. 46, 50, map 2.

Holotype (male), CAS Type No. 9019; "Tuxtla Gutierrez / 3 mi E, Chis. / Mexico. III-13-53"; "R. C. Bechtel / E. I. Schlinger / Collectors"; "HOLOTYPE / Brachynemurus / setosus / L. Stange [MA]"; "abdominal tip / in microvial / on sep. pin". (Separate pin) "Part of TYPE, / Brachynemurus / setosus / Stange".

Remarks: This species is currently placed in the genus *Dejuna* (see Stange, 1994:85).

Brachynemurus stramineus Stange.

1970, Univ. Calif. Publ. Entomol., vol. 55, pp. 63–64, figs. 45, 49, 190, map 2.

Paratype, 1 (Sinaloa).

Remarks: This species is currently placed in the genus *Dejuna* (see Stange, 1994:85).

Brachynemurus westcotti Stange.

1970, Univ. Calif. Publ. Entomol., vol. 55, pp. 109–110, figs. 122, 211, map 16.

Paratype, 1 (Arizona).

Remarks: This species is currently placed in the genus *Clathroneuria* (see Stange, 1994:85).

Chaetoleon variabilis Banks.

1942, Proc. Calif. Acad. Sci., ser. 4, vol. 24, no. 4, pp. 141–142, pl. 8 (figs. 4, 5).

Holotype (female), CAS Type No. 4914; "Triunfo / L. Cal. VII-13-38"; "Michelbacher & / Ross Collectors"; "Chaetoleon / variabilis / Type Bks".

Paratypes, 31 (Baja California Sur).

Dimarella menkei Stange.

1963, Ann. Entomol. Soc. Am., vol. 56, no. 6, p. 814, figs. 3, 6, 9, 12, 13.

Holotype (male), CAS Type No. 8558; "10 mi. S. E. / Alamos / Son. MEX. / May 22 1962"; "Jack lighting / Rio Cuchujachi"; "L. A. Stange / Collector"; "HOLOTYPE / Dimarella / [MA] menkei / L. Stange".

Dimarella psammophila Stange.

1963, Ann. Entomol. Soc. Am., vol. 56, no. 6, pp. 814–815, figs. 4, 8, 11.

Holotype (female), CAS Type No. 8559; "Veracruz / MEXICO / IV 29 1962"; " F. D. Parker / L. A. Stange / Collectors"; "at u.v. light / sand dunes"; "HOLOTYPE / Dimarella / [MA] psammophila / L. Stange".

Eremoleon affine Banks.

1942, Proc. Calif. Acad. Sci., ser. 4, vol. 24, no. 4, p. 144.

Holotype (female), CAS Type No. 4915; "Miraflores, / L. Cal. VII-8-38"; "Michelbacher & / Ross Collectors"; "Eremoleon / affine / type Bks".

Remarks: This species is currently considered a junior synonym of *Eremoleon nigribasis* Banks (see Stange, 1970b:21).

Eremoleon gracile Adams.

1957, Psyche, vol. 63, no. 3, pp. 90–91, figs. 3, 17, 29.

Holotype (female), CAS Type No. 7205; "Riverside / Cal. Ag 31.39"; "Paul DeBach / Coll."; "Eremoleon / Gracile / ADAMS / HOLOTYPE".

Eremoleon sectoralis Adams.

1957, Psyche, vol. 64, no. 1, pp. 7–8, fig. 1d, e.

Holotype (female), CAS Type No. 7206; "5 mi. s. / San Miguel, / L. Cal. VII-20-38"; "Michelbacher & / Ross Collectors"; "affine"; "Pres by / E S Ross and / A E Michelbacher"; "EREMOLEON / SECTORALIS / ADAMS / HOLOTYPE".

Gnopholeon zapotecas Stange.

1970, Univ. Calif. Publ. Entomol., vol. 55, pp. 150–151, figs. 172, 176, 182, 186, 227, map 30.

Paratype, 1 (Oaxaca).

Hesperoleon deflexus Adams.

1957, Psyche, vol. 63, no. 3, pp. 98–100, figs. 2, 31, 32, 41.

Holotype (male), CAS Type No. 7207; "Baker / S. B. Co. Cal. / VIII-23-52"; "HESPEROLEON / DEFLEXUS / ADAMS / TYPE".

Allotype (female); same data as holotype, except second label reads "HESPEROLEON / DEFLEXUS / ADAMS / ALLOTYPE".

Remarks: This species is currently placed in the genus *Scotoleon* (see Stange, 1994:87).

Hesperoleon fidelitas Adams.

1957, Psyche, vol. 63, no. 3, pp. 94, 96–98, figs. 5, 5a, 33, 34.

Paratypes, 8 (Arizona).

Remarks: This species is currently placed in the genus *Scotoleon* (see Stange, 1994:87).

Hesperoleon infuscatus Adams.

1957, Psyche, vol. 63, no. 3, pp. 104–106, figs. 4, 39, 40, 44, 45.

Holotype (male), CAS Type No. 7209; "Antioch / C. Costa Co., / Calif V.24.49"; "J. W. MacSwain / Collector"; "HESPEROLEON / INFUSCATUS / [MA] ADAMS / HOLOTYPE".

Allotype (female); same data as holotype, except third label reads "HESPEROLEON / INFUSCATUS / [MA] ADAMS / ALLOTYPE".

Paratypes, 8 (California).

Remarks: This species is currently placed in the genus *Scotoleon* (see Stange, 1994:87).

Hesperoleon minutus Adams.

1957, Psyche, vol. 63, no. 3, pp. 100–102, 104, figs. 6, 13–16.

Holotype (male), CAS Type No. 7208; "Cathedral City / Riverside Co / Cal VII-24 1950"; "L. W. Isaak / Collector"; "UCD"; "1"; "HESPEROLEON / MINUTUS / [MA] ADAMS / HOLOTYPE".

Paratype, 1 (Baja California).

Remarks: This species is currently placed in the genus *Scotoleon* (see Stange, 1994:87).

Hesperoleon peninsulanus Banks.

1942, Proc. Calif. Acad. Sci., ser. 4, vol. 24, no. 4, p. 136, pl. 8 (fig. 15).

Holotype (female), CAS Type No. 4911; "Coyote Cove / Conception Bay, / L. Cal. VII-24-38"; "Michelbacher & / Ross Collectors"; "Hesperoleon peninsulanus / type Bks".

Remarks: This species is currently placed in the genus *Scotoleon* (see Stange, 1994:87).

Maracandula minima Banks.

1942, Proc. Calif. Acad. Sci., ser. 4, vol. 24, no. 4, pp. 140–141, pl. 8 (figs. 7, 9, 14).

Holotype (female), CAS Type No. 4919; "San Miguel, / L. Cal. VII-3-38"; "Maracandula / minima / type Bks".

Paratypes, 12 (3 Baja California, 9 Baja California Sur).

Remarks: This name is considered a junior synonym of *Menkeleon bellula* (Banks) by Stange (1970a:155). One paratype has been determined as *Gnopholeon barberi* (Currie) by L. A. Stange.

Netroneurus pulchellus var. *pallescens* Banks.

1942, Proc. Calif. Acad. Sci., ser. 4, vol. 24, no. 4, p. 140, pl. 8 (fig. 12).

Holotype (male), CAS Type No. 4913; "San Domingo, / L. Cal. VII-19-38"; "Netroneurus / pulchellus / pallescens / Type Bks".

Paratypes, 31 (Baja California Sur).

Remarks: This pale variety is presently considered a junior synonym of *Brachynemurus pulchellus* Banks (see Stange, 1970a:102, 104).

Pamexis karoo Mansell.
1992, Syst. Entomol., vol. 17, no. 1, pp. 67, 69, 71, figs. 1, 6–15, 45.
Paratype, 1 (South Africa).

Psammoleon femoralis Banks.
1942, Proc. Calif. Acad. Sci., ser. 4, vol. 24, no. 4, p. 146, pl. 8 (figs. 13, 17).
Holotype (female), CAS Type No. 4917; "20 mi. N.W. / La Paz, L. Cal. / VII-16-38"; "Michelbacher & / Ross Collectors"; "Psammoleon / femoralis / type Bks".
Remarks: This species is currently placed in the genus *Eremoleon*. (see Stange, 1970b:21).

Psammoleon normalis Banks.
1942, Proc. Calif. Acad. Sci., ser. 4, vol. 24, no. 4, p. 145, pl. 8 (figs. 10, 16).
Holotype (male), CAS Type No. 4916; "Venancio, / L. Cal. VII-17-38"; "Michelbacher & / Ross Collectors"; "Psammoleon / normalis / type Bks".

Puren albovaria Banks.
1942, Proc. Calif. Acad. Sci., ser. 4, vol. 24, no. 4, pp. 146–147, pl. 8 (figs. 3, 6).
Holotype (female), CAS Type No. 4918; "Venancio, / L. Cal. VII-17-38"; "Michelbacher & / Ross Collectors"; "Psammoleon / albovaria / type Bks".

Scotoleon congener Banks.
1942, Proc. Calif. Acad. Sci., ser. 4, vol. 24, no. 4, pp. 138–139, pl. 8 (fig. 1).
Holotype (male), CAS Type No. 4912; "Chapala Dry Lk. / L. Cal. VI-21-38"; "Michelbacher & / Ross Collectors"; "Scotoleon / congener / Type Bks".
Paratypes, 22 (11 Baja California, 11 Baja California Sur).
Remarks: This species is currently considered a junior synonym of *Scotoleon longipalpis* Hagen (see Stange, 1970a:129).

Tyttholeon puerilis Adams.
1957, Psyche, vol. 63, no. 3, pp. 107–108, figs. 7, 8, 11, 12.
Holotype (male), CAS Type No. 7210; "Palm Springs / Riverside Co., Cal / V-29-1939"; "E.G. Linsley / Collector"; "UC"; "5"; "TYTTHOLEON / PUERILIS / [MA] ADAMS / HOLOTYPE".
Allotype (female); same data as holotype, except fourth label reads "15" and fifth label reads "TYTTHOLEON / PUERILIS / [FE] ADAMS / ALLOTYPE".
Paratypes, 2 (California).

Nemopteridae

Lertha sofiae Monserrat.
1989, Ann. Mus. Civ. Stor. Nat. "Giacomo Doria" (1988–1989), vol. 87, pp. 108–110, figs. 11, 12, 17, 20A–E.
Holotype (male), CAS Type No. 15953; "SPAIN: Almeria Prov. / Bulanegra 41 km W. of / Almeria, 16.VII.1966 / Edward S. Ross / (Dusk after shower)"; "LERTHA / SOFIAE [MA] / TYPUS".
Paratypes, 5 (Spain).

Polystoechotidae

Platystoechotes lineatus Carpenter.
1940, Proc. Am. Acad. Arts Sci., vol. 74, no. 7, pp. 271–272, figs. 71, 72A–E, pl. 3 (fig. 28).
Holotype (male), CAS Type No. 5593; "Sequoia Natl. / Park, Calif. / Alt. 7000–9000 ft."; "Wolverton / VI-19-29"; "Pres. by / E. C. Van Dyke / Collector"; "Type"; "Platystoechotes / lineatus Carp.".
Allotype (female); CAS Type No. 5594; "Sequoia Natl. / Park, Calif. /Alt. 7000–9000 ft."; "Wolverton / VI-23-29"; "Pres. by / E. C. Van Dyke / Collector"; "allotype"; "Platystoechotes / lineatus Carp.".
Paratypes, 4 (California).

Sisyridae

Climacia californica Chandler.
1953, J. Wash. Acad. Sci., vol. 43, no. 6, pp. 183–184, fig. 1.
Holotype (male), CAS Type No. 7196; "Clear Lake / Lake Co / Calif. sw side"; "d16-9 m5 y1949/ Elev. 1,318 / H. P. Chandler"; "Holotype / Climacia / californica".
Allotype (female), same data as holotype.
Paratype, 1 (California).

Sisyra pallida Meinander.

1978, Entomol. Scand., vol. 9, no. 3, pp. 234–235, fig. 1A, B.

Holotype (male), CAS Type No. 13114 (in alcohol); "ZAMBIA: Mpulungu / Lake Tanganyika, / 2600′ 31-I-1970 / M. E. Irwin & / E. S. Ross"; "Sisyra / pallida sp.n. [MA] / det. Meinander 1977 / HOLOTYPUS".

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Index of Species Names

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PROCEEDINGS
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A REMARKABLE NEW SPECIES OF *NEBRIA* (COLEOPTERA: CARABIDAE: NEBRIINI) FROM NORTH KOREA

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Abstract: *Nebria scaphelytra*, new species, is described from North Korea (type locality: Myohyang Mountains). Based on features of adult morphology, this species is a highly distinctive member of the *ovipennis* species group of subgenus *Catonebria* Shilenkov and is the second known Palaearctic member of this predominantly Nearctic group.

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INTRODUCTION

Knowledge of the carabid beetle fauna of both mainland and peninsular portions of North and South Korea has progressed rapidly in recent decades [e.g., compare Kano (1923) with Kwon and Lee (1986)]. Between the 1920s and 1980s, the list of nebriine carabids recorded from this region increased from two species (Csiki, 1927) to twelve species and four additional subspecies (Kwon and Lee, 1986). Individual contributions to this increase in knowledge of the fauna include both descriptions of new species or subspecies (Bänninger, 1933; Semenov Tian-Shanskij and Znojko, 1928; Horvatovich, 1973; and Shilenkov, 1983) and a synoptic faunal review for North Korea (Shilenkov, 1983). However, new information presented here suggests that the inventory of this fauna remains incomplete.

Several years ago, one of us (DHK) received a parcel, containing adult nebriine carabids from North Korea, sent by Dr. Jerzy Pawlowski [Institute of Systematic and Experimental Zoology, Krakow, Poland (ISEZ)] for identification. Among the specimens sent were a number of interesting forms, including two specimens, one male and one female, that were elegant in form and remarkable in the sculpturing and topography of their dorsal surface. They represented a species of *Nebria* Latreille unknown to either of us. Recently, having discussed the unique characteristics of these specimens, and based on our collective knowledge of known nebriine taxa, we concluded that these specimens represent an undescribed species.

Other new or little-known taxa were also represented in the North Korean material examined; but evaluation of the appropriate taxonomic status of each of these forms (i.e., whether each represents a distinct species or a subspecies of some described species) will require additional study and analysis of geographical variation in previously described forms. Therefore, the purpose of this paper is to describe this one new species and discuss its subgeneric and species-group affinities, based on synapomorphic (derived) adult features shared with other taxa.

SPECIES DESCRIPTION

Nebria scaphelytra new species

TYPE MATERIAL. — Holotype: a male, in ISEZ, labelled: "Corea sept. 1983 Mjohjang montes, Exp. Inst. Zool. Cr." / "Holotype Nebria scaphelytra Kavanaugh & Shilenkov 1995." One paratype, a female, in California Academy of Sciences, labelled: same locality label / "Paratype Nebria scaphelytra Kavanaugh & Shilenkov 1995."

TYPE LOCALITY. — Myohyang Mountains, central North Korea.

DERIVATION OF SPECIES EPITHET. — From the Latin, *scapha*, meaning a small boat, and *elytron*, referring to the resemblance between the paired elytra of adults of this species and the inverted hull of a small boat or skiff, complete with keel.

DIAGNOSIS. — The following combination of features distinguishes adults of this species from those of all other *Nebria*: body shiny black, without metallic reflection dorsally; vertex with a pair of paramedial red spots; antennal scape straight; pronotum narrow, markedly cordate, subbasal sinuation of lateral margin deep and very long, midlateral setae present, basolateral setae absent; prosternal intercoxal process with margination complete; elytral silhouette elongate, ovoid, elytron with disc distinctly depressed lateral to slightly raised sutural interval in basal fourth, intervals 3, 5, and 7 markedly catenate, each with two or more broadly foveate and deep setiferous punctures; abdominal sterna 3–5 with two or more pairs of posterior paramedial setae, without anterior paralateral setae.

DESCRIPTION. — Size medium, apparent body length (measured from apex of longer mandible to apex of longer elytron) of male 13.0 mm, of female 14.2 mm (see Table 1 for additional measurements). Body slender (Fig. 1), with long and delicate appendages. Color of body black, appendages of head and thorax piceous (tibiae and tarsi slightly paler than femora in female specimen); vertex with a pair of paramedial red spots. Body shiny, elytra more markedly so, without metallic reflection. Microsculpture of head and elytra isodiametric, that of pronotum slightly transverse, sculpticells on head and pronotum smaller and more convex than those on elytra.

Head moderate in size and width, eyes moderately convex, very slightly reduced in size; frontal furrows small, round, deep and wrinkled; antennae markedly long and slender, extended to apical one-fourth of elytra in male, to apical one-third in female; antennal scape (Fig. 2) straight, slightly narrowed basally, more convex anteriorly than posteriorly; labial palpus with penultimate palpomere trisetose; mentum with medial tooth bifid, length slightly less than one-half length of lateral lobes, M2 setae (Kavanaugh, 1979) positioned midway between basal margin and apical emargination; gula with a transverse row of 13–15 setae.

Pronotum (Fig. 3) narrow, markedly cordiform; apical angles narrow, rounded apically, moderately projected anteriorly; basal angles slightly acute, slightly projected posteriorly; sub-basal sinuation of lateral margin deep and long; apical margination restricted to lateral one-fourth; basal margination absent; lateral margination distinct and narrow in apical four-fifths of margin, absent from basal one-fifth; lateral explanation very narrow anteriorly, broadened and continuous with basal foveae posterior to middle; median longitudinal and anterior and posterior transverse impressions deep, well-defined; posterior transverse impression and lateral base with faint wrinkles, base of pronotum with a few fine, well-separated

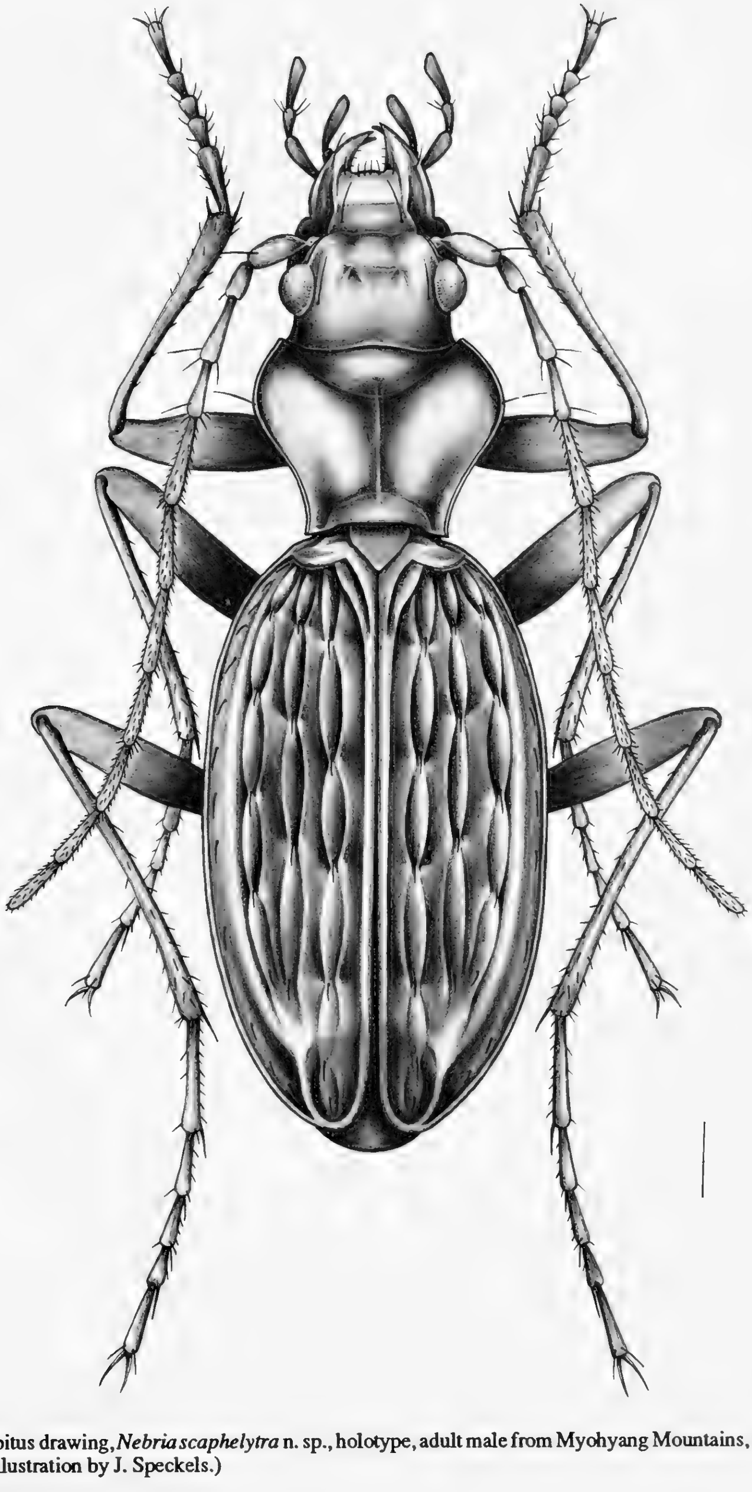


FIGURE 1. Habitus drawing, *Nebria scaphelytra* n. sp., holotype, adult male from Myohyang Mountains, North Korea; scale line = 1.0 mm. (Illustration by J. Speckels.)

TABLE 1. Measurements (in mm) of main body parts.

	Male	Female
HW	2.5	2.6
PW	3.2	3.5
PBW	1.9	2.2
EW	4.5	5.0
HL	1.5	1.5
PL	2.5	2.7
EL	7.5	9.3
SBL	11.5	12.5

Abbreviations: HW = width of head measured across compound eyes; PW = width of pronotum measured across widest point; PBW = width of base of pronotum measured between apices of hind angles; EW = width of elytra measured across widest point; HL = length of head measured along medline from apex of clypeus to a point opposite posterior margin of compound eyes; PL = length of pronotum measured along midline from apical to basal margin; EL = length of longer elytron measured along midline from apex of scutellum to elytral apex; SBL = HL+PL+EL.

punctures; midlateral setae present, positioned well anterior to midpoint; basolateral setae absent.

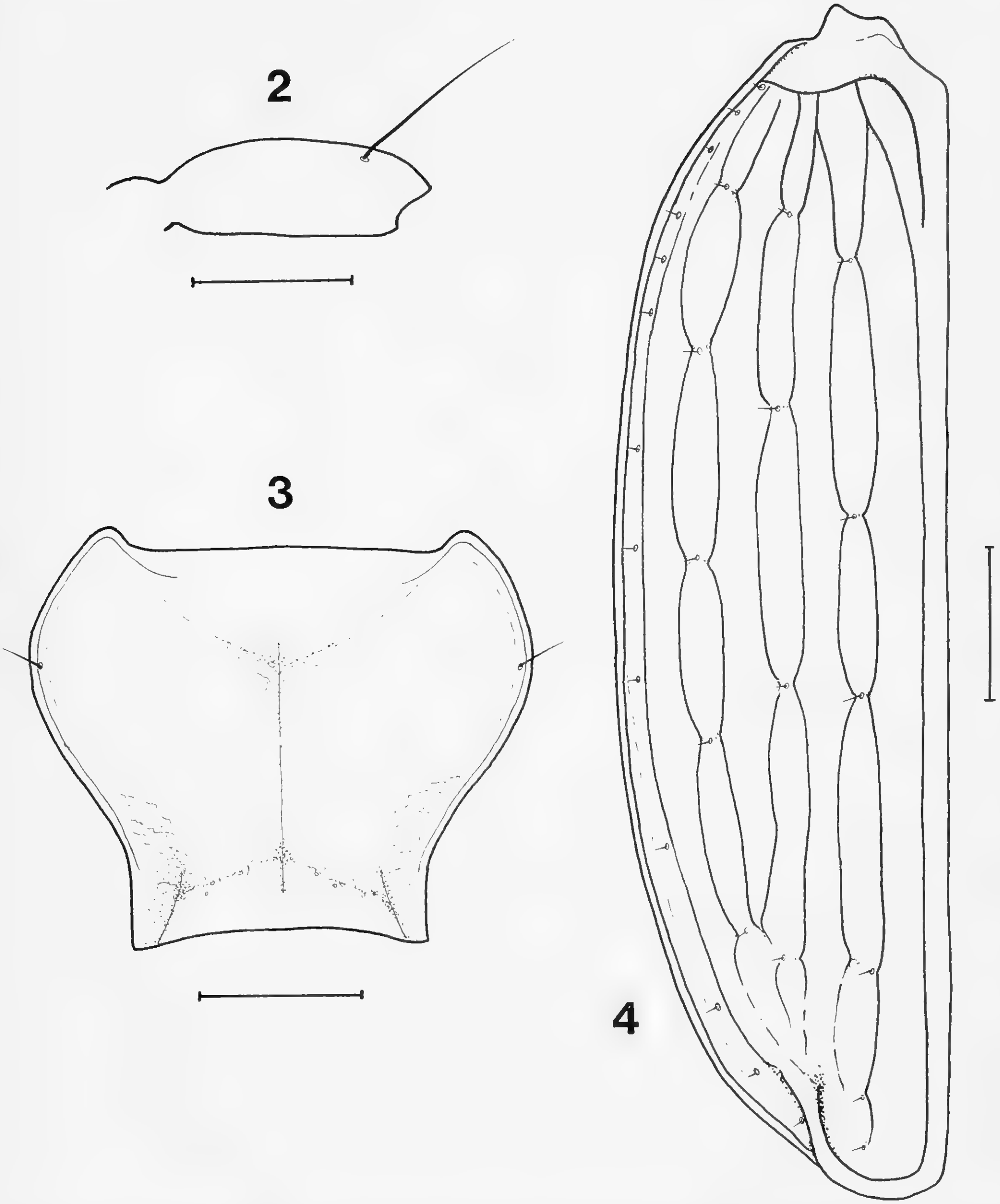
Elytral silhouette ovoid-elongate (Fig. 1), widest at middle. Elytron (Fig. 4) with disc distinctly depressed lateral to sutural interval, especially at base posterior to basal margination; humeri reduced but with marked humeral carina; basal margination markedly sinuate in male, only slightly so in female, joined with lateral margination at a markedly obtuse angle; sutural interval elevated in basal two-thirds in male, in basal one-third in female; intervals 2, 3, 4 and 6 convex basally, slightly convex at middle and apically; intervals 5 and 7 subcarinate basally, more convex than other intervals in basal three-fourths; interval 2 without basal setiferous pore; intervals 3, 5, and 7 markedly catenate, with very broad and deep setiferous foveae; interval 5 markedly carinate subapically; elytral apex broadly truncate and rounded. Hindwing present as a short, narrow, strap-like vestige.

Thoracic venter smooth, impunctate, except mesepisternum with a few fine punctulae; prosternum with margination of intercoxal process complete; metasternum short, length of portion posterior to mesocoxa slightly shorter than diameter of mesocoxa. Abdominal sterna impunctate, but slightly wrinkled laterally; sternum 2 asetose medially and paramedially; sterna 3–5 each with two or three pairs of posterior paramedial setae; anterior paralateral setae absent; sternum 6 with one pair of apical setae in male, two pairs in female.

Hind coxa with two sub-basal and one subapical setae; all tarsi without dorsal pubescence; front tarsus of male with tarsomeres 1–3 distinctly broader than those in female and with pads of adhesive setae ventrally; tarsomere 4 only slightly broader in male than in female and without ventral adhesive setae; apex of hind tarsomere 4 markedly projected lateroventrally.

MALE GENITALIA. — Median lobe (Fig. 5) thick and moderately long, slightly twisted right from base to apex (Fig. 5c), axis of curvature about 90° (Fig. 5a), straight in middle one-third, with a shallow, basally-directed invagination in the right lateral wall (Fig. 5b); mid-shaft moderately compressed in cross-section; apex broad and apically rounded, deflected ventrally (in lateral aspect, Fig. 5a) and left (in ventral aspect, Fig. 5c); apical orifice markedly deflected right; internal sac multi-lobed (Fig. 5d, e), with a faint, long, slender anterobasal sclerite and a pair of small, convex sclerites (**scl**, Fig. 5e) at the gonopore anteroapically. Left paramere (Fig. 6a) shorter than right, broad and broadly rounded apically, right paramere (Fig. 6b) slightly elongate and narrow.

FEMALE GENITALIA. — Sternum 8 (Fig. 7) with basal apodemes broad, markedly emarginate apically, medial and lateral arms equal in length. Ovipositor (Fig. 8) long and slender, medial face of gonostylus (stylomere 2) with a short diagonal row of setae dorsally. Bursa copulatrix (Fig. 9) with spermathecal chamber (**sc**, Fig. 9a, b) slightly asymmetrical and deflected right, moderately cordate, without posterodorsal accessory lobe, continuity of chambers as in Fig. 9c; spermathecal duct (**sd**, Fig. 9a) narrow, moderate in length, loosely and irregularly convoluted, inserted posterodorsally at base of spermathecal chamber of bursa; spermatheca (**sp**, Fig. 9a) lanceolate, moderately ar-

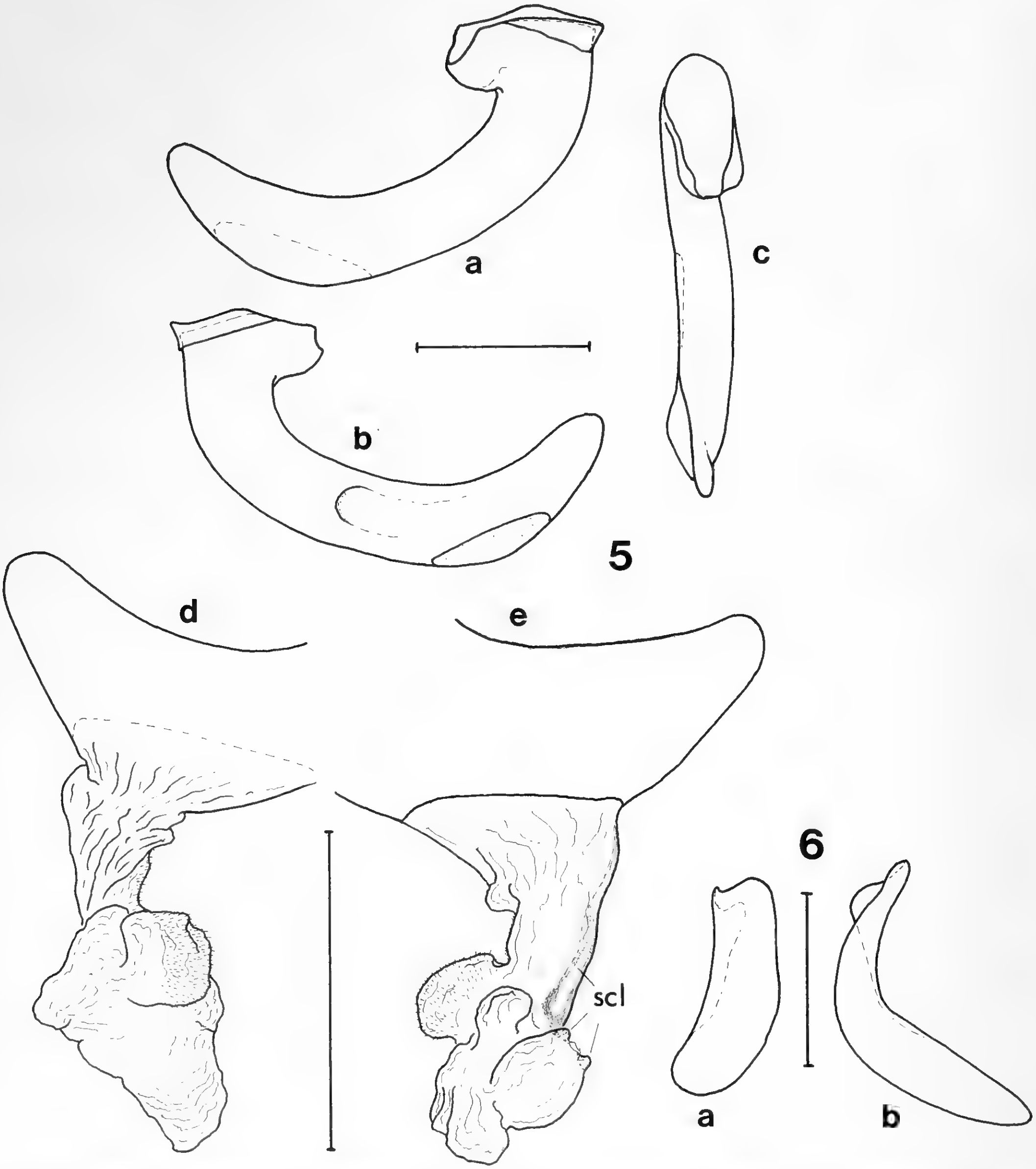


FIGURES 2–4. *Nebria scaphelytra* n. sp. FIGURE 2. Right antennal scape, dorsal aspect; scale bar = 0.5 mm. FIGURE 3. Pronotum, dorsal aspect; scale bar = 1.0 mm. FIGURE 4. Left elytron, dorsal aspect; scale bar = 1.0 mm.

cuate. Common oviduct with a small dorsal lobe (**dlco**, Fig. 9a, b), slightly deflected right.

DISTRIBUTION. — At present, known only from the Myohyang Mountains of North Korea (Fig. 10).

This isolated mountain range, located in central North Korea, forms portions of the borders between Chagang do and P'yongan-namdo and between Chgang do and Hamgyong-namdo provinces. Its axis trends northeast to southwest



FIGURES 5 and 6. Male genitalia, *Nebria scaphelytra* n. sp. FIGURE 5. Median lobe of male; a = left lateral aspect; b = right lateral aspect; c = ventral aspect; everted internal sac, d = left lateral aspect, e = right lateral aspect; scl = sclerite. FIGURE 6. Parameres; a = left paramere, left lateral aspect; b= right paramere, right lateral aspect. Scale bars = 1.0 mm.

and forms the divide between the Ch'onch'on and Taedong rivers. The precise locality at which the type series was collected is unknown.

HABITAT DISTRIBUTION AND LIFE HISTORY. — Nothing is known at present about the habitat distribution of this species, nor of the timing of its life cycle (no date of collection is recorded with the specimens).

AFFINITIES AND TAXONOMIC PLACEMENT. — Most adults of species in *Nebria* subgenus *Catonebria* Shilenkov (1976) share the following characteristics: (1) vertex with a pair of

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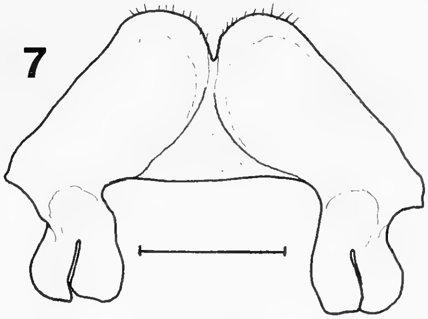

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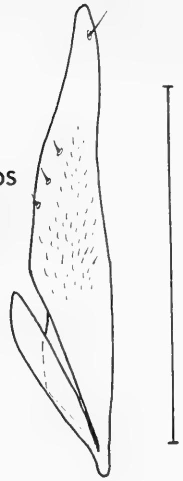

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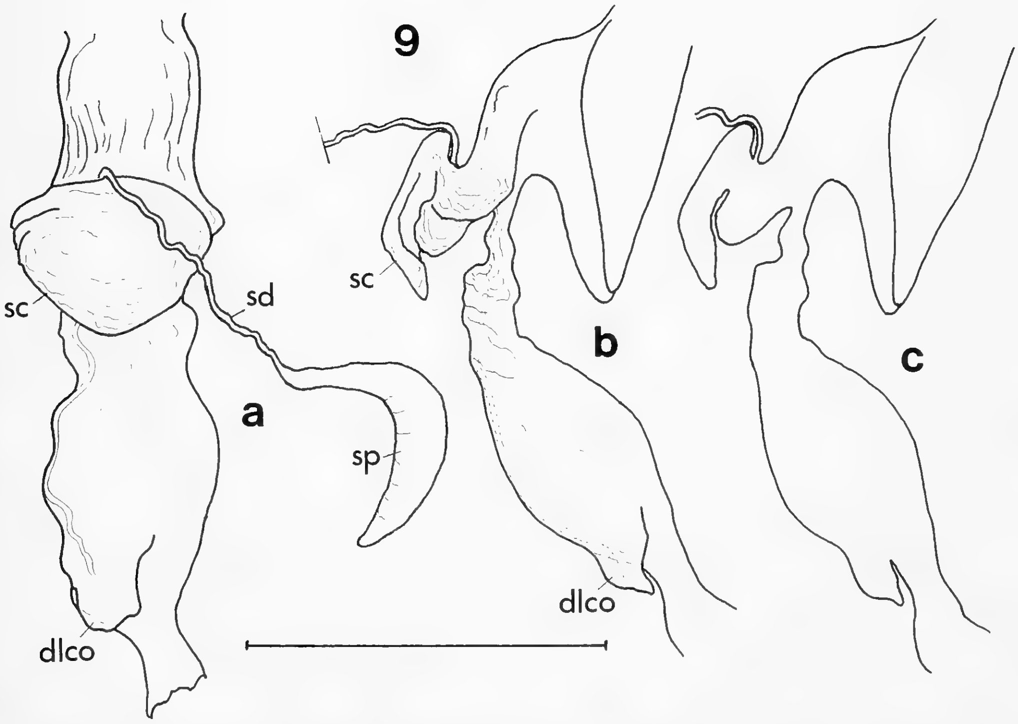

FIGURES 7–9. Female genitalia, *Nebria scaphelytra* n. sp. FIGURE 7. Sternum 8 of female, ventral aspect. FIGURE 8. Ovipositor, right coxostylus (stylomeres 1 and 2), medial aspect; mdos = row of dorsal setae. FIGURE 9. Bursa copulatrix, spermathecal duct, spermatheca, and common oviduct; a = dorsal aspect; b = left lateral aspect; c = mid-sagittal outline, left lateral aspect; dlco = dorsal lobe of common oviduct; sc spermathecal chamber; sd = spermathecal duct; sp = spermatheca. Scale bars = 1.0 mm.

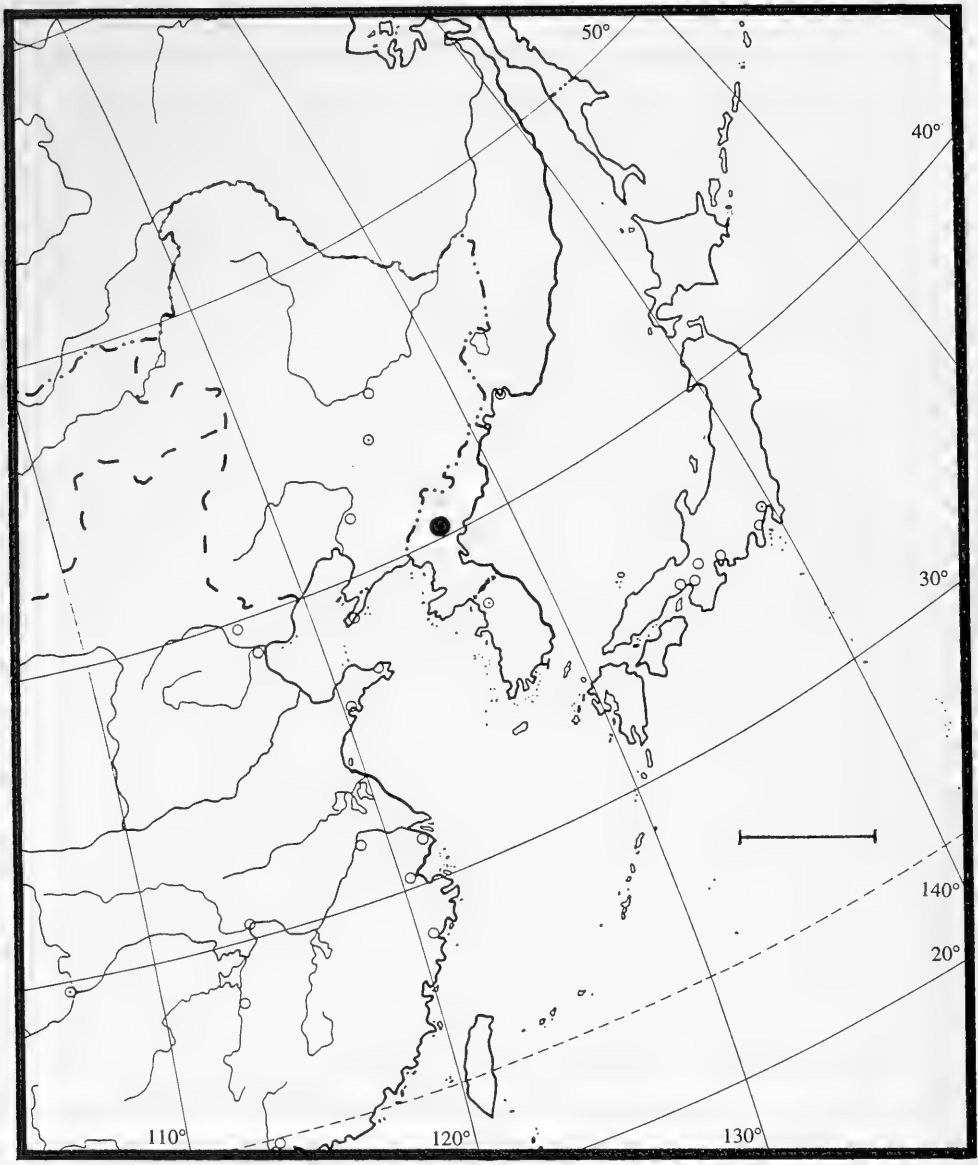

FIGURE 10. Map illustrating known geographical distribution of *Nebria scaphelytra* n. sp. (solid black dot); scale bar = 500 km.

paramedial red spots (2) upper surface with slight to marked metallic reflection; (3) longitudinal axis of antennal scape slightly arcuate; (4) midlateral pronotal seta present; (5) elytral discal setiferous punctures broadly foveate; (6) elytral intervals 3 and 7 (and also interval five in members of several species) with two to six setiferous pores; abdominal sterna 3–5 each with (7) two or more pairs of posterior paramedial setae and (8) one or more pairs of anterior paralateral setae; and (9) male median lobe with midshaft moderately compressed (in cross-section). From this list, feature (4) is plesiomorphic within Nebriini, features (1) and (7) are synapomorphic with members of subgenus *Reductonebria* Shilenkov (1976), and the remainder are synapomophies for *Catonebria.*

Adults of *Nebria scaphelytra* exhibit six of these nine subgeneric features [namely, features (1), (4) through (7), and (9)] and three of six unique synapomorphies for *Catonebria* [namely, features (5), (6), and (9)]. Adults of *N. scaphelytra* and one or more other *Catonebria* species lack metallic reflection (e.g., *Nebria vandykei* Bänninger, *Nebria trifaria* LeConte, *Nebria ovipennis* LeConte), have the antennal scape straight (e.g., *Nebria gebleri albimontis* Kavanaugh and *Nebria spatulata sierrae* Kavanaugh), and have some or all members without anterior paralateral setae on abdominal sterna 3 to 6 (most species in the *ovipennis* species group). It seems clear that *N. scaphelytra* is most closely related to at least some species in *Catonebria* and, therefore, should be placed in that subgenus.

The *ovipennis* species group (Kavanaugh, 1978) of *Catonebria* includes *Nebria gebleri* Dejean, *Nebria mellyi* Gebler, *Nebria carri* Kavanaugh, *Nebria kincaidi* Schwarz, *Nebria spatulata* Van Dyke, and *N. ovipennis*. Adults of this group share the following features: (1) prosternal intercoxal process with margination in basal half only; male median lobe with (2) longitudinal axis of midshaft bent about 90°, (3) right lateral face of midshaft with a shallow but distinct basally-directed indentation or a pouch, and (4) axis of apex slightly deflected ventrally (in lateral aspect); (5) female sternum 8 with basal apodeme deeply emarginate, with lateral arm shorter than medial arm; and (6) gonostylus (stylomere 2) of female ovipositor with dorsal row of setae on medial face diagonal. All of these features are synapomorphies for the *ovipennis* species group, and *N. scaphelytra* adults exhibit four of them [namely, features (2), (3), (4) and (6)]. These four synapomorphies for *N. scaphelytra* and members of the *ovipennis* group provide solid evidence of close phylogenetic relationship.

Adults of the *ovipennis* subgroup (Kavanaugh, 1978) (*N. carri*, *N. kincaidi*, *N. spatulata*, and *N. ovipennis*) of the *ovipennis* species group share the following features: (1) eyes slightly reduced in size; (2) elytral silhouette ovoid, (3) elytron moderately short, (4) humeri markedly to extremely rounded, (5) humeral carina present, varied from faint and vaguely linear to very well-developed, projected, and markedly linear; (6) hindwing short, slender, strap-like; (7) median lobe of male with apical orifice extremely deflected right; male parameres (8) asymmetrical, right slightly longer than left, (9) left paramere broad, pointed apically, (10) right paramere narrow, slightly elongate; (11) ovipositor of female with gonocoxa (stylomere 1) and gonostylus (stylomere 2) fused medially, narrowly divided laterally; and (12) bursa copulatrix of female with spermathecal chamber moderately cordate (in dorsal aspect).

Nebria scaphelytra adults exhibit nine of these twelve features [namely, features (1), (2), (4) through (6), (8), and (10) through (12)]. However, in *N. scaphelytra*, the elytra are elongate, not shortened; the apical orifice of the male medial lobe is markedly, but not extremely, deflected right; and the male left paramere is broadly rounded apically, not pointed. In addition, the invagination of the right lateral wall of the midshaft of the male median lobe is a shallow indentation, as in *N. gebleri* and *N. mellyi*. In contrast, members of the *ovipennis* subgroup have the invagination formed as a deep, basally-directed pouch. A feature shared by most members of *N. mellyi* and of the species of the *ovipennis* subgroup, but apparently not by members of *N. scaphelytra*, is the presence of a pair of paramedial setae (or, in some *N. ovipennis* members, a patch of short setae) on abdominal sternum 2. This synapomorphy suggests closer phylogenetic relationship between *N. mellyi* and the *ovipennis* subgroup species than between *N. scaphelytra* and either of these taxa. It seems probable to us that *N. scaphelytra* is the sister group of a clade including *N. mellyi* and the *ovipennis* subgroup; but such a relationship needs to be confirmed through formal phylogenetic analysis (currently in progress, DHK).

A particularly interesting apomorphic feature of *N. scaphelytra* adults is the absence of pronotal basolateral setae. This feature is shared with adults of *N. carri* and *N. kincaidi* of the *ovipennis* subgroup of *Catonebria*, and with members of subgenus *Eonebria* (Shilenkov, 1976; Sciaky and Pavesi, 1994), *Nebria superna* Andrewes (currently placed in subgenus *Psilonebria* Andrewes), and *Nebria nudicollis* Peyerimhoff (currently placed in subgenus *Spelaeonebria* Peyerimhoff). *Nebria scaphelytra*, *N. carri*, and *N. kincaidi* clearly are closely related to species (e.g., *N. gebleri* and *N. ovipennis*) in which basolateral setae are present. Futhermore, data already presented here suggest, for example, that *N. kincaidi* (members without basolateral setae) is more closely related to *N. ovipennis* (members with these setae) than to *N. scaphelytra*. These findings raise serious question about the usefulness of this feature as indicative of phylogenetic relationship at higher taxonomic (e.g., subgeneric and other) levels within *Nebria*, as has been suggested (see Sciaky and Pavesi, 1994).

In summary, and based on features already noted, it seems clear that *N. scaphelytra* is a member of the *ovipennis* species group of subgenus *Catonebria*. However, this distinctive taxon does not appear to be so closely related to species of the *ovipennis* subgroup as to warrant inclusion in that subgroup. This species represents only the second member of the *ovipennis* group known from the Palaearctic Region, and it does not appear to have a sister group relationship with the other Palaearctic species, *N. mellyi*.

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DENTICETOPSIS, A NEW GENUS OF SOUTH AMERICAN WHALE CATFISH (SILURIFORMES: CETOPSIDAE, CETOPSINAE), WITH TWO NEW SPECIES

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Abstract: Two species of whale catfishes from southern Venezuela, representing a new genus of the Cetopsinae, are described. The name *Denticetopsis* is proposed for this taxon, which appears to have diverged early in the evolution of whale catfishes, as evidenced by the the presence of most, but not all, characters previously thought to be diagnostic for the Cetopsinae. *Denticetopsis* is hypothesized to be monophyletic on the basis of the following series of derived whale-catfish characters: an obliquely truncate caudal fin that is joined by a membrane to the posterior margin of the anal fin, a cluster of prominent caniniform teeth at the symphysis of the dentary, a reduced lateral line canal system, and edentulous vomer.

Denticetopsis sauli is distinguished from *D. royeroi* by having a more slender body, a smaller eye, a maxilla that projects at least one eye diameter posterior of the orbit, and a deep notch in the membrane that joins the anal and caudal fins.

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Introduction

Recent attention to the freshwater fish fauna of Venezuela has uncovered a number of new and interesting species. Two species of whale catfishes (Cetopsidae, Cetopsinae), representing a new genus, were among the interesting finds and are the subject of this paper.

The whale catfishes have been recognized as a distinct family-level taxon since the publication of Gill (1872) and have almost universally been referred to as the Cetopsidae since 1912 (Miranda Ribeiro 1912). After a long period of relative neglect, whale catfish systematics has undergone considerable investigation in recent years. Two unpublished theses (Oliveira 1988 and Milani de Arnal 1991) described the morphology of selected taxa and examined the species of the family. Ferraris and Brown (1991) briefly discussed the various proposed schemes of classification of cetopsids in an effort to place their newly discovered species into an appropriate genus. Lundberg and Rapp Py-Daniel (1994) commented on the lack of explicit phylogenetic hypotheses available for the genera of whale catfishes. They observed that placement of newly discovered species into existing genera was problematic inasmuch as none of the genera are diagnosed on derived characters.

A first step toward a hypothesis of relationships of whale catfishes was provided by de Pinna and Vari (1995). Therein, the Neotropical family Helogenidae was proposed as the sister group to the whale catfish, and that the two taxa be considered as subfamilies of an expanded Cetopsidae. The whale catfishes, now the Cetopsinae, were diagnosed on a suite of derived osteological and myological characters, as well as a number of external features that, in combination, are unique to that group. Although de Pinna and Vari did not examine relationships among whale catfishes, they did provide the framework for such a study.

The two undescribed species that are the subjects of this paper were examined in the light of the contribution of de Pinna and Vari. The species can be unambiguously assigned to the Cetopsidae. Further, they exhibit none of the derived characters of one of the two included clades: the Helogeninae, and possess most, but not all of the characters of the Cetopsinae. The two species share characters that are either unique within the Siluriformes, or are otherwise unknown within the Cetopsidae. On the basis of all of these observations, the two species are thought to represent a new genus of whale catfishes that diverged early in the evolution of the Cetopsinae.

MATERIALS AND METHODS

Standard length (SL) was measured with dial calipers, to 0.5 mm, and is the measurement given for specimens; other measurements were taken with an ocular micrometer on a Wild M-5 dissecting microscope, to 0.1 mm. All measurements represent the shortest straight-line distances between points. Head length (HL) is measured from the snout tip to the end of the fleshy gill cover. Anal fin-base length is measured to the last fin ray base and does not include the membrane extending from the last ray to the first procurrent caudal-fin ray. Eye length is the horizontal diameter of the pigmented portion of the eye, as the eye is not bounded by a bony orbit. Interocular width is the shortest distance between the eyes. Vertebral counts include the single, autogenous first centrum, three for the complex centrum and count the ural complex as one.

Osteological details of *Denticetopsis* are available only for *Denticetopsis sauli*, because *D. royeroi* is known only from the holotype. Therefore, statements about the relationships of *Denticetopsis* are based on the anatomy of *D. sauli*, which is designated as the type species.

Type specimens of these species are deposited at the following institutions: Academy of Natural Sciences, Philadelphia (ANSP); National Museum of Natural History, Washington (USNM); and Museo Biología, Universidad Central de Venezuela, Caracas (MBUCV). Comparative material was examined from the collections of the American Museum of Natural History (AMNH), the California Academy of Sciences (CAS or SU) and USNM.

DESCRIPTIONS

Denticetopsis **n. gen.**

TYPE SPECIES. — *Denticetopsis sauli* n. sp.

DIAGNOSIS. — A new genus of Cetopsinae with the following combination of characters (synapomorphic characters in italics): *Caudal fin obliquely truncate, with dorsalmost principal ray longest; anal fin joined by membrane to ventral margin of caudal fin; lateral line canal not extending posteriorly past abdomen; caniniform teeth in a cluster at the symphysis of dentary; vomer edentulous; dorsal fin with four segmented rays*; gill opening not restricted, branchiostegal membranes joined only slightly to isthmus; swimbladder not encapsulated in bone by extension of Weberian complex; membranous attachment present between abdomen and basal one-third to one-quarter of innermost ray of pelvic fin.

ETYMOLOGY. — From *dentis* Latin for tooth (Brown 1956), in reference to the elevated symphyseal teeth of the dentary; and *cetopsis* Latin for whale-like, a commonly used suffix for, and source of the common name of, whale catfishes; gender is feminine.

REMARKS. — *Denticetopsis* exhibits the osteological characters described in de Pinna and Vari (1995) that diagnose the Cetopsidae. For example, the anterior cartilage of the palatine is flared anteriorly and extended onto the mesial surface of the bone (Fig. 1); and the interopercle broadly contacts, and overlaps, the anteroventral margin of the opercle (Fig. 2). *Denticetopsis* further exhibits the external characters listed in de Pinna and Vari (1995) as useful for recognition of the cetopsids, including: an elongated anal fin base (Figs. 3, 4), the absence of nasal barbels, the orbital margin obscured by a

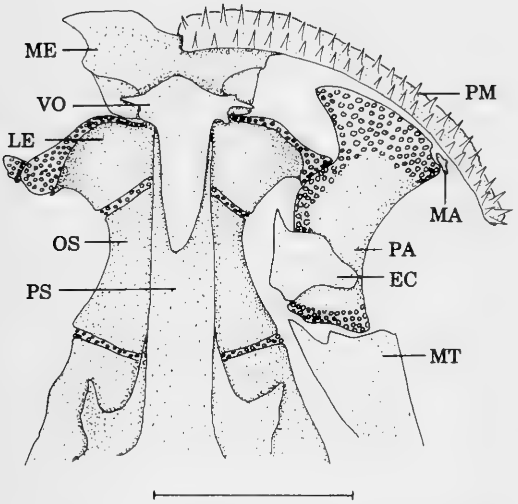

FIGURE 1. *Denticetopsis sauli*, ANSP 161432, ventral view of ethmoid region, anterior at top. Scale bar represents 1 mm. EC - ectopterygoid; LE - lateral ethmoid; MA - maxilla; ME - mesethmoid; MT - metapterygoid; OS - orbitosphenoid; PA - palatine; PM - premaxilla; PS - parasphenoid; VO - vomer.

thick epidermal layer, and slender, thread-like barbels.

None of the derived characters listed in de Pinna and Vari (1995) supporting the monophyly of the Helogeninae are found in *Denticetopsis*. Similarly, the external characters that are useful in the recognition of helogenines are not found in these fishes. In contrast, most of the characters that diagnose the whale catfish, the Cetopsinae, are found in *Denticetopsis*. The basipterygium exhibits an enlarged, ramified posterior cartilage (Fig. 5); the hyomandibula has a basal, laminar sheet extending anteriorly from the neurocranial articular head (Fig. 2); and hypertrophied levator arcus palatini and adductor mandibulae muscles (Fig. 6) extend onto the dorsal surface of the neurocranium, although the latter is in a somewhat modified form (see below). Two characters cited in de Pinna and Vari as either diagnostic of cetopsines, or valuable in their recognition, are not found in *Denticetopsis*. The anterior tip of the third epibranchial is not curved anteriorly, and it appears to contact the cartilages of both the third and fourth pharyngobranchial elements. This resembles the primitive catfish condition and not the derived cetopsine state. Similarly, *Denticetopsis* lacks furrows in the skin into which the mental barbels fit. This, too, reflects the absence of a derived cetopsine character. Thus, it appears that while *Denticetopsis* can unambiguously be assigned to the Cetopsinae on the basis of some of the characters listed in de Pinna and Vari, the curved epibranchial and mental barbel furrows may be derived for a more restricted subgroup of that clade.

The monophyly of *Denticetopsis* is supported by several derived characters, all of which are listed in the diagnosis (above). Interpretation of some of these characters is not problematic, as they represent either unique features in catfishes (e.g., the enlarged symphyseal teeth on an expanded oral surface of the dentary) or features that are only rarely found in catfishes (e.g., obliquely truncate caudal fin, and the membranous attachment between the caudal fin and the anal fin)(Figs. 7, 8). Other features, such as the low number of dorsal fin rays, absence of teeth on the vomer, and the truncated lateral line canal system, are not rare in catfishes. They are, however, derived within the Cetopsidae and can be considered diagnostic for the genus. However, features such as these are cited in Weitzman and Vari (1988) as typical reductive features of miniature species and may be related to the small size of the species. A search for equivalent sized cetopsines for comparison uncovered two *Pseudocetopsis* specimens (USNM 226147, 17.6 mm; and SU 50456, 27 mm) from Surinam. These specimens have fully-developed vomerine tooth patches and lateral line canal systems as well as obvious

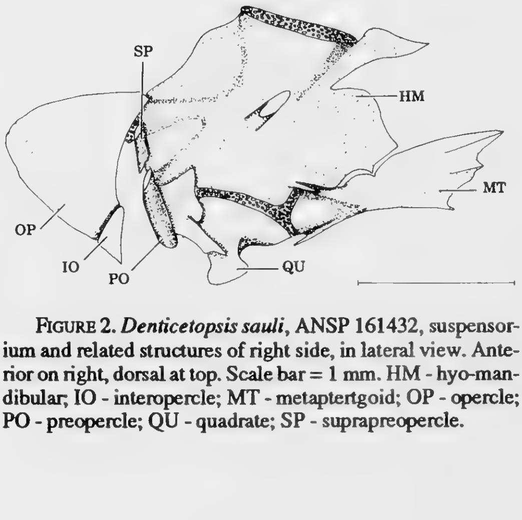

FIGURE 2. *Denticetopsis sauli*, ANSP 161432, suspensorium and related structures of right side, in lateral view. Anterior on right, dorsal at top. Scale bar = 1 mm. HM - hyo-mandibular; IO - interopercle; MT - metaptertgoid; OP - opercle; PO - preopercle; QU - quadrate; SP - suprapreopercle.

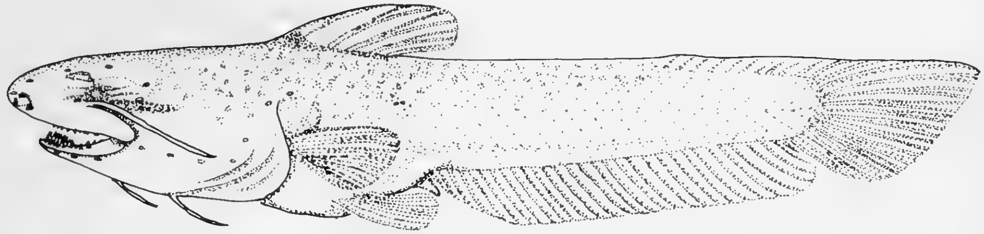

FIGURE 3. *Denticetopsis sauli*, MBUCV-V-20300 (20.5 mm SL), holotype.

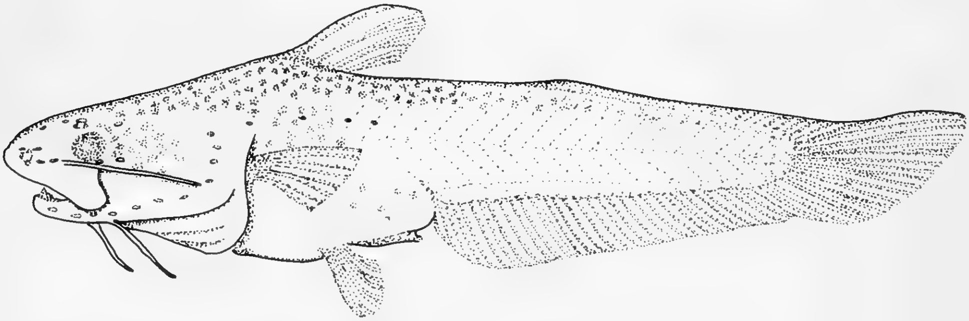

FIGURE 4. *Denticetopsis royeroi*, MBUCV-V-26785 (18.7 mm SL), holotype.

furrows associated with the mental barbels. Thus, it appears that these features develop in comparably small individuals of related species and their absence need not be considered the result of paedomorphosis.

Several additional features that are not mentioned in the diagnosis are not easily interpreted in a phylogenetic context but are worth pointing out. The posterior fontanelle is greatly enlarged (Fig. 9) and covers much of the posterior portion of the dorsal neurocranium. A condition similar to this is found in *Bathycetopsis* (Lundberg and Rapp Py-Daniel 1994). As mentioned above, the adductor mandibulae is unusual among cetopsines inasmuch as it originates only along the posterior margin of the supraoccipital (Fig. 6). In all other cetopsines (except *Bathycetopsis* which, according to Lundberg and Rapp Py-Daniel [1994], lacks an expanded adductor mandibulae) the muscle is broadly attached over the posterior half of the dorsal midline of the neurocranium (de Pinna and Vari 1995). In *Cetopsis coecutiens* (CAS 78929), *Hemicetopsis candiru* (CAS 65902), and *Pseudocetopsis* sp. (SU 50456) the adductor mandibulae extends to the posterior margin of the supraoccipital as well (pers. obs.). The polarity of this variation among species, as well as the relationship of the enlarged fontanelle to this variation, must await a more thorough study.

Denticetopsis sauli n. sp.
(Figs. 3, 10, 11)

HOLOTYPE. — MBUCV-V-20300 (20.5 mm) Venezuela: Estado Amazonas, outflow stream from series of morichales, ca. 5.0 km from mouth of Río Pamoni, 2°48′N, 65°53′W, 18 Mar 1987, B. Chernoff et al.

PARATYPES. — (all taken with holotype) MBUCV-V-20301 (2, 20.0–21.0 mm); ANSP 161432 (4:2 as prepared skeletons in glycerine, 16.5–21.0 mm).

DIAGNOSIS. — A relatively slender species of *Denticetopsis* in which the body depth at the point of insertion of the epaxial musculature is less than 20% SL. The eye is less than 11% SL. The fleshy maxilla extends approximately one eye diameter past the posterior margin of

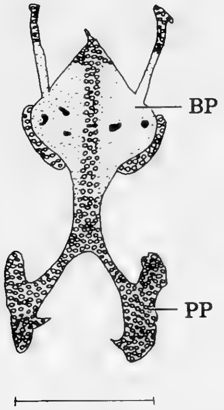

FIGURE 5. *Denticetopsis sauli*, ANSP 161432, ventral view of pelvic girdle, anterior at top. Scale bar represents 1 mm. BP - basipterygium; PP - posterior process of basipterygium.

the eye, and the membrane that joins the caudal fin to the anal fin is distinctly incised.

DESCRIPTION. — Selected measurements for the type specimens are given in Table 1.

Body terete, deepest at dorsal fin base; dorsal profile of head and body nearly straight, with only a slight elevation in the vicinity of the dorsal spine; body depth at supraoccipital spine less than 20% SL; in cross section, body rounded at abdomen, becoming compressed posteriorly; body depth in caudal region decreasing uniformly posteriorly.

Head large, depressed anteriorly; head length one-third of SL, depth at eyes approximately 40% HL; dorsal profile of head convex, especially in region of enlarged adductor mandibulae; snout bluntly rounded, extending beyond anterior margin of dentary; anterior naris a short, anteriorly directed, tube at snout margin, posterior naris a short broad tube situated above anterior half of eye, directed posterodorsally; eye small, lateral, diameter of pigmented portion approximately one-tenth HL and between one-third and one-half snout length; eye covered with thick epidermal layer, not bounded by bony orbit; maxillary barbel originates in fleshy groove between upper jaw and middle of eye, barbel tip not reaching opercular margin; mental barbels not lying in grooves, medial mental barbel originates anterior to equally long lateral mental; mental barbels not extending to posterior opercular margin; postorbital region of head dominated by massive adductor mandibulae that originates near to, but not contacting, dorsal midline of neurocranium; branchiostegal rays 10–12, opercular membranes joined to isthmus anteriorly, not extending to tip of first branchiostegal ray, gill openings not restricted, extending from above origin of pectoral fin to vertical line at anterior margin of eye.

Mouth large, subterminal; gape extends posterior of eye by at least one eye diameter; upper jaw teeth small, conical, uniform in size; in two rows from symphysis to below middle of eye; dentary with single row of small conical teeth from base of coronoid process midway to symphysis; more anteriorly, a second row lateral to primary row; at symphysis, oral surface of dentary expanded medially with irregular patch of large conical teeth, smaller teeth of primary row continue to symphysis anterior to enlarged teeth; teeth absent from palate. Seven or eight rakers on outer surface of lower limb of first gill arch, none on upper limb. Rakers increase in size posteriorly, anterior ones smaller than interval between successive rakers, posterior ones longer than interval.

Cephalic lateral-line canal system with indis-

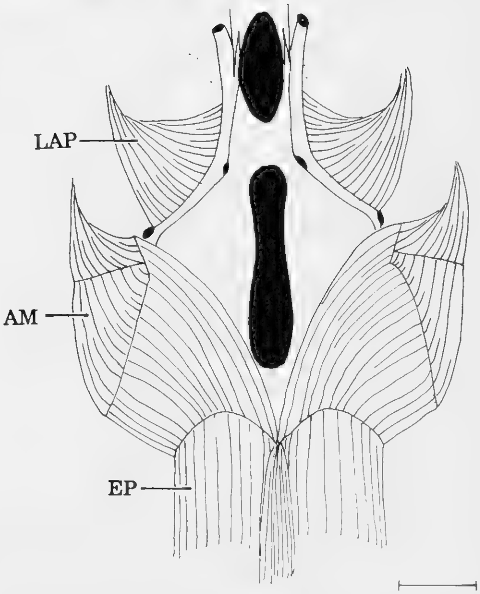

FIGURE 6. *Denticetopsis sauli*, MBUCV-V-20301, dorsal view of posterior portion of head showing superficial muscles, anterior at top. Scale bar represents 1 mm. AM - adductor mandibulae; EP - epaxialis; LAP - levator arcus palatini.

TABLE 1. Selected measurements for *Denticetopsis sauli* and *Denticetopsis royeroi*. All values represent percentages. Mean and range values are for the entire type series.

	Denticetopsis sauli			***D. royeroi***
	holotype	mean	range	holotype
Standard length (mm)	20.5		16.5–21.0	18.5
Predorsal length (in SL)	38.5	38.35	34.3–40.6	37.4
Head length (in SL)	34.6	33.17	30.8–36.4	32.1
Body depth at epaxial origin (in SL)	19.0	18.94	17.1–19.5	23.5
Body depth at anus (in SL)	14.6	16.34	14.6–18.2	18.2
Depth at caudal peduncle (in SL)	8.3	8.28	7.2–9.1	7.5
Body width at anus (in SL)	8.8	10.42	8.7–12.7	9.1
Anal fin base length (in SL)	39.0	41.89	39.0–44.9	39.0
Preanal length (in SL)	54.2	51.91	47.7–55.0	50.3
Interorbit width (in HL)	28.2	32.90	28.2–38.3	28.3
Head width (in HL)	54.9	58.25	53.3–62.1	58.3
Snout length (in HL)	26.8	25.80	23.3–30.0	26.7
Eye (in HL)	8.5	9.70	8.5–10.6	11.7

tinct pores along mandibular, infraorbital, and supraorbital series; canals deep beneath skin and visible only in skeletal preparations; canals on body consist of one or two disjunct segments bordered by one pore at each end; canals restricted to abdomen and only visible after removing superficial mucus.

Dorsal fin well-developed, origin approximately one-third SL behind snout tip; margin rounded, second branched ray longest; first ray spinous for basal half, segmented and flexible distally, without filamentous extension; 4 branched rays (one specimen with 3); dorsal-fin spinlet absent; distinct adipose-dorsal fin absent, but low ridge of adipose-like tissue extends from dorsal procurrent caudal-fin rays to vertical above anterior half of anal fin; caudal fin obliquely truncate, dorsal principal rays longest, 13 branched rays; anal fin-base long, extending from anus to caudal fin, posterior ray attached to first two procurrent caudal fin rays by membrane, with distinct notch at confluence; anterior margin of anal fin broadly rounded, ventral margin straight, 29 to 32* unbranched rays; pelvic fin short, rounded, fin origin in advance of vertical of posterior dorsal-fin base, adpressed fin extends to anal fin origin, rays: i,5; pectoral fin rounded, first ray spinous to just past middle of ray, flexible distally; spinous portion of first ray without serrations; adpressed fin extends to vertical through anus, but not reaching anal-fin origin; rays: I,6 or I,7*. (NOTE. — The count for the holotype is indicated by an asterisk *.)

PIGMENTATION IN ALCOHOL. — Pigmentation primarily from scattered brown stellate chromatophores approximately one eye diameter in size when fully expanded on head and lateral abdominal wall; caudal chromatophores noticeably smaller; body appears light brown when chromatophores are fully expanded, or creamy white with fine brown flecks when contracted.

Chromatophores evenly distributed over most of caudal region except for denser concentration on dorsal midline and at caudal-fin base; chromatophores more sparse on anterior caudal region and lateral abdominal walls; chromatophores concentrated in diffuse triangular blotch in humeral region, extending for length of adpressed pectoral fin; dorsal and lateral surface of nape, snout, and head (to level of eyes) with few scattered chromatophores; cheek ventral of eye, operculum, ventral surface of head and abdomen without, or with few widely-scattered chromatophores. Barbels without pigment or with one or two spots basally. Dorsal fin with spot covering base of first two rays, spot no larger than eye. Pectoral, pelvic, and anal fins immaculate; caudal fin dusky, small chromatophores scattered irregularly along dorsal and ventral margins of rays.

DISTRIBUTION. — The species is known from the Río Pamoni, a north-flowing river at the

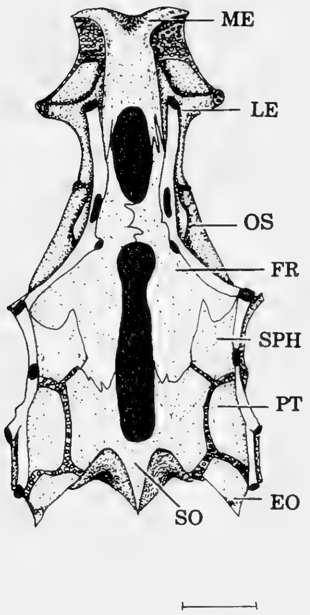

FIGURE 7. *Denticetopsis sauli*, ANSP 161432, dorsal view of neurocranium and associated structures, anterior at top. Scale bar represents 1 mm. EO - epioccipital; FR - frontal; LE - lateral ethmoid; ME - mesethmoid; OS - orbitosphenoid; PT - pterotic; SO - supraoccipital; SPH - sphenotic.

northeastern end of Brazo Casiquiare, in southern Venezuela.

ETYMOLOGY. — I take great pleasure in naming this fish for William G. Saul, collection manager of the Ichthyology Department of the Academy of Natural Sciences, Philadelphia, who participated in the collection of the type series of this species and who brought these fishes to my attention.

SIZE. — The largest individual examined, 21 mm SL., possessed mature testes. It is presumed, therefore, that the species does not grow substantially larger than this, making it the smallest species of whale catfishes.

Denticetopsis royeroi n. sp.

(Figs. 4, 10, 12)

HOLOTYPE. — MBUCV-V-26785 (formerly USNM 268643) (1, 18.5 mm), Venezuela: Estado Amazonas, Caño Chola at crossing of San Carlos de Río Negro to Solano road, 1°58′N, 67°00′W, 5 Dec 1984, R. P. Vari, C. J. Ferraris, and A. Machado-Allison.

DIAGNOSIS. — A species of *Denticetopsis* in which the maxilla extends only slightly past the posterior margin of the eye; the eye is almost 12% HL; the body depth at the supraoccipital spine is 23% SL; and the membranous connection between the anal fin and the caudal fin is without a distinct notch.

DESCRIPTION. — Selected measurements for the holotype are given in Table 1.

Body terete, deepest at dorsal fin base; dorsal profile of head and body distinctly flexed at dorsal fin origin; in cross section, body rounded at abdomen, becoming compressed posteriorly; abdomen globose; body depth in caudal region decreasing uniformly posteriorly.

Head large, slightly depressed anteriorly; depth at eyes approximately 40% HL; head depth and width nearly equal at opercle; head length one-third of SL; dorsal profile of head straight to dorsal-fin origin, except for slight notch at juncture of adductor mandibulae and epaxialis; snout bluntly rounded, extending beyond anterior margin of dentary; anterior naris a short anteriorly directed tube at snout tip, posterior naris a short tube above anterior half of eye directed dorsolaterally; eye small, lateral, greater than 11% HL and less than one-half snout length; eye covered with thick epidermal layer, not bounded by bony orbit; maxillary barbel originates in fleshy groove between upper jaw and middle of eye, barbel tip not reaching opercular margin; mental barbels not lying in grooves, medial mental barbel originates anterior to lateral mental; mental barbels not reaching posterior margin of gill cover; postorbital region of head dominated by massive adductor mandibulae that originate on dorsal surface of neurocranium, reaching near to, but not contacting dorsal midline; branchiostegal membranes not connected to isthmus, gill openings

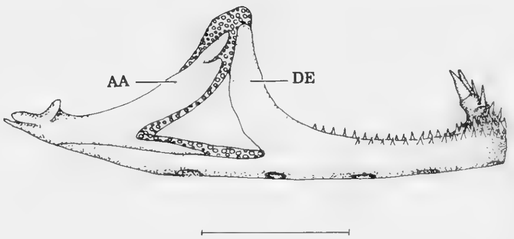

FIGURE 8. *Denticetopsis sauli*, ANSP 161432, lateral view of right dentary, anterior to right, dorsal at top. Scale bar represents 1 mm. AA - anguloarticular; DE - dentary.

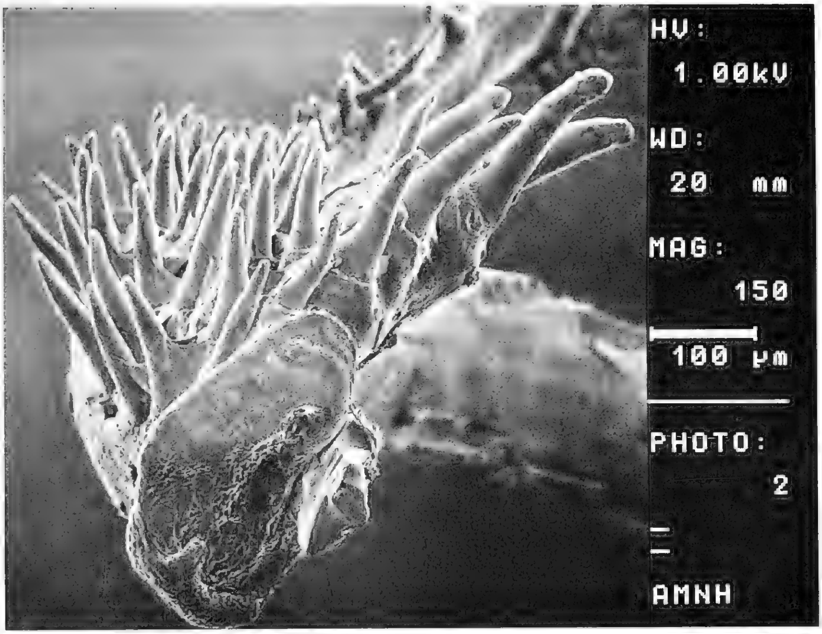

FIGURE 9. *Denticetopsis sauli*, ANSP 161432, scanning electron micrograph of mesial view of symphysis of right dentary, anterior to left, dorsal at top.

extend from above origin of pectoral fin to vertical line through anterior margin of eye.

Mouth large, subterminal; gape does not extend beyond posterior margin of eye; teeth on both jaws small, conical; symphysis of lower jaw with posteriorly expanded oral surface covered by somewhat larger teeth.

Cephalic lateral-line canal system with indistinct pores along mandibular, infraorbital, and supraorbital series; canals not visible; one pair of pores connected by slender canal observed midlaterally on body slightly posterior to vertical through posterior extent of dorsal fin base.

Dorsal fin well-developed, origin approximately 40% SL behind snout tip, margin rounded; first ray spinous for basal third, segmented distally, without filamentous extension; 4 branched rays; dorsal-fin spinlet absent; distinct adipose-dorsal fin absent, but low ridge of adipose-like tissue extends from dorsal procurrent caudal-fin rays to vertical above anterior half of anal fin; caudal fin obliquely truncate, dorsal principal rays longest, 13 branched rays; anal fin-base long, extending from anus to caudal fin, membranous extension from posterior ray broadly attached to caudal fin, without distinct notch at confluence; anterior margin of anal fin broadly rounded, ventral margin straight, 31 unbranched rays; pelvic fin short, rounded, fin origin anterior to vertical of posterior dorsal-fin base, adpressed fin extends to anal fin origin, rays: i,5; pectoral fin rounded, first ray not spinous, but slightly stiffened, visibly segmented and flexible distally; spinous portion of first ray without serrations; adpressed fin not reaching vertical through anus, but not reaching anal-fin origin; rays: I,7.

PIGMENTATION IN ALCOHOL. — Pigmentation primarily from scattered brown stellate chromatophores approximately one-half eye diameter or less in size when fully expanded on head and lateral abdominal wall; caudal chromatophores noticeably smaller; body creamy white with fine brown flecks.

Chromatophores evenly distributed over most of caudal region except for denser pattern on, and along side of, dorsal midline; single row of chromatophores dorsal to anal fin base; dorsal and lateral surface of nape, snout, and head (to level of eyes) with few scattered chromatophores; cheek ventral of eye, operculum, ventral surface of head and abdomen without, or with few widely scattered chromatophores. Barbels without pigment or with one or two spots

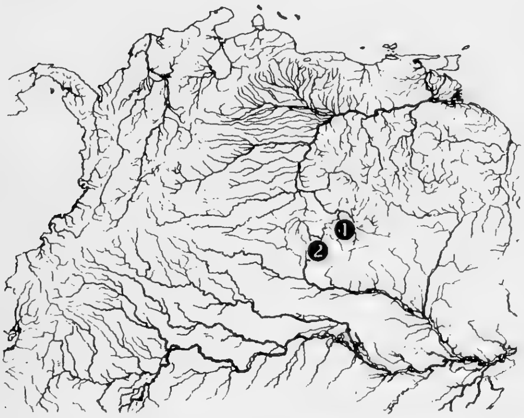

FIGURE 10. Drainage map of northern South America from the Amazon River northwards, with the type localities of *Denticetopsis sauli* (1) and *D. royeroi* (2) indicated. Scale 1 cm equals approximately 210 km.

basally. Dorsal fin with diffuse spot covering base of first two rays, spot no larger than eye. Pectoral, pelvic, and anal fin rays and membranes immaculate; caudal fin with small chromatophores scattered irregularly along dorsal and ventral margins of each ray.

DISTRIBUTION. — The species is known only from the Río Negro drainage of southern Venezuela.

ETYMOLOGY. — The new species is named for Ramiro Royero, a Venezuelan ichthyologist, who accompanied me on all of my field work in Venezuela.

SIZE. — This species is known from the 18.7 mm holotype. The sex and state of maturation for this specimen are unknown.

ACKNOWLEDGMENTS

The holotype of *Denticetopsis royeroi* was collected with Richard Vari during fieldwork that was supported by funding from the International Environmental Sciences Program (IESP), Neotropical Lowland Research Program of the Smithsonian Institution. The specimens of *Denticetopsis sauli* were studied with the permission of Barry Chernoff and Scott Schaefer. This study was initiated while I was at AMNH and completed at CAS. Access to the collections and equipment at these institutions was provided by Gareth Nelson, C. Lavett Smith, Tomio Iwamoto, and William Eschmeyer. Photographs of the holotypes were taken by Susan Middleton and Dong Lin at CAS. The manuscript was reviewed by Mário de Pinna and John Lundberg. The assistance of these individuals and organizations is appreciated.

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FIGURE 11. *Denticetopsis sauli*, MBUCV-V-20300 (20.5 mm SL), holotype.

FIGURE 12. *Denticetopsis royeroi*, MBUCV-V-26785 (18.7 mm SL), holotype.

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MESOAMERICAN *BACTRIS* (PALMAE)

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Mesoamerican *Bactris* (Palmae). The genus *Bactris* Jacq. ex Scop. in Mesoamerica is reviewed, based on field and herbarium study of morphology. A key is provided to distinguish the twenty species, two with two varieties each, recognized from the region. Each species and variety is described, including distribution and habitat. Four species are new to science (*B. charnleyae*, *B. grayumii*, *B. kunorum*, and *B. panamensis*) and two varieties (*B. mexicana* var. *trichophylla* and *B. glandulosa* var. *baileyana*) represent new combinations. The synonymy which is provided accounts for all names which have been used in the Mesoamerican region.

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The Neotropical *Bactris* Jacq. ex Scop. (Palmae, Arecoideae, Cocoëae) is notorious among students of palms. Specimens are difficult to prepare because of the spininess of the plants, and so there are relatively few collections in herbaria. Those that do exist are often fragmentary, and flowers are seldom represented because of the short time of anthesis. Natural variation has been misunderstood, and a surplus of names has been proposed. The types of many of these have been destroyed in both Brazil (those of Barbosa Rodrigues and Wallace) and Berlin (those of Burret). The major publications on the genus (Burret 1933, 1933–1934) contain neither keys nor illustrations, and are difficult to use. They are actually a catalogue of names. The species are readily recognizable, both in the field and from well-collected specimens, and the number of species is certainly much smaller than the 250-plus names suggest. Henderson et al. (1995) recognize 64 species. Recent intensive collecting in Central America, together with the publication of a cladistic study of *Bactris* (Sanders, 1991), has made the genus less difficult to understand.

Sanders (1991) emphasized fruit characters for phylogenetic analysis. We have experienced difficulties in interpreting some of these characters. We could not see tubercules or papillae at the bases of the endocarp fibers in the Central American members of the Tuberculate clade (*B. coloniata*, *B. major*, *B. maraja*, *B. militaris*, *B. pilosa*), with the possible exception of *B. militaris*. We had difficulty seeing displaced endocarp pores in the Mesomerican members of the Tuberculate clade; indeed we considered that *B. pilosa* had the most symmetrical endocarp pores of any Mesomerican *Bactris*, and some non-members of the clade had more or less asymmetrical endocarp pores (e.g., *B. coloradonis*). The interpretation of the endocarp pores depends on how many character states one can distinguish; Sanders distinguished three states, we saw two. We had difficulty interpreting pitted endocarps. *Bactris militaris* has two populations, one with pitted endocarps and the other with smooth endocarps (see discussion under that species). A second species, *B. kunorum*, also has pitted endocarps, but this species appears to belong to the nonfibrous clade. We had difficulty interpreting juice sacs attached to endocarp fibers. In most members of the Atropurpureous clade these were obvious, but we also saw them in an orange-fruited species, *B. charnleyae*. We also had difficulty interpreting rachis bracts of the inflorescence, because they are hard to see and the shapes are difficult to divide into discrete character states.

This paper treats all of the *Bactris* species of Mesoamerica, and refers to synonymy the excess names that have been applied to the genus in the region. Synonyms from outside the region are excluded. We cite specimens only from Mesoamerica. This forms part of a treatment of the Palmae for *Flora Mesoamericana*, and a revision of the whole genus which is in preparation by Henderson.

There are problems with lectotypification in the genus. Some have considered that citation of a specimen by Burret (1933, 1934), Dahlgren (1936, 1959) or Glassman (1972) constitutes lectotypification. However, according to Greuter (1988, art. 8.3), unless the word "type" is specifically used in reference to a specimen, that specimen cannot be considered to have been designated as lectotype.

BACTRIS JACQ. EX SCOP.

Small to large, solitary or (usually) clustered, spiny, pleonanthic, monoecious, protogynous palms. Leaves pinnate, or pinnately veined if simple; sheath open, with or rarely without an ocrea; petiole very short to long; rachis usually long; pinnae regularly arranged or clustered, variously shaped, acuminate or rarely praemorse apically, or often the leaf simple and bifid. Inflorescences interfoliar, rarely infrafoliar, once-branched or spicate; prophyll much shorter than the peduncular bract; rachillae usually covered with trichomes; flowers arranged in triads, these regularly arranged proximally along the rachillae or more often scattered amongst paired or solitary staminate flowers, staminate flowers only distally; staminate flowers sessile or pedicellate, asymmetrical; sepals connate into a 3-lobed calyx; petals connate basally, free apically (in Mesoamerica); pistillode absent; stamens 6 (in Mesoamerica), dorsifixed, filaments inflexed apically; pistillate flowers sessile; sepals connate into a tubular or annular calyx; petals connate into a tubular corolla; staminodes absent, small and triangular, or connate into a staminodial ring; gynoecium trilocular, triovulate; fruits 1-seeded, small to large, variously shaped, usually orange or yellow, or purple-black; mesocarp floury or juicy; endocarp with or without fibers attached, the pores at or above the equator; endosperm homogeneous; eophyll bifid; germination adjacent-ligular.

KEY TO MEXICAN AND CENTRAL AMERICAN SPECIES OF BACTRIS

1. Stems 4–15 m tall, 10–14 cm diam; sheaths lacking an ocrea; petiolar spines in 3 longitudinal lines; fruits to 5 cm long, 3 cm diam; always cultivated or planted .... 7. *B. gasipaes.*

1. Stems 0.8–10 m tall, 0.5–8 cm diam; sheaths with an ocrea; petiolar spines not in 3 lines; fruits less than 4.5 cm long; naturally occurring.

    2. Rachillae (24–) 40–90, filiform; triads ± regularly arranged on proximal part of rachillae.

        3. Fruits glabrous; pinnae pubescent abaxially (almost glabrous in var. *baileyana*), linear to narrowly elliptic,without prominent cross-veins.................. 8. *B. glandulosa.*

        3. Fruits covered with short bristles; pinnae glabrous abaxially, linear, with prominent cross-veins .... 1. *B. barronis.*

    2. Rachillae 3–34 (–51), not filiform; triads scattered amongst paired or solitary staminate flowers.

        4. Ripe fruits yellow, orange, or red.

            5. Leaves simple, elongate with parallel sides; peduncle erect, not recurved; Costa Rica and Panama .... 18. *B. militaris.*

            5. Leaves pinnate, or simple but then not elongate and parallel-sided; peduncle erect or recurved.

                6. Peduncle erect, not recurved; stems small, 1–3 m tall, 0.5–1.5 cm diam; rachillae 3–12, 2–5 cm long.

                    7. Leaves pinnate with numerous, glabrous pinnae .... 19. *B. panamensis.*

                    7. Leaves usually simple, often pilose abaxially.

                        8. Pinnae pilose abaxially; peduncle with appressed, brown spines; fruits 1.2–1.5 cm diam; endocarp fibers absent or few .... 12. *B. hondurensis.*

                        8. Pinnae glabrous; peduncle with elongate, black spines; fruits 5–8 mm diam; endocarp with numerous fibers .... 3. *B. charnleyae.*

                6. Peduncle strongly recurved; stems large, 2.5–6 m tall, 2–6 cm diam; rachillae 8–51, 4.3–29 cm long.

                    9. Leaves simple or irregularly divided, glabrous, thick and leathery; fruits ovoid, not rostrate, fruiting calyx truncate; lowlands in Nicaragua (Chontales, Zelaya) and Costa Rica (Limón, San José) .... 10. *B. grayumii.*

                    9. Leaves pinnate to simple, glabrous to pubescent, not thick and leathery (except *B. kunorum*); fruits ovoid, obovoid, or turbinate, rostrate or not; fruiting calyx crenate, irregularly divided or truncate; widely distributed.

                        10. Leaves thick and leathery, glabrous; fruits 1.1–1.2 cm long, prominently rostrate; Panama (Panamá, San Blas) .... 13. *B. kunorum.*

                        10. Leaves not thick and leathery, glabrous to pubescent; fruits variously sized, not prominently rostrate; widespread.

                            11. Rachillae 14–29 cm long; fruits ca. 1.5 cm long, briefly rostrate; pinnae usually with prominent cross-veins .... 5. *B. coloradonis.*

                            11. Rachillae 6–16 cm long; fruits mostly smaller, rostrate or rounded; pinnae usually without prominent cross-veins.

                                12. Fruiting calyx 3-lobed; fruits prominently rostrate; rachillae few (7–17); sheath, petiole and rachis densely and minutely spinulose; mostly above 600 m elevation .... 6. *B. dianeura.*

                                12. Fruiting calyx truncate; fruits rounded or obscurely rostrate; rachillae many (15–35); leaves not minutely spinulose; mostly below 600 m elevation.

                                    13. Inflorescences compact with closely spaced rachillae, these 5–10 cm long; pinnae glaucous, concave below; Atlantic slope of Nicaragua, Costa Rica and Panama .. 2. *B. caudata.*

13. Inflorescences lax with loosely spaced rachillae, these 7–16 cm long; pinnae green, not concave below; widespread.
    14. Leaf rachis with black spines; pinnae linear to linear-lanceolate, 35–85 cm long, usually pubescent abaxially; rachillae 26–38; Mexico to NE Nicaragua .... 17. *B. mexicana.*
    14. Leaf rachis without any spines; pinnae, ± sigmoid, 25–35 cm long, often glabrous abaxially; rachillae 15–21; SE Nicaragua to Panama.................................. 9. *B. gracilior.*

4. Ripe fruits purple-black or yellowish brown.
    15. Pistillate flowers and fruiting perianth without staminodial ring; fruits 1.5–2.5 cm long, 1.3–2 cm diam.
        16. Fruits either covered in short, brown bristles or minutely spinulose; fruiting perianth only slightly shorter than the corolla.
            17. Fruits yellowish brown, covered in short, brown bristles; leaf spines yellowish brown; pinnae glabrous....................... 4. *B. coloniata.*
            17. Fruits purple-black, minutely spinulose; leaf spines black; pinnae pubescent .... 20. *B. pilosa.*
        16. Fruits glabrous; fruiting perianth much shorter than the corolla.
            18. Pinnae ± equally and briefly bifid at the apex; pinnae pale green and easily falling from dried specimens .... 11. *B. guineensis.*
            18. Pinnae not bifid at the apex; pinnae dark green and not falling from dried specimens.
                19. Leaf spines flattened, yellowish brown; pinnae sigmoid, lacking marginal spines .... 16. *B. maraja.*
                19. Leaf spines terete, black; pinnae linear, with marginal spines 2–3 cm long .... 14. *B. longiseta.*
    15. Pistillate flowers and fruiting perianth with staminodial ring; fruits 3.3–4.5 cm long, 2.3–3.5 cm diam .... 15. *B. major.*

1. **Bactris barronis** L. H. Bailey, Gentes Herb. 3:101. 1933.

TYPE. — PANAMA. **Canal Area:** Barro Colorado Island, 6 Jul 1931, *L. Bailey 503* (holotype, BH).

Stems cespitose, forming dense colonies, 2–8 m tall, 3.5–8 cm diam, the internodes prominently spiny. **Leaves** 4–9; sheath 30–84 cm long, sheath and petiole densely black-spiny with spines to 11 cm long; petiole 14–57 cm long; rachis 0.7–2.4 m long; pinnae 31–45 per side, linear to linear-lanceolate, conspicuously cross-veined, setose marginally, usually regularly arranged and spreading in the same plane, occasionally irregular or with gaps; middle pinnae 47–72 cm long, 1.5–5.3 cm wide. **Inflorescences** interfoliar; peduncle (9–) 16–25 cm long, densely brown-spiny, tightly curved in fruit; prophyll 6–19 cm long; peduncular bract 18–51 cm long, covered with dense black spines to 1 cm long, after anthesis; rachis 3–8 (–17) cm long; rachillae 80–90, filiform, to 12 cm long, ca. 1 mm diam; triads more or less regularly arranged on proximal part of rachillae, but sometimes intermixed with paired or solitary staminate flowers; **staminate flowers** deciduous, not seen; **pistillate flowers** 3 mm long, arranged on 1 side of rachillae; calyx minutely 3-lobed; corolla tubular, truncate, pubescent; staminodia absent; **fruits** densely clustered, subglobose or turbinate, with prominent, abrupt stigmatic residue, 1–1.6 cm diam, orange-red, covered with short bristles, glabrescent; mesocarp mealy; endocarp turbinate; endocarp fibers few, free, terete; endocarp pores equidistant; fruiting calyx minute, corolla 2–3 mm long, crenate, irregularly split by the enlarging fruit.

ADDITIONAL SPECIMENS EXAMINED. — PANAMA. **Canal Area:** Río Chilibre, *Cook & Martin 67* (F, US); Barro Colorado Island, *Bartlett 16727* (MICH), *16734* (MICH), *16872* (MICH), *Croat 5500* (SCZ), *5867* (SCZ), *6534* (MO), *6541* (MO, SCZ), *8627* (MO),

8792 (MO), *9030* (MO, SCZ), *9127* (MO, SCZ), *9272* (MO, SCZ), *9450* (MO), *10297* (MO, SCZ), *10805* (MO), *10826* (MO), *10980* (MO), *11024* (MO), *11199* (MO), *15417* (MO), *16513* (MO), *Shattuck 1080* (F, MO, US); trail from Chagres River to Agua Clara, *Bartlett & Lasser 16890* (MICH), *16891* (MICH); Pipeline road 4 mi. N of Gamboa, *Gentry 6052* (MO, PMA); near Gamboa, 9°05′N, 79°40′W, 50 m, *McPherson 11705* (MO); Santa Rita Ridge, E of Colón, 200–300 m, *Gómez-Pompa et al. 3190* (MO), *de Nevers et al. 10651* (CAS, NY, COL); 4 km N of Arriaján, 115 m, *Nee 7159* (MO, PMA, US). **Darién**: Parque Nacional del Darién, Estación Rancho Frío at N base of Cerro Pirre, ca 9 km S of El Real, along Quebrada Peresenico, 8°01′N, 77°44′W, 70–270 m, *de Nevers et al. 8264* (CAS); Río Perresenico, *Duke & Bristan 243* (MO, US). **Panamá**: Río La Maestra, 0–25 m, *Allen 9* (MO); along PanAm Highway halfway between El Llano and Río Mamoní, *Duke 5612* (MO); 2 km W of Gamboa, near Chagres air strip, 30 m, *Nee 7560* (CAS, MO, PMA). **San Blas**: Yar Bired, 9°20′N, 79°08′W, *de Nevers 6943* (MO); near Cangandí, 9°24′N, 79°24′W, 3–30 m, *de Nevers et al. 7415* (MO).

DISTRIBUTION AND HABITAT. — Eastern Panama (Canal Area, Darién, Panamá, San Blas) and western Colombia (Antioquia, Chocó, Valle); lowland rainforest below 700 m elevation.

LOCAL NAMES AND USES. — Panama: *alar* (Kuna), *caña conga* (Spanish). The stems are used for making floors in Darién Province, Panama.

DISCUSSION. — This species is characterized by its compact inflorescences, numerous, filamentous rachillae, regularly arranged triads, lepidote to setose pistillate corolla, and spinulose fruits. Rarely, hybridization between this species and *Bactris gasipaes* occurs in the Chocó, Colombia (Bernal & Henderson, in prep.).

2. Bactris caudata H. Wendl. ex Burret, Repert Spec. Nov. Regni Veg. 34:230. 1934.

TYPE. — COSTA RICA. **Alajuela**: Río Sarapiquí, San Miguel, May 1857, *H. Wendland 53* (holotype, B, destroyed; lectotype, GOET [here designated]; isolectotype, K).

Bactris dasychaeta Burret, Repert. Spec. Nov. Regni Veg. 34:215. 1934.

TYPE. — COSTA RICA. **Cartago** ("San José"): Tucurrique, 635–700 m, May 1899, *A. Tonduz 13310* (holotype, B; isotypes BM, P, US).

Stems solitary or cespitose, 1–5 m tall, 2–2.4 cm diam, spiny on the internodes or lacking spines. **Leaves** 5–8; sheath 41–67 cm long, sparsely spiny; petiole 40–54 cm long, with a few black spines to 5 cm or more long; rachis to 98 cm long, lacking spines or with a few, black, terete spines to 6.5 cm long; pinnae 19–26 per side, irregularly arranged in clusters and spreading in various planes, linear to ovate, concave, smooth to plicate with veins prominent adaxially, long-acuminate, middle pinnae (21–) 40–50 cm long, 2.5–5 cm wide (apical one wider, narrowly obovate), glaucous, dark green adaxially, paler abaxially, glabrous, with forward- or backward-pointing spinules 1–3 mm long on the margins. **Inflorescences** interfoliar; peduncle to 11 cm long, 1–2 cm wide, sparsely to densely spiny, strongly recurved; prophyll 5.5–8.5 cm long, 2–2.5 cm wide; peduncular bract 16–36 cm long, 3–5.5 cm wide, sparsely to densely black-spiny; rachis 1.5–2 cm long; rachillae 18–31, 5–10 cm long, ca. 1 mm diam; triads scattered amongst paired or solitary staminate flowers proximally; **staminate flowers** not seen; **pistillate flowers** with calyx shallowly cupuliform, acutely 3-lobed, 0.5 mm long; corolla tubular, acutely 3-lobed, 2.5 mm long; **fruits** in a tight bunch, obovoid, with prominent stigmatic residue, orange-red, 0.9–1.3 cm long, 1.1–1.2 cm diam, glabrous; endocarp turbinate; endocarp fibers lacking; endocarp pores equidistant; fruiting calyx minute, corolla truncate to crenate, 3 mm long.

ADDITIONAL SPECIMENS EXAMINED. — NICARAGUA. **Río San Juan**: 1 km E of Río Sábalos, 11°02′N, 84°27′W, 100 m, *Moreno 23185* (MO). **Zelaya**: Caño Montecristo, E of Germán Pomares camp, 11°36′N, 83°52′W, 60–90 m, *Moreno 15134* (MO); Caño Montecristo, "La Grupera," 11°33′N, 87°48′W, 10 m, *Moreno & Sandino 14652* (MO).

COSTA RICA. **Alajuela**: Highway 15 between Naranjo and Aguas Zarcas, 8 km NE of Quesada, 600 m, *Croat 46954* (MO); Guatuso de San Rafael, 10°43′N, 84°48′W, 80–100 m, *Holm & Iltis 909* (MO), *Holm & Iltis 910* (MO); 5 mi. from San Miguel, *Langlois 1* (BH); 8 km NE of Villa Quesada, *Molina et al. 17152* (F, NY). **Cartago**: Turrialba, *Boynton 14* (BH), *Boynton 17* (BH), 500–600 m, *Córdoba 1* (BH), *Córdoba 2* (BH), *Córdoba 35* (BH), *Córdoba 36* (BH), *Córdoba 51* (NY), *Córdoba 52* (BH), *Córdoba 106* (BH), *Grayum et al. 8475* (MO), *Moore 6709* (BH); *Sánchez 2* (CR); Pavones, *Moore 6749* (BH).

Heredia: between Corazón de Jesus and La Virgen, *Moore 6633* (BH).

PANAMA. **Bocas Del Toro:** Chiriquí Lagoon, Cayo Solarte (Nancy Island), near town of Bocas Del Toro, 9°20′N, 82°15′W, 5 m, *McPherson 11486* (MO).

DISTRIBUTION AND HABITAT. — Nicaragua (Río San Juan, Zelaya), Costa Rica (Alajuela, Cartago, Heredia), and Panama (Bocas Del Toro); lowland rain forest below 800 m elevation.

DISCUSSION. — This species is characterized by its glaucous, linear to ovate, concave pinnae with spinules 1–3 mm long on the margins, and compact inflorescences with short rachillae.

3. Bactris charnleyae de Nevers, A. Henderson & Grayum, sp. nov.
Fig. 1.

TYPE. — PANAMA. **San Blas:** El Llano-Cartí road, 19.1 km from Interamerican highway, 9°19′N, 78°55′W, 150–350 m, 8 Jan. 1985, *G. de Nevers et al. 4463* (holotype, MO; isotype, NY).

Statura parva foliis simplicibusque *Bactris hondurensi* similis sed fibris endocarpii numerosis distinctis spinis pedunculi longis nigrisque.

Stems cespitose, 0.5–2 m tall, 6–9 mm diam. **Leaves** 3–6; sheath 5–6 cm long, not deeply split opposite the petiole, truncate, sheath, petiole and rachis not spiny; petiole 7–11 cm long; rachis 11–15 cm long; blade simple, bifid, the lobes 13–18 cm long from top of rachis to apex, 4.5–9 cm wide at apex of rachis, with 10–14 main veins, these raised above, glabrous, veins with minute setae abaxially, leaf margins setose apically with spinules 1–7 mm long. **Inflorescences** interfoliar, projecting from the top of the sheath; peduncle 3–5 cm long, densely spiny with fine, straight spinules 6–8 mm long; prophyll 2–3 cm long; peduncular bract 8–8.5 cm long, 1.5–2.3 cm wide, moderately covered with fine, straight spinules 1.5–2.3 cm long; rachis 2–2.6 cm long; rachillae 5–8, 1.5–3 cm long, ca. 1 mm diam; triads irregularly arranged amongst paired or solitary staminate flowers; **staminate flowers** not seen; **pistillate flowers** 2 mm long; calyx 3-lobed, 0.5 mm long; corolla 3-lobed, 2 mm long; staminodes present or absent; **fruits** globose, rostrate, 5–8 mm diam, orange or yellow, striate; mesocarp mealy; endocarp turbinate; endocarp fibers numerous, with juice sacs attached; endocarp pores equidistant; fruiting perianth with crenate corolla, 2 mm long, staminodes visible or absent.

ADDITIONAL SPECIMENS EXAMINED. — PANAMA. **San Blas:** El Llano-Cartí road, 19.1 km from Interamerican highway, 9°19′N, 78°55′W, 100–350 m, *de Nevers 5982* (MO), *6187* (MO), km 32, *Henderson & Herrera 715* (NY), km 12, *Henderson & Herrera 731* (NY); Cangandí, 9°24′N, 79°24′W, *de Nevers et al. 5714* (MO, NY), *Herrera 205* (CAS).

DISTRIBUTION AND HABITAT. — Panama (San Blas); lowland rainforest at 25–300 m elevation.

LOCAL NAMES AND USES. — Panama: *bor* (Kuna), *uga wawad* (Kuna).

DISCUSSION. — This species is distinguished by its small size, simple, glabrous leaves, and densely spinulose peduncle and peduncular bract. There is only one specimen with ripe fruits, but these appear to have endocarp fibers with juice sacs attached. This situation is anomalous, since Sanders (1991) considered that orange-fruited species of *Bactris* lacked endocarp fibers with juice-sacs attached. Apart from this, *B. charnleyae* is very similar to *B. hondurensis*, from which it differs in its densely spiny peduncle and peduncular bract.

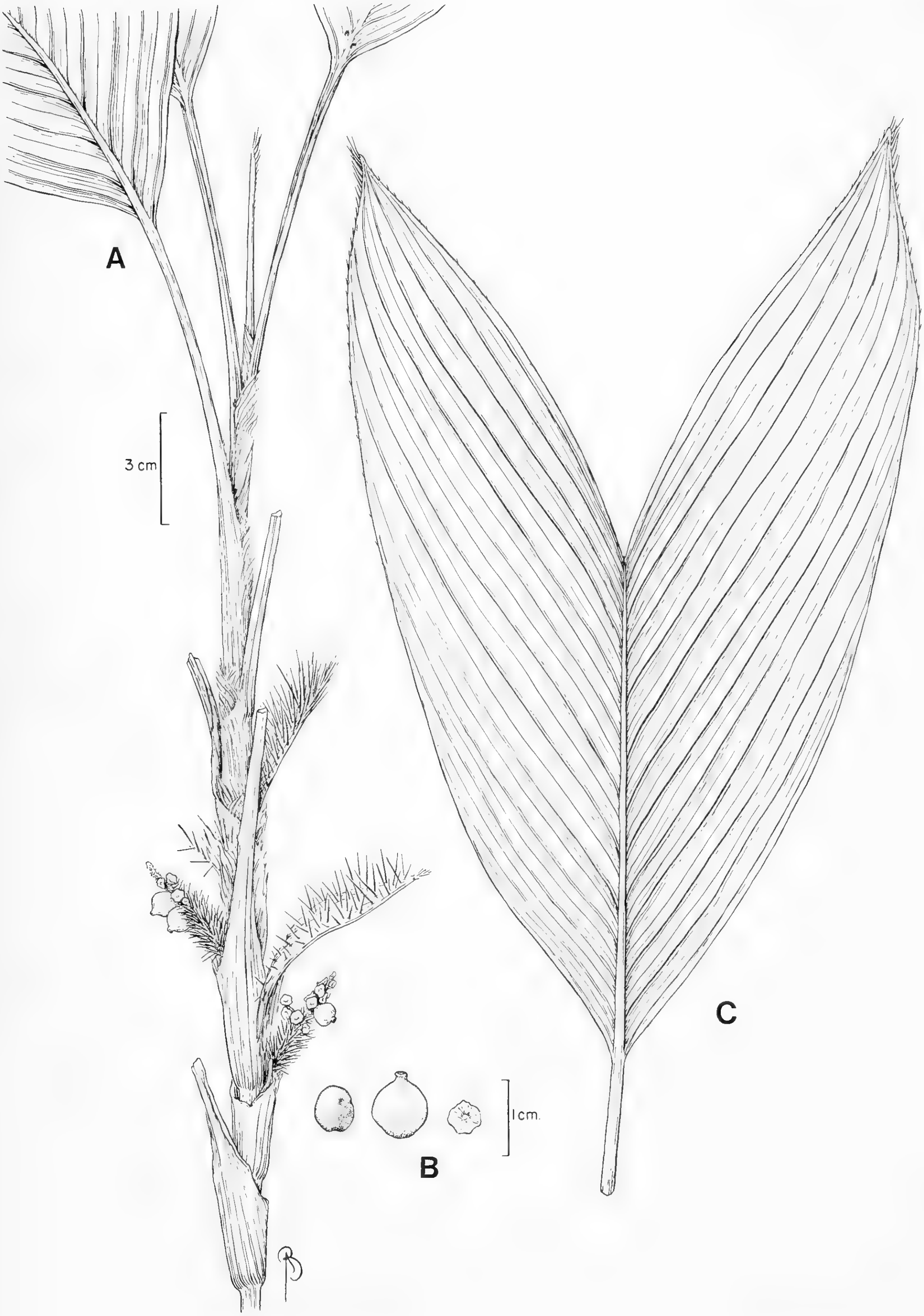
4. Bactris coloniata L. H. Bailey, Gentes Herb. 3:106. 1933.

TYPE. — PANAMA. **Canal Area:** Barro Colorado Island, 29 Jun 1931, *L. Bailey 77* (lectotype, BH [here designated]).

Stems cespitose, rarely solitary, forming open colonies, 3.5–7 m tall, 2–5 cm diam, with spiny

→

FIGURE 1. *Bactris charnleyae* (*de Nevers et al. 4463*). A. Habit. B. Left to right: endocarp, fruit, fruiting calyx. C. Leaf blade. A & C same scale.


A
3 cm
B
1cm.
C

internodes. **Leaves** 5–7; sheath 27–80 cm long, sheath, petiole (and rachis) reddish-brown-tomentose, densely to moderately covered with yellowish brown to black, somewhat flattened spines; petiole 39–70 cm long; rachis (0.45–) 1.2–1.4 m long; pinnae (4–) 14–23 per side, regularly or irregularly arranged in clusters of 4–12, spreading in the same or various planes, linear-lanceolate, elliptic or slightly sigmoid, the apex long-caudate and drooping; middle pinnae 30–75 cm long, 2.5–7.2 cm diam, without conspicuous cross-veins, glabrous. **Inflorescences** interfoliar; peduncle 16–25 cm, strongly curved in fruit; prophyll 15–49 cm; peduncular bract (26–) 42–60 cm long, densely covered with appressed, brown, flattened spines, after anthesis; rachis 4–10 cm long; rachillae 9–16, 14–25 cm long, thick, to 3 mm diam in fruit; triads scattered amongst paired or solitary staminate flowers; **staminate flowers** 4 mm long; sepals free, linear, 1 mm long; petals connate below for ca. one-third their length, free and valvate above, 4 mm long; **pistillate flowers** 5 mm long; calyx tubular, 4 mm long; corolla tubular, 2 mm long, with minute bristles; staminodes absent; **fruits** very widely obovoid, markedly rostrate, 1.5–2.5 cm long, ca. 1.5 cm diam, yellowish brown, covered with short brown hairs; mesocarp floury; endocarp turbinate; endocarp fibers numerous, wiry, with juice sacs attached; endocarp pores equidistant; fruiting calyx only slightly shorter than the corolla, 4–5 mm long, both crenulate-margined.

ADDITIONAL SPECIMENS EXAMINED. — PANAMA. **Canal Area:** Barro Colorado Island, *Bangham 555* (US), *Bartlett 16716* (MICH), *16745* (MICH), *Croat 5306* (MO), *5307* (MO), *6174* (MO), *6772* (MO), *7141* (MO, SCZ), *7434* (MO), *7439* (MO), *8039* (MO), *8343* (MO), *8787* (MO, SCZ), *8799* (MO), *9230* (MO), *11010* (MO), *11013* (MO), *11018* (MO), *11021* (MO), *11022* (MO, SCZ), *11102* (MO), *11103* (MO), *11144* (MO), *11198* (MO), *11642* (MO), *15252* (NY), *15257* (MO), *15408* (MO, NY), *Kenoyer 161* (US); *Oppenheimer 67-1-3-1020* (MO); between Fort Sherman and Fort San Lorenzo, *Croat 15422* (MO); between Gatún and Fort Sherman, *Croat 15408* (MO, NY); Margarita Swamp, *Cook & Martin 5* (US); Frijoles, *Cook & Martin 65* (US); Agua Salud, *Cook & Martin 68* (US). **Colón:** Santa Rita Ridge, 9°20′N, 79°47′W, 200 m, *Churchill 5564* (MO). **Darién:** Parque Nacional del Darién, Estación Rancho Frío at N base of Cerro Pirre, ca 9 km S of El Real, along Quebrada Perisenico, 8°01′N, 77°44′W, 70–270 m, *de Nevers et al. 8242* (CAS). **Panamá:** Cerro Azul, *Croat 17279* (MO); 4.5 km N of Lago Cerro Azul, vicinity of Finca Vega, 675 m, *Nee 7020* (MO, WIS). **San Blas:** El Llano-Cartí road, km 19.1, 9°19′N, 78°55′W, 200 m, *de Nevers et al. 4464* (MO, NY), *Mori & Kallunki 5547* (MO), km 26.5, along Río Cartí Chico, 9°19′N, 78°55′W, 200 m, *de Nevers et al. 5343* (MO, NY, PMA); Cangandí, 30 m, *Herrera 166* (CAS, MO); Miria Ubigandup, 9°26′N, 78°56′W, 20 m, *Herrera & Pérez 304* (CAS).

DISTRIBUTION AND HABITAT. — Eastern Panama (Canal Area, Colón, Darién, Panamá, San Blas), northwestern Colombia (Antioquia, Chocó) and Amazonian Peru (Amazonas); tropical wet forest at elevations below 700 m.

LOCAL NAMES AND USES. — Panama: *signugar* (Kuna, literally translated "peccary teeth"), *sadu wala* (Kuna); *uvita*, *uvito*, *caña brava* (Spanish). The Kuna make a comb from the stem which is used medicinally to augment intelligence. *Kwi*, *dior*, and *maske*, are all general Kuna names for plants of the genus *Bactris*.

DISCUSSION. — This species is characterized by its large size, open habit of growth, subequal fruiting calyx and corolla, and hairy fruits which are widest at the middle. We have seen only leaves of the type. *Nee 7020* has the subequal fruiting calyx and corolla and bristly fruits of *B. coloniata* and the plicate leaves of *B. kunorum*, and pinnae with numerous 1–3 mm long, black, marginal spines.

5. **Bactris coloradonis** L. H. Bailey, Gentes Herb. 3:104. 15 Mar 1933.

TYPE. — PANAMA. **Canal Area:** Barro Colorado Island, 6 Jul 1931, *L. & Z. Bailey 502* (lectotype, BH [here designated]).

Bactris porschiana Burret in Cufod., Ann. Naturhist. Mus. Wien 46:229. Jul 1933.

TYPE. — COSTA RICA. **Limón:** Río Reventazón, La Castilla-Los Negritos, 3 Apr 1930, *G. Cufodontis 724* (holotype, B, destroyed; F negs. 30905, 30906).

NEOTYPE. — COSTA RICA. **Limón:** Dist. Guácimo, between Guácimo and Santa Rosa, 19 Jun 1991, *Mattos 2892* (NY, here designated).

Stems cespitose or solitary, 1.5–10 m tall, 3–8 cm diam, with spines on the internodes. **Leaves** 2–6; sheath 43–60 (–100) cm long, sheath, petiole (and rachis) usually white, woolly-tomentose, densely to moderately covered with terete, black spines to 8.5 cm long; rachis 0.9–2.1 m long, normally without spines; pinnae 17–38 (–80) cm long (or the leaves rarely simple), irregularly arranged in clusters, spreading in the same or in various planes, linear-lanceolate, aristate, glabrous, the middle ones 21–86 cm long, 3–7 cm wide, usually spiny on the margins, usually with obvious cross-veins. **Inflorescences** interfoliar; peduncle 9.5–23 cm long, recurved, flattened; prophyll 9–23 cm long; peduncular bract 27–37 cm long, sparsely to densely covered with spreading, terete, black or brown spines to 1 cm long; rachis 3.5–9 cm long; rachillae 20–51, 14–29 cm long, with long, brown hairs; triads irregularly arranged amongst paired or solitary **staminate flowers**; staminate flowers 3 mm long (immature); sepals connate below, free above, 2 mm long; petals connate below for ca. half their length, free and valvate above, 3 mm long; **pistillate flowers** 2.5 mm long (immature); calyx tubular, 1 mm long; corolla tubular, 2 mm long; staminodes 6, mi-nute; **fruits** very widely obovoid, briefly rostrate, to 1.5 (–2.5) cm long, 1.4–1.5 (–2) cm diam, orange-red, smooth; meoscarp mealy, fibrous; endocarp turbinate; endocarp with few fibers, without juice sacs; endocarp pores equidistant; fruiting perianth with calyx less than 1 mm long, obscure, and corolla 4–5 mm long, truncate or with slightly undulate margins.

ADDITIONAL SPECIMENS EXAMINED. — COSTA RICA. **Heredia**: Finca La Selva, Río Sarapiquí, *Hammel 8345* (MO), *Holdridge 5121* (BH), *Moore & Hartshorn 10123* (BH), *Moore & Dransfield 10233* (BH), Finca El Bejuco, *Henderson 63* (NY). **Limón**: 14 airline km SW of Barra del Colorado, 83°40′W, 10°40′N, 10–120 m, *Davidse & Herrera 31101* (MO); 7 km S of Bribrí, 100–250 m, *Gómez et al. 20453* (MO); Dist. de Los Angeles de Jiménez, Finca Copasa, *Mattos 2891* (NY); Tortuguero, 70 m, *Robles 1604* (MO), *Robles 1198* (MO); Cerro Coronel, 10–40 m, *Stevens 24350* (MO).

PANAMA. **Canal Area**: Mojinga swamp, *Bartlett 16873* (MICH); Balboa, *Cook & Martin 6* (F); Barro Colorado Island, *Croat 10946* (MO, SCZ), *10947* (MO), *11322* (MO); road S-10 N of Escobal, *Croat & Porter 12478* (MO, PMA); near Coco Solo weather station, *Duke 4269* (MO); Río Chinilla, *Maxon 6904* (US), *6908* (US), *Cook & Martin 21* (US); Fort Sherman, *Mori & Kallunki 3664* (F, MO); Loma La Toba, 3 km SW of mouth of Río Chagres, *Nee 8933* (MO, PMA, US); Gatuncillo, *Smith et al. 3335* (US). **Coclé**: Atlantic slope 9.4 km above El Copé, 750–900 m, *Croat 44663* (MO), 8°38′N, 80°39′W, 650–750 m, *de Nevers et al. 6374* (MO, PMA), 700–850 m, *Folsom et al. 5746* (MO), 3000 ft., *Hammel 2628* (MO), *Read et al. 81-25* (US); Coclecito road, trail along continental divide, 8°42′N, 80°28′W, 500 m, *de Nevers et al. 6731* (MO); El Valle, Cerro Gaital, 8°37′N, 80°07′W, 800–900 m, *McPherson 11198* (CAS, MO), *Mori & Kallunki 2969* (MO). **Colón**: N of Diamante, NW of abandoned mine on Quebrada de la Mina, 9°24′N, 79°35′W, *Churchill & de Nevers 4223* (MO); Santa Rita Ridge, ca. 1 mi. from Boyd-Roosevelt Highway, *Croat 15322* (MO), 9°25′N, 79°40′W, 500 m, *McPherson 11752* (MO), *Porter et al. 4730* (BH, MO); end of Río Boquerón road, 1500–2000 ft., *Hammel 2464* (MO). **Darién**: Cerro Pirre, 700–950 m, *Mori & Kallunki 5505* (MO). **Panamá**: Cerro Jefe, *Davidse & D'Arcy 10120* (MO), *Lewis et al. 263* (BH, MO), 2900 ft., *Gentry et al. 3451* (MO, PMA); *Busey & Croat 257* (MO), *Croat 11550* (MO), *Read et al. 81-42b* (US); El Llano-Cartí road km 14, 350–400 m, *Correa A. et al. 1839* (MO, PMA), *Folsom et al. 6160* (MO), km 22.3, 350 m, *Mori & Kallunki 5103* (MO, PMA); Cerro Campana, 1000 m, *Croat 22838* (MO), *Porter et al. 4209* (MO); El Llano, Río Mamoni, *Duke 5612* (MO); Pipeline road, *Gentry & Hamilton 41119* (MO, NY). **San Blas**: El Llano-Cartí road, km 26.5, along Río Cartí Chico, 9°19′N, 78°55′W, 200 m, *de Nevers et al. 5351* (CAS, MO, NY), *Henderson & Herrera 716* (BH, CAS, NY), km 19.1, 350 m, *de Nevers et al. 6216* (MO, PMA), *de Nevers et al. 7314* (MO); Yar Bired (Cerro San José), 9°20′N, 79°08′W, 400–500 m, *de Nevers & Herrera 6946* (MO); Cangandí, 9°24′N, 79°24′W, 30 m, *de Nevers & Herrera 7077* (MO), *de Nevers et al. 7549* (MO); 50 m, *Herrera & Pérez 126* (CAS, PMA); Aila Tiwar (Río Acla), 8°48′30″N, 77°40′30″W, 25–100 m, *Mabberley & Sugden 1852* (MO). **Veraguas**: Santa Fe, 8°31′N, 81°08′W, 700 m, *Churchill et al. 5965* (MO), 700–1200 m, *Liesner 999* (MO), *Croat & Folsom 33910* (MO), *de Nevers et al. 10555* (CAS, NY); mouth of Río Concepción, *Lewis et al. 2815* (MO);

DISTRIBUTION AND HABITAT. — Costa Rica (Heredia, Limón), Panama (Canal Area, Coclé, Colón, Darién, Panamá, San Blas, Veraguas), western Colombia (Antioquia, Chocó, Nariño, Valle), and western Ecuador (Esmeraldas); lowland or premontane rainforest below 900 m elevation.

LOCAL NAMES AND USES. — Nicaragua: *coyolito*. Panama: *arar*, *sin nuar* (Kuna).

DISCUSSION. — *Bactris coloradonis* is distinguished from related species by its longer rachillae with larger fruits. Panamanian material usually has prominent cross-veins and marginal setae on the pinnae; that from Costa Rica usually does not. However, this variation is not consistent, and flowers and fruits from both countries are identical. One specimen from near La Selva, at Finca El Bejuco (*Henderson 63*) is unusual. It is large and superficially resembles *Bactris coloradonis*, but has the fruiting calyx and corolla like those of *B. major*. *Gómez et al. 20453*, from extreme southeastern Costa Rica, agrees well with *B. coloradonis*, but has unusually large fruits (2.5 × 2 cm).

Bactris coloradonis, as here circumscribed, is a variable species, with several more or less geographically distinct races that may ultimately be found deserving of taxonomic recognition. We currently distinguish four such entities, including typical *B. coloradonis*, widespread in the Panamanian lowlands. Costa Rican material, for which the name *B. porschiana* Burret is available, differs from the typical "race" in having less formidably spiny leaves without conspicuous cross-veins, as well as somewhat smaller, more globose, and less prominently rostrate fruits. Panamanian specimens from higher elevations in the provinces of Coclé (El Copé) and Veraguas (Santa Fe region) tend to have proportionately broader and more conspicuously caudate-tipped pinnae than material from the adjacent lowlands, as well as shorter rachillae and larger, more prominently rostrate fruits. A specimen from Coclé (*de Nevers et al. 6731*) is unique in having simple leaves. These Panamanian upland collections seem to approach *B. dianeura*, another mid-elevation species, especially in their fruits. *Mabberley & Sugden 1852*, from the Comarca de San Blas, Panama, is the sole Mesoamerican collection of a "race" which, judging from herbarium material, ranges through the Pacific lowlands of Colombia south to the Bajo Calima region of the Department of Valle. This material is characterized by very densely white-tomentose petioles and leaf rachises, inconspicuous cross-veins in the pinnae, and densely spinulose rachillae. The distinctive rachilla spinules are black, somewhat contorted and to ca. 3 mm long. This last "race" may occur sympatrically with typical *B. coloradonis*, and may even merit specific status. Additional collections are necessary to resolve the issue.

6. Bactris dianeura Burret, Repert. Spec. Nov. Regni Veg. 34:217. 1934.

TYPE. — NICARAGUA. **Matagalpa:** Camino Real de Casica, 850 m, 8 Aug 1893, *E. Rothschuh 237* (holotype, B, destroyed).

NEOTYPE. — COSTA RICA. **Alajuela:** Monteverde Cloud Forest Nature Reserve, 9°17′N, 84°86′[sic]W, 1250–1350 m, *Burger et al. 10753* (F, isoneotype MO, here designated).

Stems cespitose, forming small colonies of 2–8 stems, 2–5 (–10) m tall, 1–3 cm diam, the internodes with spines to 2.8 cm long. **Leaves** 5–7; sheath 17–45 or more cm long, sheath and petiole densely black- or ± reddish spiny, with spines to 6.5 cm long; petiole 26–80 cm long; rachis 58–90 (–125) cm long, with few spines to ca. 7.5 cm long; pinnae 14–20 per side, irregularly arranged in clusters of 2–3, lanceolate to oblanceolate, the middle ones 26–44 (–56) cm long, (1.4–) 2.7–4.5 (–6.3) cm wide, obscurely to clearly cross-veined, setose marginally (the setae to ca. 6 mm long). **Inflorescences** interfoliar; peduncle 6–12.5 cm long, tightly curved in fruit, with fine spines to ca. 1 cm long; prophyll 10–11 cm long; peduncular bract to at least 26 cm long, densely covered with stramineous to blackish spines to 2 cm long, inserted 0.5–3 cm above base of peduncle, rarely subbasal; rachis 1.6–3.4 cm long; rachillae 7–17, 4.3–11 cm long, 1–1.5 mm wide; triads irregularly arranged on proximal two thirds of rachillae; **staminate flowers** 3–4 mm long; calyx 1–1.5 mm long, hyaline, divided nearly to the base, the lobes narrowly lanceolate or subulate; **pistillate flowers** 3.5–5.5 mm long; calyx 1–2 mm long, shallowly cupuliform, acutely 3-lobed, striate, glabrous; corolla 3–5 mm long, campanulate to tubular, acutely 3-lobed to about halfway (lobes sometimes with subsidiary teeth); staminodes 1–3, scutellate, extremely minute; **fruits** subglobose or usually obovoid, prominently rostrate, 1.2–1.8 cm long, 1.2–1.6 cm diam, bright orange, glabrous, striate; mesocarp very thin, mealy; endocarp turbinate; endocarp not pitted, fibers few or lacking; endocarp pores equidistant; fruiting calyx minute; corolla 2–3 mm long, irregularly split at apex by enlarging fruit, without visible staminodia.

ADDITIONAL SPECIMENS EXAMINED. — COSTA RICA. **Alajuela:** Monteverde Cloud Forest Nature

Reserve, 10°18′N, 84°47′W, 1450–1650 m, *Burger & Baker 9646* (F); Reserva Biológica de San Ramón, 10°04′N, 84°32′W, 850–1100 m, *deNevers et al. 7794* (MO); Montes del Aguacate, 10°02′N, 84°28′W, *Grayum et al. 9103* (MO). **Cartago**: 0.8 km W of Tapantí, *Lent 971* (F); S of Muñeco, *Utley & Utley 767* (F, MO). **Guanacaste**: Monteverde Cloud Forest Nature Reserve, 10°18′N, 84°50′W, *Gentry et al. 71590* (MO). **Heredia**: 5.5 km N of Vara Blanca, 1200 m, *Croat 36054* (MO); Volcán Barva, Río San Rafael, 10°13′N, 84°05′W, 1500 m, *Grayum 7028* (CR, MO); Reserva Forestal de San Ramón, 600–800 m, *Sánchez s.n.* (CR). **Limón**: between Río Pacuare and Grano de Oro, 7 km below Hacienda Moravia, *Moore & Córdoba 6700* (BH). **Puntarenas**: Monteverde, 10°17′N, 84°50′W, *Dryer 1415* (F), 1450–1550 m, *Gentry & Haber 48776* (MO), 1400 m, *Haber ex Bello & Lierheimer 4670* (MO), 1500 m, *Hammel 13865* (MO). **San José**: La Palma, 1520 m, *Pittier 396* (BR).

PANAMA. **Chiriquí**: 7.2 mi. beyond Los Planes de Hornito, 8°44′N, 82°14′W, 1165–1200 m, *Croat 67824* (CAS); *de Nevers 8747* (CAS). **Veraguas**: Santa Fe, *de Nevers et al. 8986* (CAS).

DISTRIBUTION AND HABITAT. — Nicaragua (Matagalpa), Costa Rica (Alajuela, Cartago, Guanacaste, Heredia, Limón, Puntarenas, San José) and Panama (Chiriquí, Veraguas); premontane rainforest between 600 and 1650 m elevation.

DISCUSSION. — This species is similar to *Bactris mexicana*, but the sheath, petiole and rachis are minutely spinulose, the rachillae are fewer, and the fruits are rostrate. It also occurs at higher elevations.

Our application of the name *Bactris dianeura* Burret to this species demands some explanation, as no original material or illustration is extant, and we have seen no specimens from Nicaragua, where the type was collected. In the first place, Burret's lengthy description agrees quite well with the material cited above, especially in terms of relatively small stature, extreme spininess ("ganze Pflanze sehr stachelig") with the spines often pale colored and black-tipped ("stramineis, superne atris"), and prominent cross-veins on the adaxial laminar surface. Furthermore, the type locality at 850 m in Matagalpa Department is in a "cloud-forest" habitat (W. Stevens, pers. comm.), and this is the only cloud-forest *Bactris* species we are aware of in the Mesoamerican region. In any case, we have seen no collections of any other *Bactris* species from Matagalpa Department. Thus, the evidence presently available strongly suggests that *Bactris dianeura* represents the species here circumscribed.

7. Bactris gasipaes Kunth, in Humbl., Bonpl. & Kunth, Nov. gen. sp. 1:302. 1816. nom. cons. *Guilielma gasipaes* (Kunth) L. H. Bailey, Gentes Herb. 2: 187. 1930.

TYPE. — COLOMBIA. **Tolima**: Ibagué, n.d., *A. Bonpland s.n.* (holotype, P; F neg. 38701).

Martinezia ciliata Ruiz & Pav., Syst. veg. fl. peruv. chil. 295. 1798. *Bactris ciliata* (Ruiz & Pav.) Mart., Hist. nat. palm. 2:95, t. 71, fig. 3. 1826.

TYPE. — PERU. **Huánuco**: "in nemoribus Pozuzo, Cuchero, Chanchamayo et Huayabal," *Pavon s.n.* (holotype, MA, n.v., isotypes, BM, n.v., M, n.v.).

Guilielma utilis Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjöbenhavn 1858:46. 1859. *Bactris utilis* (Oerst.) Benth. & Hook. f. ex Hemsl., Biol. centr.-amer., Bot. 3:413. 1885.

TYPE. — COSTA RICA. Without locality, n.d., *A. Oersted s.n.* (holotype, C?, n.v.).

Stems cespitose or solitary, 4–15 m tall, 8–14 cm diam, spiny at internodes, rarely without spines. **Leaves** 9–20; sheath lacking an ocrea; sheath and petiole 1–1.1 m long, sheath, petiole and rachis moderately to densely covered with black or brownish spines to 1 cm long, these in three lines on the abaxial surface of sheath and petiole; rachis 1.9–2.6 m long; pinnae 92–123 per side, arranged in obscure clusters of 3–5, spreading in several planes, linear, 52–75 cm long, 2–3 cm wide, unequally bifid with midrib terminating subapically. **Inflorescences** at first interfoliar; peduncle 20–28 cm long, gently recurved, non-spiny; prophyll 20–21 cm long; peduncular bract 47–70 cm long, moderately to densely covered with blackish or brownish spines to 1 cm long; rachis 15–23 cm long; rachillae 46–57, 17–28 cm long; triads irregularly arranged amongst paired or solitary staminate flowers; **staminate flowers** to 4 mm long, deciduous; sepals 2 mm long, united into a spreading, triangular calyx; petals united for ca. one-third their length, free and valvate above, obovate, 3.5 mm long; **pistillate flowers** 6 mm long; calyx 2 mm long; corolla 4.5 mm long; staminodes absent; **fruits** widely ovoid, to 5 cm long, to 3 cm diam, yellow, orange or red at maturity; mesocarp mealy; endocarp ellipsoid; endocarp fibers stout, flattened, adnate to the endocarp; endocarp pores with the sterile pores close together and the fertile pore displaced towards apex; fruiting perianth with very small calyx with undulate margins and much longer, scarcely lobed corolla, staminodial ring absent.

ADDITIONAL SPECIMENS EXAMINED. — HONDURAS. **Atlántida:** Lancetilla, near Tela, 20-600 m, *Standley 55564* (US). COSTA RICA. **Heredia:** Finca La Selva, *Hammel 10045* (MICH), *Henderson 43* (NY); Río Hondo, Plains of Santa Clara, 100 m, *Cook & Doyle 342* (US); *634* (US).

PANAMA. **Canal Area:** Barro Colorado Island, *Croat 11798a* (MO), *14479* (MO, SCZ), *14497* (MO); Juan Minas, Chagres River, *Doyle 7* (US); Las Cascadas, 11 April 1925, *Cook s.n.* (US); end of Pipeline road, 19 km W of Gamboa, 25–50 m, *Nee & Smith 11063* (MO). **Darién:** near camp Pico Pendejo and also upstream on the Río Sabana from Santa Fe, *Duke 14075* (MO, PMA). **San Blas:** Cangandí, 30 m, 9°24′N, 79°24′W, *de Nevers et al. 7469* (MO).

DISTRIBUTION AND HABITAT. — Widely and commonly cultivated throughout tropical areas of Central and northern South America, almost always associated with current or past human dwellings. There are many cultivated varieties, including one without spines on the stems and leaves, and another with seedless fruits. Its place of origin is not known, but the wild ancestor is probably *B. macana* (Mart.) Pittier from the Andean region of Colombia and Venezuela and the southwestern Amazon region in Peru, Brazil and Bolivia.

LOCAL NAMES AND USES. — Costa Rica: *pejibaye, pejivalle*. Panama: *nalup*, (Kuna). The fruits of *Bactris gasipaes* are an important food item in many parts of Central America, for example the Kuna of Panama. Although we have observed spineless clones in Cangandí these are not favored nor propagated preferentially by the Kuna. The Kuna use the fallen fruits as bait in hunting (Ventocilla 1992:107), and the trunks in construction (Castillo & Beer 1983). Currently agriculturalists are working to improve yields in this species, and are promoting its use as a source of palm hearts (e.g., Clement & Mora Urpí, 1987).

DISCUSSION. — This species is characterized by its tall, thick stems, sheath without ocrea, petiole spines in three lines, and endocarp fibers flattened and adnate to the endocarp.

Bernal (1989) proposed conservation of *Bactris gasipaes* over the earlier name, *B. ciliata* (Ruiz & Pav.) Mart., and his proposal has been accepted (Brummitt, 1993).

8. Bactris glandulosa Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjöbenhavn 1858:184. 1859. *Bactris bifida* Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjöbenhavn 1858:44. 1859, non Mart. (1826). *Bactris oerstediana* Trail, J. Bot. 15:43. 1877, nom. superfl.

TYPE. — COSTA RICA. **Puntarenas:** Puntarenas, n.d., *A. Oersted 6536* (inflorescence only).
LECTOYPE. — C (here designated), F neg. 21108.

Stems cespitose or solitary, 1.5–5 m tall, 2–4.5 cm diam, spiny. **Leaves** 4–6; sheath 26–86 cm long, sheath and petiole sparingly armed with round, black or yellowish spines to 5 cm long; petiole 16–80 cm long; rachis 1–1.7 m long; pinnae 16–29 per side (or occasionally leaf simple), linear to narrowly elliptic, without prominent cross-veins, both surfaces (or sometimes only abaxially) bearing a fine, short, golden pubescence, irregularly arranged in clusters of 2–7 and spreading in different planes, middle pinnae 30–60 cm long, 3–7 cm wide. **Inflorescences** interfoliar; peduncle 8–13 cm long, recurved, spinulose; prophyll 8–16 cm; peduncular bract 15–30 cm long, densely hirsute with fine, soft to stiff, black spines and golden hairs; rachis 3–6 cm long; rachillae (24–) 40–50, crowded, slender, 5–11 cm long, densely glandular; triads regularly arranged on proximal part of rachillae, staminate paired or solitary distally; **staminate flowers** 3.5–4 mm long, usually along only one side of the rachillae, usually persistent in fruit; sepals connate into a shallow, 3-lobed cupule, 1 mm long; petals connate below for ca. half their length, free and valvate above, 3.5–4 mm long; anthers exserted laterally from petals at anthesis; **pistillate flowers** 3 mm long; calyx 1 mm long, glabrous; corolla 3 mm long, usually pubescent with soft, thin, wavy spines to 1 mm long, occasionally glandular, rarely glabrescent, minutely 3-toothed; staminodia absent; **fruits** globose, 0.5–1.6 cm diam, red, glabrous, striate, with abrupt stigmatic residue; mesocarp mealy; endocarp fibers absent; endocarp turbinate, black or white, the pores ± equidistant or displaced, all at same latitude; fruiting calyx minute, corolla 2 mm, irregularly parted.

DISTRIBUTION AND HABITAT. — Costa Rica (Cartago, Heredia, Limón, Puntarenas, San José), Panama (Bocas Del Toro, Canal Area, Chiriquí, Coclé, San Blas, Veraguas) and Colombia (Antioquia, Chocó); tropical wet forest below 1000 m elevation.

DISCUSSION. — Oersted (1859:44) originally called this species *Bactris bifida*, but between the time he submitted his manuscript and the date it was printed he became aware that the name was preoccupied by *Bactris bifida* Mart. (Hist. Nat. Palm. 2:105, t. 73C fig. 3, 1826.). He corrected his mistake on page 184 of the same volume, substituting the name *B. glandulosa* for *B. bifida*. In 1863 Oersted illustrated *B. glandulosa*, referring to its original publication in his paper of 1859. In neither publication did Oersted cite a specimen. Trail (1877) understandably overlooked Oersted's correction.

Neither Dahlgren (1936) nor Burret (1933–34) nor Glassman (1972) lectotypified the name *B. bifida* Oerst. *Oersted 6536* consists of an inflorescence and part of a leaf. The leaf apparently belongs to *B. gasipaes* (and may be part of the original, now missing, type of *Guilielma utilis*). The inflorescence alone is here lectotypified as *B. glandulosa*, and matches perfectly Oersted's (1863) plate of that species.

Two subtaxa of this species occur, almost always together, and some intermediates are found. Here we recognize these two subtaxa as varieties.

Key to the varieties of *B. glandulosa*

1. Petiole and rachis not or sparsely spiny; pinnae densely pilose abaxially; pistillate corolla with long, contorted setae..8a. *B. glandulosa* var. *glandulosa*.

1. Petiole and rachis densely spiny; pinnae sparsely pilose abaxially, mainly along veins; pistillate corolla glabrous or minutely spinulose.................. 8b. *B. glandulosa* var. *baileyana*.

8a. **Bactris glandulosa** var. **glandulosa**

Fig. 2.

Bactris fusca Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjöbenhavn 1858:43. 1859.

TYPE. — COSTA RICA. **Cartago:** Turrialba, 1845–48, *A. Oersted 6535* (excluding inflorescence).

LECTOYPE. — C, n.v. (here designated); F neg. 21107.

Bactris alleniana L. H. Bailey, Gentes Herb. 6:228. 1943.

TYPE. — PANAMA. **Coclé:** El Valle de Antón, 700 m, 2 Jul 1942, *P. Allen 2574* (holotype, BH; isotype, MO).

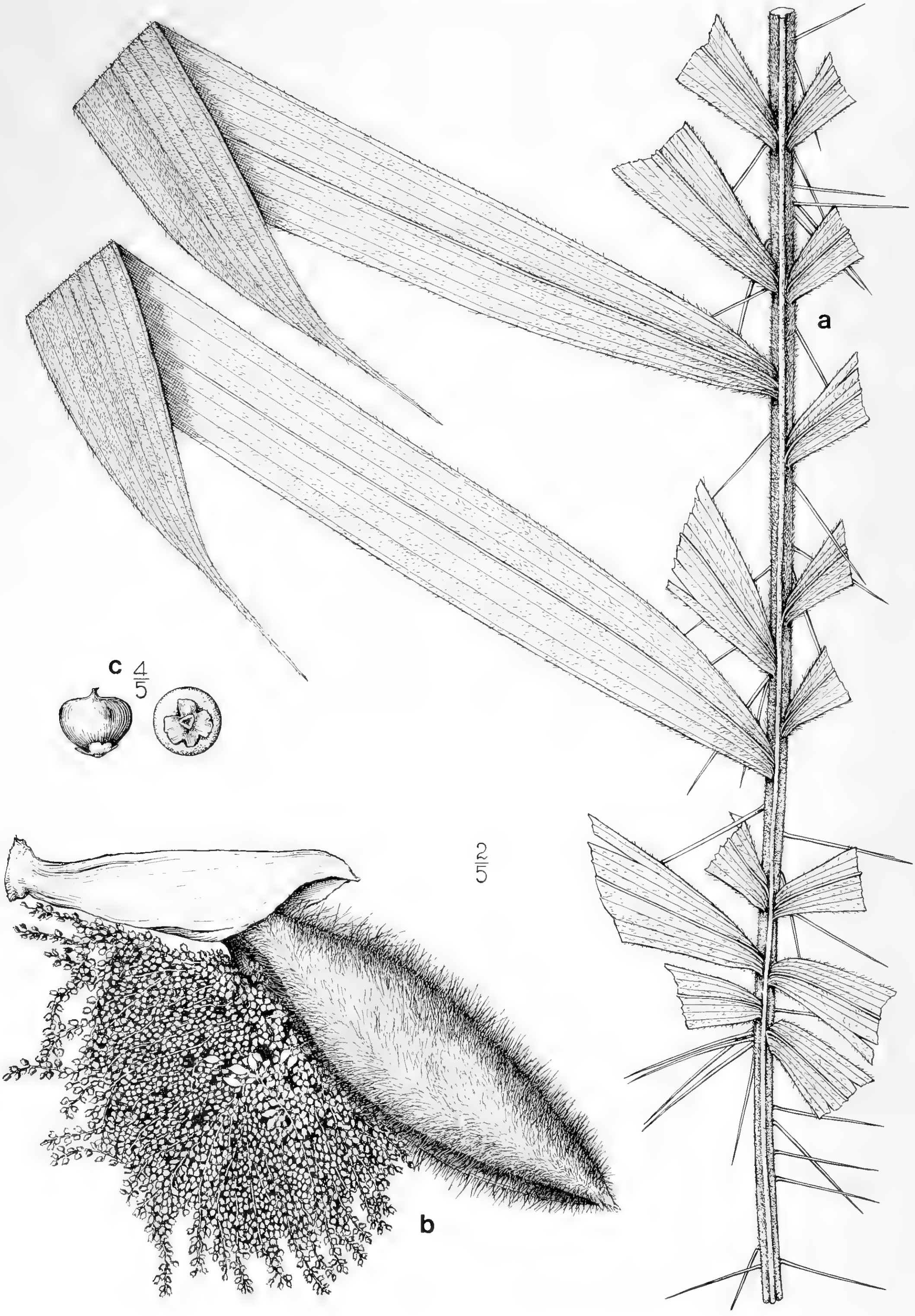
ADDITIONAL SPECIMENS EXAMINED. — COSTA RICA. **Cartago:** Juan Viñas, *Cook & Doyle 219* (US). Turrialba, 9°53′N, 83°39′W, 560–600 m, *Grayum 8476* (MO), *Read & Daniels 74-58* (US). **Limón:** Cairo, *Loomis 9* (US). **Puntarenas:** 5 km W of Rincón de Osa, 8°42′N, 83°31′W, *Burger & Liesner 7297 (F)* Sirena Field Station, Corcovado National Park, Osa Peninsula, 8°30′N, 83°35′W, *Gentry 48498* (MO); *Gentry 48535* (MO); Golfito, Fila Gamba, 8°35′N, 83°12′W, 140–180 m, *Grayum & Herrera 9137* (MO), *Grayum & Herrera 9235* (MO); ca. 15 km W of Rincón, 8°42′N, 83°33′W, *Henderson et al. 1812* (NY); ca. 5 km W of Rincón, 8°42′N, 83°31′W, *Henderson et al. 1819* (NY), *Henderson et al. 1820* (NY), *Henderson et al. 1824* (NY); Rincón de Osa, 20–300 m, *Liesner 2090* (MO). **San José:** Reserva Biológica Carara, Río Carara, 9°47′N, 84°32′W, 130–170 m, *Grayum 10441* (MO).

PANAMA. **Bocas Del Toro:** hill above RR station at Milla 7.5, *Croat & Porter 16404* (MO). **Canal Area:** road S-11, NW of Escobal, *Croat 12462* (MO). **Chiriquí:** 1 mi. E of Cañas Gordas near Costa Rican border on road to Volcán, *Croat 22303* (MO); Burica Peninsula, 8 mi. W of Puerto Armuelles, 200 m, *Croat 22478* (MO, PMA). **Coclé:** El Valle de Antón, *Allen 1804* (BH, MO), *Allen 2951* (BH). **Colón:** Río Guanche, sea level, *de Nevers 10703* (CAS). **San Blas:** Río Taindi (Taimdi of maps) 6 km above confluence with Río Mandinga, 9°25′N, 79°11′W, 30–100 m, *de Nevers & Herrera 7645* (MO); trail to Cerro Obu from Río Urgandi (Río Sidra), 9°23′N, 78°48′W, *de Nevers et al. 7999* (CAS, MO).

8b. **Bactris glandulosa** var. **baileyana** (H. E. Moore) de Nevers, comb. & stat. nov. *Bactris baileyana* H. E. Moore in L. H. Bailey, Gentes Herb. 8:155. 1949.

TYPE. — PANAMA. **Chiriquí:** Cerro Galera Chorcha, Gualaca, 1000 ft, 1 Aug 1947, *P. Allen 5023* (holotype, MO; isotype, BH).

ADDITIONAL SPECIMENS EXAMINED. — COSTA RICA. **Cartago:** Tucurrique, Turrialba, 820 m, *Mat-*


a
c
4/5
2/5
b

tos et al. 2895 (NY). **Limón:** between Punta Manzanillo and Punta Mona, 9°38′N, 82°38′W, *Grayum & Schatz 5254* (MO); Colonía Maceo, *Cook & Doyle 739* (US). **Puntarenas:** Interamerican Highway, km 287, 3 km W of Chacarita, 8°84′N, 83°17′W, *de Nevers et al. 7754* (MO); Osa Peninsula, Corcovado, *Gentry et al. 48571* (MO); fila before Rancho Quemado, near Rincón, 8°42′N, 83°33′W, 300 m, *Gentry et al. 78762* (MO); Osa Peninsula, near Palmar Norte, *Grayum et al. 9137* (MO); Osa, road to Puerto Jiménez, 100 m, *Gómez P. 19513* (CAS, MO); Finca El Edén, 400 m E of Santa Marta [Valle de El General], *Gómez 22953* (MO); Esquinas, ca. 25 km from Palmar Sur on Golfito railroad, *Moore 6556* (BH); between Las Cruces Botanical Garden and Río Jaba, ca 4 km SE of San Vito de Coto Brus, 8°47′N, 82°58′W, 1150 m, *Grayum et al. 7575* (MO); 8 km from Chacarita, 8°45′N, 83°18′W, *Henderson et al. 1806* (NY).

PANAMA. **Chiriquí:** Progreso, *Cooper & Slater 189* (US). **Veraguas:** mountains of southern Azuero Peninsula, ca 10 km SW of El Cortezo, El Pavo ridge above river Los Changuales, 1500–2000 ft, *Hammel 5438* (MO); Cerro Alto Higo, 2000–3000 ft., *Hammel 4316*.

DISCUSSION. — The question of priority must be carefully considered with regard to the binomials *Bactris fusca* and *B. glandulosa*, published by Oersted in the same volume of the Danish journal *Videnskabelige Meddelelser fra den naturhistoriske forening i Kjöbenhavn*, and here treated as synonyms. The unnumbered volume comprises papers presented in 1858, but was published in 1859. It is divided into three sections, as follows: "Nr. 1–4" (pp. 1–64), "Nr. 5–7" (pp. 65–128), and "Nr. 8–11" (pp. 129–184). *Bactris fusca* and *B. bifida* Oerst., the basionym of *B. glandulosa*, were published on pp. 43 and 44, respectively, of the first section, while *B. glandulosa* (a nomen novum for *B. bifida*) appeared on the very last page of the final section. If it could be established that the three separate sections were issued sequentially at different times, then the name *Bactris fusca* would have to be used for this species as having priority over *B. glandulosa*; however, if the entire volume had been issued at once, then either name could be chosen (provided no precedent existed for preferring one name over the other).

Unfortunately we can find no wording anywhere in the volume that definitely clears up this problem. However, based on indirect evidence, we believe that the entire volume appeared as a single unit in 1859 (the date of publication given on the title page). The volume was reviewed (apparently by F. L. von Schlechtendal) in *Botanische Zeitung* Vol. 18, beginning with Oersted's paper on Central American palms, dealt with on pp. 46–47 of issue No. 5, which appeared on 3 February 1860. This portion of the review terminated with the words "Beschluss folgt" ("Conclusion follows"), marking it as a single, if interrupted, piece which was completed in issue No. 6 (pp. 54–55), published on 10 February 1860, beginning with the heading "Beschluss" ("Conclusion"). Three additional articles were reviewed in issue No. 6, including one from section "Nr. 8–11." Thus it seems virtually certain that the 1858 volume of the journal containing Oersted's paper was published all at once, probably in late 1859; otherwise, a weekly publication such as *Botanische Zeitung* would surely have reviewed the sections separately. Unfortunately, the detailed review of Oersted's paper does not mention *Bactris glandulosa*, which would have clinched the matter; however, that item would have been easily overlooked.

We conclude, therefore, that priority of initial publication is not a factor in selecting between the names *Bactris fusca* and *Bactris glandulosa*. In the case of names published simultaneously, priority is established according to the earliest publication in which said names were treated as synonyms. Although this can be extremely difficult to determine, we feel relatively certain that *Bactris fusca* and *B. glandulosa* have never been previously treated as synonyms, and that our present action in preferring *B. glandulosa* establishes a precedent in this regard. We select *Bactris glandulosa*, since the element chosen to lectotypify that binomial is that which most unequivocally belongs to the species we are dealing with. *Bactris fusca* is a very uncertain entity,

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FIGURE 2. *Bactris glandulosa* var. *glandulosa* (*Allen 2574*). A. Midsection of leaf rachis (× 2/5). B. Inflorescence (× 2/5). C. Fruit in two views. Courtesy of the L. H. Bailey Hortorium, Cornell University.

assigned here only on the basis of a very poorly preserved leaf fragment.

9. Bactris gracilior Burret, Repert. Spec. Nov. Regni Veg. 34:216. 1934.
Fig. 3

TYPE. — COSTA RICA. **Alajuela**: San Carlos, *Koschny* (holotype, B, destroyed).
NEOTYPE. — COSTA RICA. **Alajuela**: Finca Vera Cruz, Pital de San Carlos, 60 m, 7 Apr 1990, *J. Sánchez s.n.* (CR [here designated]).

Bactris aureodrupa L. H. Bailey, Gentes Herb. 6:232. 1943.
TYPE. — PANAMA. **Coclé**: El Valle de Antón, 1000 m, 23 Jun 1940, *P. Allen 2150* (holotype, BH).

Stems cespitose, 2–4 m tall, ca. 2 cm diam, spiny on internodes. **Leaves** 5–9; sheath to 28 cm long, moderately to densely covered with short, black spines; petiole 0.2–1.1 m long, without spines; rachis 42–96 cm long, without spines; pinnae 10–24 per side, irregularly arranged in clusters on alternating sides of the rachis distally, more regularly arranged apically, spreading in different planes, narrowly elliptical, gradually aristate, glabrous, middle pinnae 18–39 (–45) cm long, 2.5–4.4 cm wide, dull green adaxially, brownish abaxially on drying, sometimes with minute, forward pointing marginal spines. **Inflorescences** interfoliar; peduncle 6–10 cm long, not spiny or sparsely appressed-spiny, curved; prophyll 8–12 cm long, thin, chartaceous; peduncular bract 15–24 cm long, sparsely covered with short, black or brown spines, occasionally almost glabrous; rachis 3–3.6 cm long; rachillae 8–23, 7–10 cm long; triads irregularly arranged amongst paired or solitary staminate flowers; **staminate flowers** 3 mm long; sepals very briefly connate below, spreading above, 1 mm long; petals connate below for ca. half their length, free and valvate above, 3 mm long; pistillode absent; **pistillate flowers** 3 mm long; calyx 1 mm long; corolla 3 mm long; staminodes minute; **fruits** obovoid, bluntly rostrate, 1–1.3 cm long, 0.9–1.1 cm diam, orange, glabrous; mesocarp mealy, fibrous; endocarp turbinate; endocarp not pitted, with a few, flattened fibers; endocarp pores equidistant; fruiting perianth with a minute, 1 mm long calyx and truncate, 3 mm long corolla.

ADDITIONAL SPECIMENS EXAMINED. — NICARAGUA. **Zelaya**: Bluefields, Cerro El Panteón, 12°S, 83°46'W, 60–100 m, *Moreno 14585* (MO); Caño Costa Riquita, ca. 1.8 km SW of Colonia Naciones Unidas, ca. 11°43'N, 84°18'W, 150–180 m, *Stevens 5083* (NY); along Río Rama above Rápido Machuca, ca. 11°56'N, 84°16'W, 10 m, *Stevens 8906* (MO).

COSTA RICA. **Alajuela**: San Carlos, *Cook & Doyle 51* (US); between San Lorenzo and Los Angeles de San Ramón, 10°14'S, 84°32'W, ca. 620 m, *Burger & T. Antonio 11197* (F); Reserva Biológica de San Ramon, road from Las Lagunas to Colonia Palmareña, 850–1100 m, *de Nevers et al. 7794* (MO); San Miguel de Sarapiquí, *Wendland 62* (GOET), *Wendland 70* (GOET). **Cartago**: above Turrialba, 800 m, *Read & Daniels 74-64* (US). **Heredia**: 8 km SW of Puerto Viejo on road to San José, 10°26'N, 84°02'W, *Burger & G. Matta 4303* (NY, US); N of Puerto Viejo, 10 km down road, then 7–8 km W, *Garwood et al., 857* (BM); Río Sarapiquí, *Wendland s.n.*, 1857 (K); La Selva, Río Sarapiquí near Puerto Viejo, 10°26'N, 84°01'W, 100 m, *Gentry & Ortiz 78575* (MO); Finca El Bejuco, 6 km W of Puerto Viejo, 10°27'N, 84°04'W, *Grayum & Jacobs 5344* (MO), *Henderson et al. 60* (NY); between Corazón de Jesús and La Virgen, *Moore 6629* (NY). **Limón**: 7 km SW of Bribrí, 100–250 m, *Gómez et al. 20454* (MO, NY); Parque Nacional Tortuguero, 10°26'N, 83°23'W, 80–100 m, *Robles 1668* (MO); Cerro Coronel, E of Laguna Danto, 10°41'N, 83°38'W, 20–170 m, *Stevens 23685* (MO), *Stevens 23707* (MO), *Stevens & Montiel 24490* (MO); Cairo, *Loomis 2* (US); Port Limón, 0-10 m, *Cook & Doyle 426* (US); Río Reventazón below Cairo, 25 m, *Standley & Valerio 48944* (US).

PANAMA. **Province unknown**: May 1928 *Cooper s.n.* (MO). **Bocas Del Toro**: Chiriquí Grande near Rambala, 8°45'N, 82°15'W, 250 m, *McPherson 11151* (MO), *Hart 143* (US). **Coclé**: Coclecito road, 8°42'N, 80°28'W, 200 m, *de Nevers & McPherson 6709* (MO, NY); 27 km N of Penonomé on road to Coclesito, 1500 ft, *Hammel 1620* (MO); El Copé, *Hammel 2392* (MO). **Colón**: Santa Rita ridge, ca. 6 mi. from Transisthmian Highway, 800–900 ft., *Anto-*

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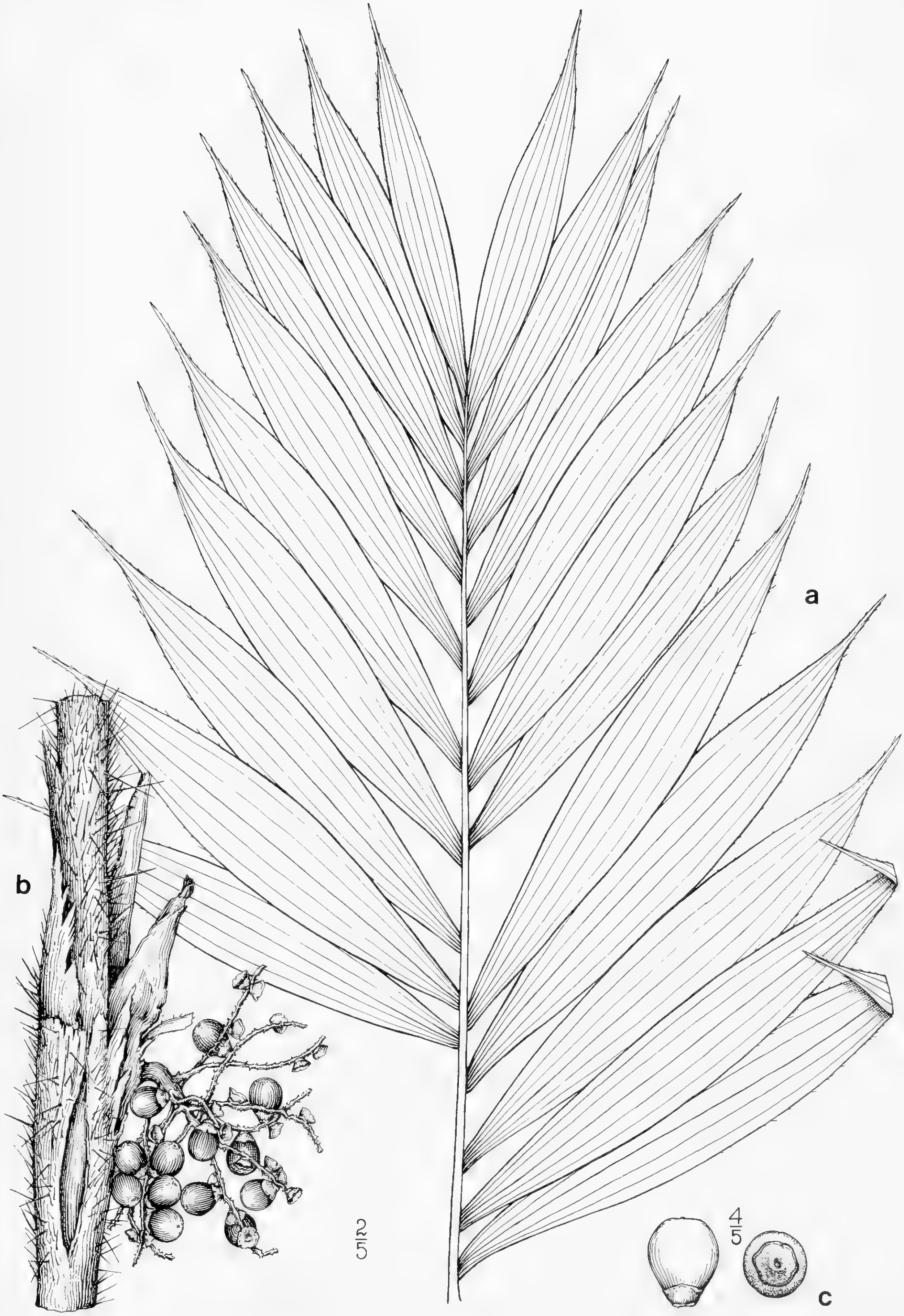
FIGURE 3. *Bactris gracilior* (*Allen 2150*). A. Leaf apex (× 2/5). B. Infructescence. (× 2/5). C. Fruit in two views. Courtesy of the L. H. Bailey Hortorium, Cornell University.


a
b
2/5
4/5
c

nio 1786 (MO); 12 mi. from highway, 9°20′N, 79°45′W, 500 m, *McPherson 10254* (CAS); ridge top leading N from Río Escandaloso towards Cerro Bruja, 1500 ft., *Hammel 2722* (MO). **Darién**: trail N from Ensenada del Guayabo, 18 km SE Jaqué, *Garwood et al. 211* (MO). **Panamá**: Rancho Chorro, above Tortí Arriba, 400–700 m, *Folsom et al. 6655* (MO); Cerro Jefe, *Gentry & Dwyer 3441* (CAS); 2600 ft., *Hammel 4864* (MO); just W of El Llano, *Gentry 5099* (MO); 16 km above Pan-Am Highway on road from El Llano to Cartí-Tupile, 350–400 m, *Kennedy 2541* (MO); along road between El Llano and Cartí-Tupile, 200–500 m, *Liesner 1327* (MO). **San Blas**: El Llano-Cartí road, km 19.1, 9°19′N, 78°55′W, 350 m, *de Nevers & Cavagnaro 4828* (MO); km 27, 9°19′N, 78°55′W, 250 m, *de Nevers & Charnley 5082* (MO); km 26.5, 9°19′N, 78°55′W, 200 m, *de Nevers et al. 5267* (MO); km 16, 9°19′N, 78°55′W, *de Nevers 5976* (MO, NY); km 19.1, *de Nevers et al. 6168* (MO, NY), *de Nevers et al. 5626* (MO); km 20, *Paredes et al. 774* (SCZ); km 22, 9°19′N, 78°55′W, 350 m, *de Nevers & Herrera 7848* (MO); near Nusagandi, 9°15′N, 79°W, 250–300 m, *McPherson 11020* (MO); Cangandí, 9°24′N, 79°24′W, 100 m, *de Nevers et al. 5726* (MO), *de Nevers et al. 6466* (MO), *de Nevers et al. 7579* (MO); trail to Cerro Obu (Habu of maps) from Río Urgandi (Río Sidra), 9°23′N, 78°48′W, 100–300 m, *de Nevers et al. 7978* (MO).

DISTRIBUTION AND HABITAT. — Atlantic slope from southern Nicaragua (Zelaya), Costa Rica (Alajuela, Heredia, Limón) and Panama (Bocas Del Toro, Coclé, Colón, Darién, Panamá, San Blas); lowland rainforest below 800 m elevation.

LOCAL NAMES AND USES. — Costa Rica: *biscoyol.*

DISCUSSION. — This is the species referred to as "*Bactris* sp nov. fide Moore" by Chazdon (1985, 1987). Several specimens are somewhat aberrant: *Gentry & Dwyer 3441* and *Robles 1668* have the typical leaves of the species but have spines on the rachis. Some specimens from Costa Rica and Nicaragua have black, 2–11 mm spines on the nerves abaxially (*Moore 6629, Robles 1668, Stevens 5083*).

10. Bactris grayumii de Nevers & A. Henderson, sp. nov.

Fig. 4

TYPE. — COSTA RICA. **Limón**: Barra del Colorado, 10°47′N, 83°35′W, 1–5 m, 12 Sep 1986, *G. Davidse & G. Herrera 30954* (holotype, MO).

Forma fructuum *Bactris mexicana* similis sed foliis simplicibus plicatisque.

Stems usually solitary, rarely cespitose, 1.5–3.5 m tall, 2.2–3 cm diam, usually spiny on internodes. **Leaves** 4–9; sheath 20–29 cm long, sparsely covered with black spines to 3 cm long; petiole 40–45 cm long, with black spines to 6 cm long; rachis 29–70 cm long, without spines or with round black spines to 6 cm long; blade usually simple and deeply bifid, concave, glabrous, leathery, with very prominent veins adaxially, occasionally irregularly pinnate, when bifid the lobes 11–20 cm wide at apex of rachis, 35–60 (–90) cm long from apex of rachis to tip, when pinnate the pinnae 55–90 cm long, 2.5–10 cm wide, the apical one much wider. **Inflorescences** interfoliar; peduncle 10–11 cm long, 8–10 mm wide, strongly recurved at anthesis, glabrous or covered with short spines; prophyll 11–12 cm long, 3–4 cm wide; peduncular bract 23–27 cm long, 3 cm wide, sparsely covered with short black spines to 0.5 cm long, occasionally almost glabrous; rachis 1.8–3 cm long; rachillae 18–25, 5–6 cm long, 1 mm diam at anthesis; triads irregularly arranged amongst paired or solitary staminate flowers; flowers not seen; **fruits** obovoid with prominent stigmatic residue, 1.1–1.2 cm long, 0.9–1.1 cm diam, orange, glabrous; mesocarp mealy, fibrous; endocarp turbinate; endocarp fibers few, free, terete; endocarp pores equidistant; fruiting perianth with a minutely 3-lobed, 1 mm long calyx and truncate 3 mm long corolla.

ADDITIONAL SPECIMENS EXAMINED. — NICARAGUA. **Chontales**: 4 km N of Santo Domingo, ca. 12°17′N, 85°6′W, 280 m, *Grijalva 3784* (NY). **Zelaya**: Monkey Point, Caño El Pato, 11°35′N,

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FIGURE 4. *Bactris grayumii* (*Davidse & Herrera 30954*). A. Leaf blade. B. Infructescence. C. Fruit in two views and seed (right). A & B same scale.


3 cm
a
b
c
1 cm

83°42′W, 10 m, *Moreno 12427* (MO); Comarca "Bodega," 30 km NE of Río Blanco, 13°03′N, 84°58′W, 80–100 m, *Moreno 24040* (MO); 30 km N of Río Blanco, 13°03′N, 84°58′W, 80–100 m, *Moreno 24075* (MO); Caño Sardina, 11°40′N, 84°26′W, *Stevens 6362* (NY); Caño Zamora, Río Rama, ca. 11°57′N, 84°16′W, 10 m, *Stevens 8874* (MO).

COSTA RICA. **Limón**: Refugio Barra del Colorado, 10°38′N, 83°45′W, 10–15 m, *Grayum et al. 8995* (MO); Parque Nacional Tortuguero, 10°32′N, 83°30′W, 2–4 m, *Robles 1856* (MO), *Solano 20* (MO). **San José**: along Río Negro, ca. 1.5 km E of Santa Rosa de Puriscal, 9°42′N, 84°23′W, 320 m, *Grayum et al. 8310* (MO).

DISTRIBUTION AND HABITAT. — Nicaragua (Chontales, Zelaya) and Costa Rica (Limón, San José); lowland rainforest below 350 m elevation, usually near sea level.

DISCUSSION. — This species sometimes occurs sympatrically with *Bactris militaris*, which it resembles in its usually simple leaves, but these are ovate, shorter and wider, and do not have parallel margins. *Bactris grayumii* is further distinguished from *B. militaris* by its recurved inflorescence. The fruits very much resemble those of *B. mexicana*.

11. Bactris guineensis (L.) H. E. Moore, Gentes Herb. 9:251. 1963. *Bactris minor* Jacq., nom illeg., Select. stirp. amer. hist. 234. 1780–1781. *Cocos guineensis* L., Mant. pl. 137. 1767.
Fig. 5

TYPE. — Jacq., Select. stirp. amer. hist., pl. 171, fig. 1, 1763 (lectotype, designated by Moore, 1963).

Bactris rotunda Stokes, Bot. mat. med. 4:394. 1812. Nom. superfl.

Bactris horrida Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjöbenhavn 1858:41. 1859.
TYPE. — Nicaragua. **Granada**: Granada, n.d., *A. Oersted 6531* (lectotype, here designated).

Bactris oraria L. H. Bailey, Gentes Herb. 6:232. 1943.
TYPE. — PANAMA. **Panamá**: Taboguilla Island, Panama Bay, 1 Jun 1941, *P. Allen 2543* (holotype, BH).

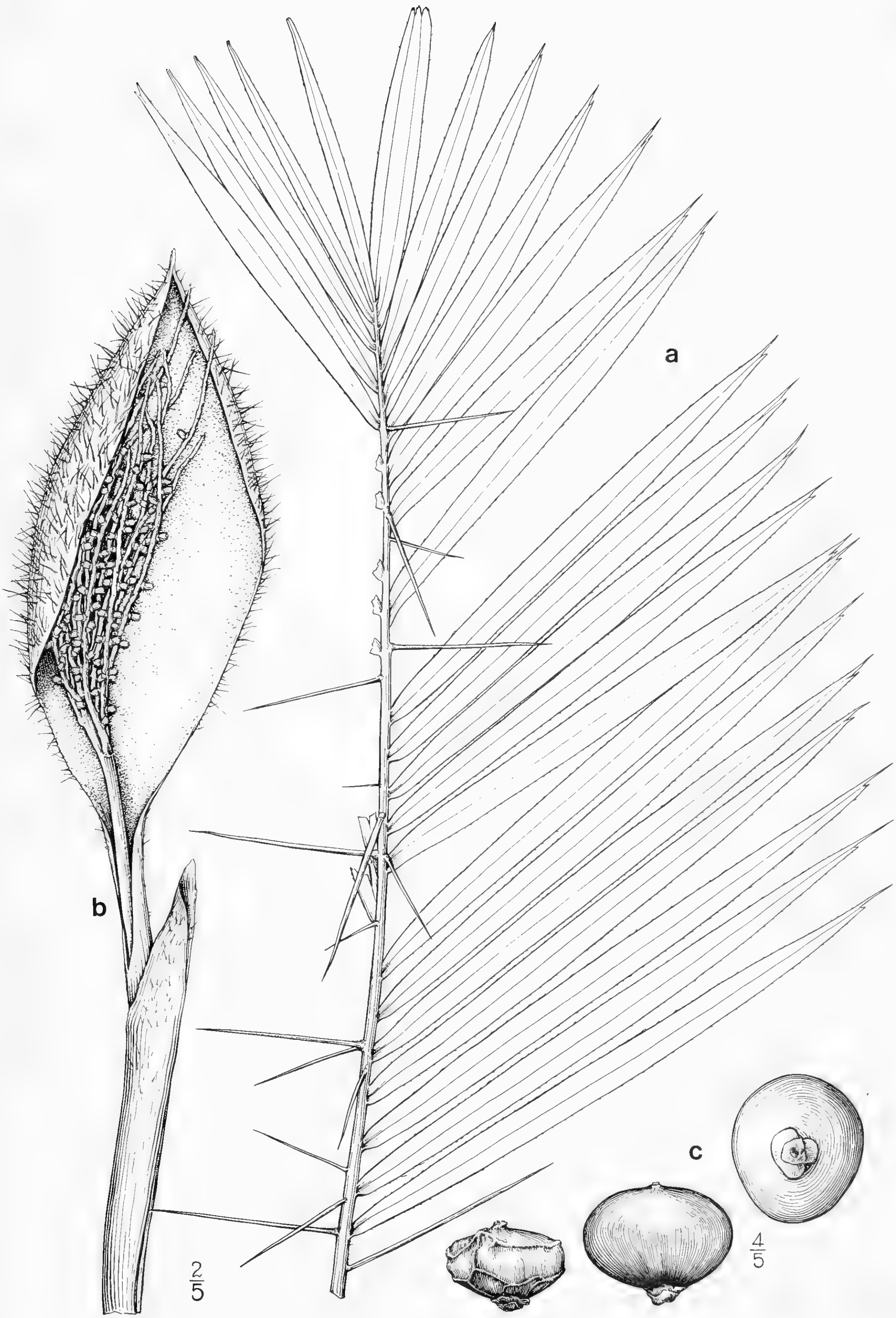
Stems cespitose, 0.8-3 m tall, 2.6–3 cm diam, often covered with dead, persistent leaf bases. **Leaves** 5–6; sheath 15–60 cm long, fibrous; sheath, petiole and rachis densely to moderately covered with yellowish (black at base and apex), terete spines to 9 (–15) cm long; petiole short, to 5 cm long; rachis 20–40 cm long; pinnae 20–42 per side, regular or slightly irregularly arranged (often with gaps), spreading ± in the same plane or in various planes, linear, ± equally and briefly bifid at the apex, pale green and easily falling on dried specimens; middle pinnae 15–30 cm long, 0.9–2 cm wide. **Inflorescences** interfoliar; peduncle 10–20 cm long, straight to slightly curved in fruit, spiny; prophyll to 20 cm long; peduncular bract 25–35 cm long, moderately covered with spreading, yellowish spines to 1 cm long; rachis 2–5 cm long; rachillae 11–30, 8–11 cm long, slender; triads irregularly arranged amongst paired or solitary staminate flowers; **staminate flowers** 4 mm long; sepals very briefly connate below, free above, narrowly triangular, 2 mm long; petals connate below for ca. half their length, free and valvate above, 4 mm long; **pistillate flowers** 3.5 mm long; calyx 3-lobed, 1 mm long; corolla tubular, lobed at the apex, 3 mm long; staminodes absent; **fruits** depressed globose, briefly rostrate, 1.5–2 cm diam, purple-black; mesocarp juicy; endocarp depressed-oblong; endocarp fibers numerous, with juice sacs attached; endocarp pores offset; fruiting calyx minute, corolla 3 mm, truncate.

ADDITIONAL SPECIMENS EXAMINED. — NICARAGUA. **Chontales**: Highway 7 between Boaco and Acoyapa, 100–250 m, *Bunting & Licht 734* (F). **Granada**: Granada, *Baker 193* (CAS, DS, MICH), *654* (US); Realejo, *Oersted 6537* (C); Lago de Nicaragua, Las Isletas, Isleta de Cementerio, *Guzmán & Castro 106* (MO).

COSTA RICA. **Guanacaste**: Hacienda La Pacifica, 10°30′N, 85°10′W, 50 m, *Gentry & Woodruff 71520* (MO); Comelco, 5 km W of Bagaces, *Opler 930* (F). **Puntarenas**: Playas Doña Ana, near Barranca, *Crow*

→

FIGURE 5. *Bactris guineensis* (*Allen 2543*). A. Leaf apex. B. Infructescence. C. Left to right: dry, shriveled fruit; mature fruit in two views. Courtesy of the L. H. Bailey Hortorium, Cornell University.


a
b
c
2/5
4/5

& Rivera 6218 (F, MO); El Ostillero, Nicoya Penninsula, 0-10 m, *Cook & Doyle 639* (US).

PANAMA: **Province unknown:** *Allen 2551* (MO). **Canal Area:** Balboa, *Standley 25496* (US); La Jagua, *Bartlett 16390* (MICH), *16996* (MICH); 3 mi. E of Panama City, *Maxon et al. 7100* (US), *Doyle 20* (US); Matías Hernández *Pittier 6953* (US). **Coclé:** Aguadulce, *Pittier 4975* (US); 20 mi. S of Natá, *Croat 9644* (MO, SCZ); Cerro Mangote, *McPherson 10047* (CAS). **Los Santos:** 7 mi. S of Chitre, *Croat 9710* (MO, SCZ). **Panamá:** E of Río Venado, 8°45′N, 79°39′W, *Knapp 1929* (MO); Lago Sororia, NE of Nueva Gorgona, S of Chamé, 8°33′N, 79°51′W, 5 m, *de Nevers & Piperno 10547* (CAS, PMA).

DISTRIBUTION AND HABITAT. — Pacific slope of Central America in Nicaragua (Chontales, Granada), Costa Rica (Guanacaste, Puntarenas), Panama (Canal Area, Coclé, Los Santos, Panamá), and in northern Colombia (Atlántico, Bolívar, La Guajira, Magdalena) and Venezuela (Apure, Cojedes, Guárico, Monagas, Portuguesa); open, often disturbed areas, and deciduous or semi-deciduous forest, often near the coast, in areas that experience prolonged dry seasons, to 850 m elevation.

LOCAL NAMES AND USES. — Costa Rica: *viscoyol*. Nicaragua: *coyolito*. Panama: *uvita de monte*.

DISCUSSION. — This is one of the most easily recognized species in the genus. The plants are small, the pinnae are short, glabrous, narrow and bifid, the spines of the stem and leaves are terete and usually yellowish, and the armature of the peduncular bracts is sparse. Most of these characters are shared with other species individually, but in combination they serve to distinguish this species. *Bactris guineensis* is further distinguished by occurring in the driest conditions of any Central American *Bactris*. Dahlgren (1959) presents two plates of *Bactris horrida*; plate 50 figures *A. Oersted s.n.* (C sheet 6537), but the leaf shown is actually *B. major*. The numerically corresponding bottled inflorescence (C *6537A*, not figured by Dahlgren) is *B. horrida*.

12. Bactris hondurensis Standl., Trop. Woods 21:25. 1930.
Fig. 6

TYPE. — Honduras. **Atlántida:** Lancetilla Valley, near Tela, 150 m, 6 Dec 1927–20 Mar 1928, *P. Standley 56798* (holotype, F; isotype, US).

Bactris pubescens Burret, Repert. Spec. Nov. Regni Veg. 34:197. 1934.
TYPE. — COSTA RICA. **Alajuela:** San Carlos, 8 Jun 1901 *Koschny s.n.* (holotype, B, destroyed).
NEOTYPE. — COSTA RICA. **Alajuela:** Río San Carlos, 1 km E of Jabillos, 10°22′N, 84°32′W, 150 m, 1 Jun 1986, *G. de Nevers 7808* (MO, here designated).

Bactris wendlandiana Burret, Repert. Spec. Nov. Regni Veg. 34:198. 1934.
TYPE. — COSTA RICA. Sarapiquí, n.d., *H. Wendland s.n.* (holotype, B, destroyed).
LECTOYPE. — COSTA RICA. **Province Unknown:** "flum. Sarapiquí," 1857, *H. Wendland s.n.* (K, here designated).

Bactris standleyana Burret, Repert. Spec. Nov. Regni Veg. 34:199. 1934.
TYPE. — COSTA RICA. **Guanacaste:** Tilarán, 500–650 m, 10–31 Jan 1926, *P. Standley & J. Valerio 44446* (holotype, US).

Bactris paula L. H. Bailey, Gentes Herb. 6:226. 1943.
Yuyba paula (L. H. Bailey) L. H. Bailey, Gentes Herb. 8:173. 1949.
TYPE. — PANAMA. **Coclé:** El Valle de Antón, La Mesa, 1000 m, 22 Jun 1941, *P. Allen 2567* (holotype, BH).

Stems cespitose or apparently sometimes solitary, 1–2.5 (–4) m tall, 0.5–1.5 cm diam. **Leaves** 5–9; sheath 9–25 cm long, sheath and petiole with few, black spines to 1 cm long, occasionally interspersed with longer, yellowish or black spines to 2 cm long; petiole 16–27 cm long; rachis 15–50 cm long; blade usually simple, bifid, 36–71 cm long, 26–39 cm wide, often with a pair of broad (rarely narrow) apical pinnae and 1–8 (–15) narrower, irregularly spaced, sigmoid basal pinnae, occasionally with cross-veins, usu-

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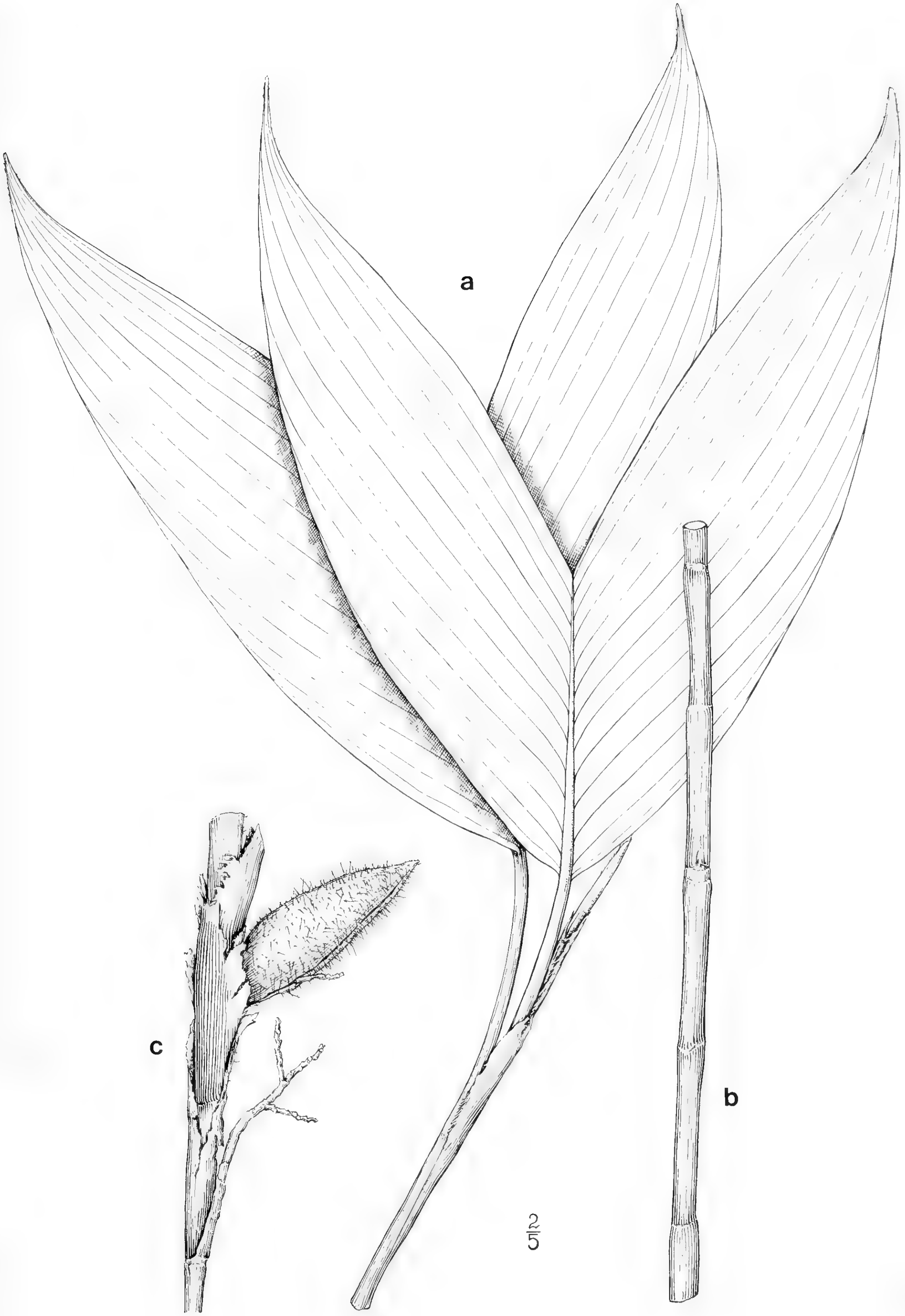
FIGURE 6. *Bactris hondurensis* (*Allen 2567*). A. Leaves. B. Stem. C. Infructescence. All × 2/5. Courtesy of the L. H. Bailey Hortorium, Cornell University.


a
b
c
2/5

ally minutely, densely and softly white-pubescent abaxially. **Inflorescences** interfoliar; peduncle 7–11 cm long, terete, straight at anthesis, becoming arched in fruit; prophyll 8–9 cm long; peduncular bract 13–18 cm long, densely to moderately covered with soft, spreading, yellowish, black or brown spines to 1 cm long; rachis 1–3 cm long; rachillae 3–7, 2–5 cm long, slender; triads irregularly arranged amongst paired or solitary staminate flowers; **staminate flowers** 7 mm long; sepals connate below, free above, 1.5 mm long; petals connate below for ca. half their length, free and valvate above; **pistillate flowers** (immature) 2 mm long; calyx 1 mm long; corolla 2 mm long, lobed at the apex; staminodes minute or absent; **fruits** very broadly obovoid, briefly rostrate, 1.2–1.5 cm diam, orange or red, glabrous; mesocarp mealy; endocarp turbinate; endocarp fibers few or absent, without juice sacs; endocarp pores symmetrical; fruiting calyx minute, corolla 2 mm, irregularly parted.

ADDITIONAL SPECIMENS EXAMINED. — HONDURAS. **Atlantidá**: Lancetilla valley near Tela, 20–600 m, *MacDougal et al. 3335* (MO), *Standley 54212* (F). **Gracias a Diós**: Río Platano, Quebrada Tiro, 15′43″N, 84′50″ W, 200 ft., *Saunders 1180* (US).

NICARAGUA. **Bluefields**: 3.6 km SE of Cerro San Isidro, Río Kama, Río Escondido, 12°05′–12°15′N, 83°45′–84°20′W, 0–65 m, *Proctor et al. 26907* (NY). **Chontales**: Cerro Oluma, top of Cordillera Amerisque, 12°18′N, 85°24′W, 840 m, *Gentry et al. 43892* (MO). **Jinotega**: Salto Kayaska, Río Bocay, ca 13°51′N, 85°22′W, 190–340 m, *Stevens et al. 16458* (MO). **Rio San Juan**: Bocas de Sábalo, 11°03′N, 84°27′W, 70–100 m, *Moreno 26773* (MO); El Castillo, 11°02′N, 84°24′W, *Salick 7813* (MO). **Zelaya**: between El Muelle de los Bueyes and Villa Somoza, *Bunting & Licht 1079* (F); Mpio. Siuna, Comarca Danlí, *Ortiz 236* (NY).

COSTA RICA.**Alajuela**: Río Sarapiquí, 10°16′N, 84°11′W, 830 m, *Croat 68334* (MO); Monteverde Cloud Forest Reserve, Peñas Blancas river valley, 10°20′N, 84°40′W, 840–900 m, *Haber 5458* (MO), *7344* (MO); Plains of San Carlos, 100 m, *Cook & Doyle 86* (US); between Tronadora & Arenal, *Read & Daniels 74-10* (US); between Tronadora & Tilarán, 600 m, *Read & Daniels 74-15b* (US); *74-15c* (US); Ciudad Arenal, *Read & Daniels 74-18* (US); Turrialba, 695 m, *Read & Daniels 74-60* (US); *74-61* (US); **Guanacaste**: along Río Las Flores between Quebrada Desprendimiento and Q. Sanguijuela, Hacienda Montezuma, 450 m, 10°40′N, 85°04′W, *Grayum et al. 4935* (MO); 4.7 km before Tronadora on road to Tilarán, 600 m, *Read & Daniels 74-15* (US); El Arenal, 485-600 m, *Standley & Valerio 45309* (US); *45313* (US); La Tejona, north of Tilarán, 600-700 m, *Standley &Valerio 46005* (US). **Heredia**: Finca La Selva, near Río Puerto Viejo, about 2 km upstream from confluence with Río Sarapiquí, 10°26′N, 84°W, 100 m, *Burger & Stolze 5891* (F, NY), *Gentry & Ortiz 78616* (MO), *Hammel 12166* (MO), *Henderson 46* (NY), *McDowell 967* (MO); between Río Peje and Río Sardinalito, 10°17′N, 84°04′W, 700–750 m, *Grayum & Jermy 6803* (MO). **Limón**: between Fila Dimat and Río Urén, *Gómez et al. 23749* (CAS, MO); Refugio Nacional Barra del Colorado, 10°38–47′N, 83°35–45′W, 0–15 m, *Grayum 9833* (MO), *Grayum 9835* (MO), *Stevens 24112* (MO, NY); Cairo, Río Reventazon, 25 m, *Standley & Valerio 48942* (US), *Loomis 4* (US); vicinity of USDA Rubber Experiment Station, Los Diamantes, on Río Santa Clara, 1.6 km E of Guápiles, 200 m, *Holm & Iltis 323* (BH, WIS), Astúa Pirie Reserve, United Fruit Company, *Seibert 1598* (US); *Standley 37190* (US); Parque Tortuguero, 10°31′N, 83°30′W, 4 m, *Robles 1466* (MO, NY). **Puntarenas**: Reserva Biológica Carara, 9°46′N, 84°34′W, 480–520 m, *Grayum et al. 9610* (MO); Coto Brus Guaymí Reserve E of Limoncito ford/bridge, 600 m *Kosear 282* (CAS). **San José**: Río Naranjo, 200–250 m, *Tonduz 7638* (BR).

PANAMA. **Bocas Del Toro**: Changuinola, *Correa et al. 3905* (PMA); above RR station at Milla 7.5, *Croat & Porter 16397* (MO). **Coclé**: El Valle de Antón, ca. 1000 m, *Allen 2695* (BH, US); 7 km from Llano Grande on road to Coclesito, 1200 ft., *Antonio 1402* (MO, PMA); Coclecito rd., 4 mi. beyond continental divide, 8°42′N, 80°24′W, *de Nevers & McPherson 6707* (MO, NY); near sawmill 16.7 km N of turnoff to Coclesito from Llano Grande, 700 ft., *Hammel 1859* (MO); Coclesito road, 1500 ft., *Hammel 3479* (MO); El Copé on Pacific side, 2400 ft., *Antonio 2102* (MO); *Read & Watson 84-52* (US); La Mesa above El Valle, ca. 800 m, *Croat 25336* (MO); 3000 ft., *Duke & Lallathin 15021* (MO); Alto Calvario, 7+ km N of El Copé, 700–900 m, *Folsom 3259* (MO, PMA). **Colón**: near Guásimo, *Croat 9922* (MO); trail from Alto Pacora to Cerro Brewster, 9°18′N, 79°16′W, *de Nevers et al. 6240* (BH, MO, PMA). **Darién**: Parque Nacional del Darién, ridge between Río Topalisa and Río Pucuro, ca 13 km E of Pucuro, 8°03′N, 77°20′W, 450–600 m, *de Nevers et al. 8329* (CAS, MO); S of Garachiné above Casa Vieja, W flank Serranía Sapo, 7°58′N, 78°23′W, 500–800 m, *Hensold 1130* (MO), *Herrera et al. 996* (MO); Río Tuquesa, camp called Charco Peje, ca. 250 m, *Mori 7075* (MO). **Panamá**: El Llano-Cartí road, km 14, 350–500 m, *Folsom et al. 1489* (MO), km 19, ca. 500 m, *Busey 882* (MO); Gorgas Memorial Labs yellow fever research camp, 5–10 km NE of Altos de Pacora, ca. 600 m, *Mori & Kallunki 3404* (MO, PMA). **San Blas:** Yar Bired (Cerro San José), continental divide between Cangandí and San José, 400–500 m, 9′20″N, 79′08″W, *de Nevers & Herrera 6940* (MO), *7005* (MO, NY); Cerro Brewster, 9°18′N, 79°16′W, 800–850 m, *de Nevers et al. 6281* (MO), *5558* (MO, NY), El Llano-Cartí rd., km 18.3, 9°19′N, 78°55′W, *de Nevers 5982* (MO), *4858* (MO), *5883* (MO, NY), *7682* (MO), km 26.5, 200 m, *de Nevers et al. 5250* (MO); near Cangandí, 9°27′N, 79°07′W, *Herrera 205* (CAS); Campamento Kariadi, Río Ispergandi, 3 km upriver, 9°15′N, 78°15′W, 50 m, *Herrera et al. 1080* (MO); Isla de Nargana, 9°22′N, 78°35′W, 50–100 m, *Herrera et al. 1254* (MO); Aila Tiwar (Río Acla), 8°48′30″N, 77°40′30″W, 25–100 m, *Sugden 350* (MO); (San Blas) Armila, 8°39′N, 77°27′W, 0–400 m, *de Nevers & Herrera 10697* (CAS, PMA). **Veraguas:** valley of Río Dos Bocas along road between Escuela Agrícola Alto Piedra and Calovébora, 15.6 km NW of Santa Fe, 450–550 m, *Croat 27666* (MO, PMA); *Mori & Bolten 7656* (MO); trail to Cerro Tute, 800–1000 m, *de Nevers et al. 10554* (CAS, NY, COL), *10588*; trail from Bajo Chitra to Río Gatu, 8°34′N, 80°56′W, *de Nevers & McPherson 6787* (MO, PMA); Río Concepción to Río Barrera, 0–200 m, *Hammel 5149* (PMA).

Distribution and Habitat. — Honduras (Atlantidá), Nicaragua (Bluefields, Chontales, Jinotega, Río San Juan, Zelaya), Costa Rica (Alajuela, Guanacaste, Heredia, Limón, Puntarenas, San José), Panama (Bocas Del Toro, Coclé, Colón, Darién, Panamá, San Blas, Veraguas) to northwestern Colombia (Antioquia, Chocó); lowland rain forest at elevations below 1000 m.

Local Names and Uses. — Costa Rica: *biscoyol, caña brava* (Spanish); *kaa* (Guaymí). Nicaragua: *coyolillo, huiscoyol, montiel* (Spanish). Panama: *pacaya de danto* (Spanish), *uga wawad* (Kuna). In Kuna "wawad" means hairy, and "uga" is a generic term for palms of the genus *Geonoma*, thus to the Kuna *Bactris hondurensis* is the "hairy *Geonoma*," an apt association for this non-spiny species.

Discussion. — Although Standley's minimal description in *Tropical Woods* (21:25, March 1930) constituted valid publication of *Bactris hondurensis*, no specimens were cited. We thus accept as holotype the specimen cited as such in Standley's much more detailed description that appeared in *Publ. Field Columbian Mus., Bot. Ser.* (8:4, July 1930).

The soft, almost invisible pubescence and often complete lack of spines of *B. hondurensis* render it perhaps the most distinctive species of the genus in Central America. It is variable in degree of blade division (from simple and bifid to pinnate with wide apical pinnae) and habit (from solitary to cespitose and from 0.5 to 3 m in height). The inflorescence is typically small and erect at anthesis. It could easily be confused with *B. charnleyae*, which is distinguished by its abundant endocarp fibers with juice sacs attached; without fruits, the latter species can be separated by the elongate, soft, black spines on the peduncle and peduncular bract. The endocarp sometimes has scattered fibers, contra Sanders (1991).

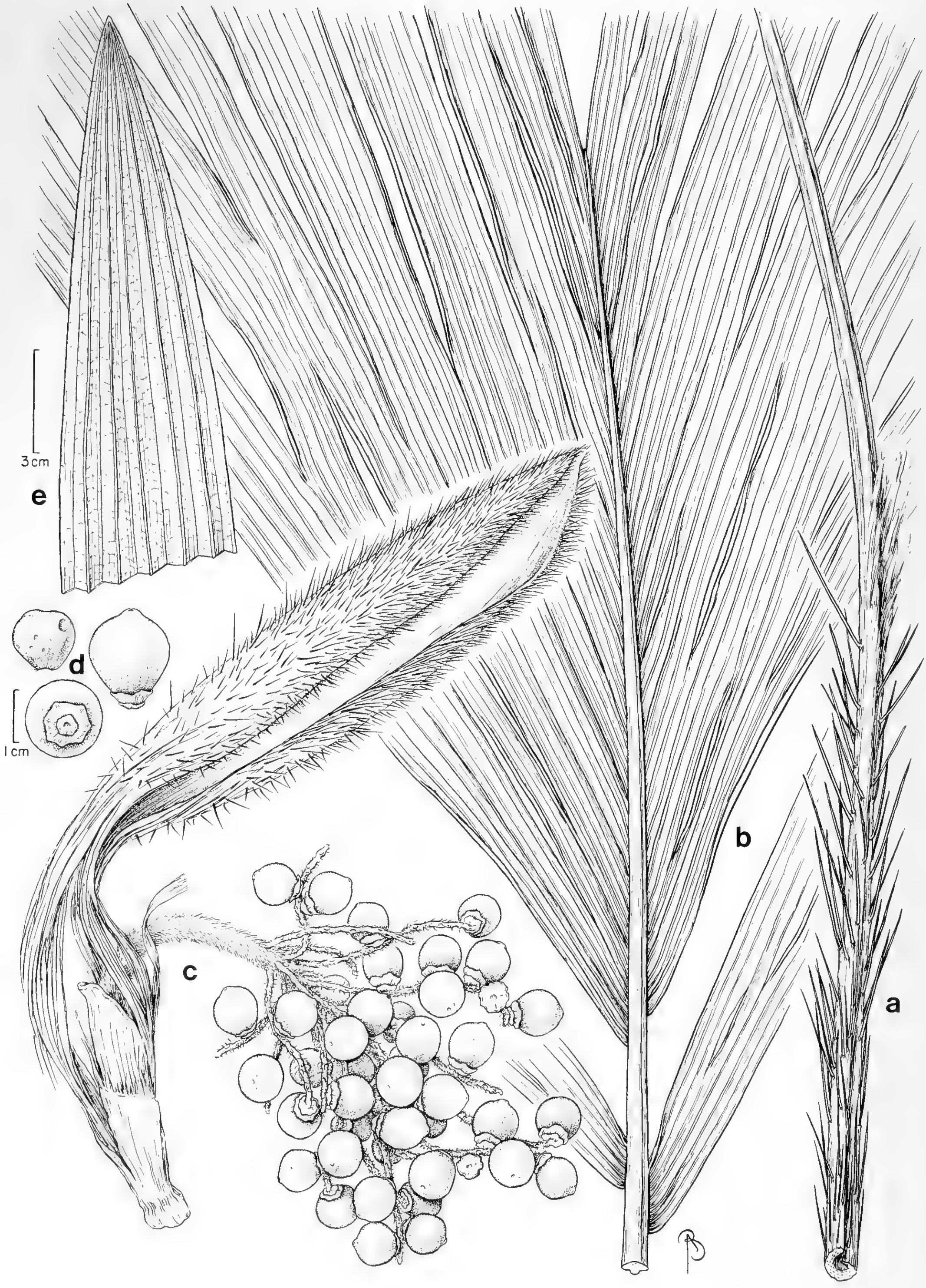
13. **Bactris kunorum** de Nevers & Grayum, sp. nov.

Fig. 7

Type. — PANAMA. **San Blas:** Río Esadi to Cerro Banega, 9°23′N, 78°51′W, 300–530 m, 21 Dec 1985, *G. de Nevers & H. Herrera 6672* (holotype, MO; isotype, NY).

Fructibus grandibus aurantiacis *Bactris coloradonidis* similis sed foliis simplicibus pinnatisve plicatis.

Stems cespitose in tight clumps of 4–6 stems 50–60 cm wide, 2–6 m tall, to 5 cm diam, usually spiny on internodes. **Leaves** 4–9; sheath 22–54 cm long, densely black-spiny; petiole 20–27 cm long, without spines or with black spines to 6 cm long; rachis (42–) 65–135 cm long, without spines or with round black spines to 6 cm long; pinnae 4–14 per side, irregularly arranged in clusters and spreading in various planes, forming a 10–40° angle with the rachis, concave, glabrous, leathery, strongly plicate with prominent veins adaxially, the middle ones 45–87 cm long, 3.5–5.5 cm wide (distal and sometimes proximal ones much wider), blade occasionally simple, bifid, the lobes 11.5–18 cm wide at apex of rachis, 46–52 cm long from apex of rachis to tip. **Inflorescences** interfoliar; peduncle 10–29 cm long, strongly recurved at anthesis, densely spiny; prophyll 11–14 cm long, 3–4 cm wide, thin, chartaceous; peduncular bract 30–45 cm long, 3–5 cm wide, sparsely covered with short black spines to 0.5 cm long; rachis 3–7 cm long;


3 cm
e
d
1 cm
c
b
a

rachillae 24–30, 8–14 cm long, 1 mm diam at anthesis; triads irregularly arranged amongst paired or solitary staminate flowers; **staminate flowers** 2–3 mm long; sepals very briefly connate below, lanceolate, 1 mm long; petals 3 mm long; **pistillate flowers** 3 mm long; calyx 1 mm long; corolla minutely 3-lobed apically, 3 mm long; staminodes minute; **fruits** obovoid, flat-topped but with prominent stigmatic residue, 1.4–1.9 cm long, 1.3–2 cm diam, orange or red, glabrous; mesocarp mealy, fibrous; endocarp turbinate; endocarp pitted or smooth, with a few, terete or flat fibers; endocarp pores equidistant; fruiting perianth with a minutely 3-lobed calyx 1 mm long, and crenate corolla 3–4 mm long.

ADDITIONAL SPECIMENS EXAMINED. — PANAMA. **Panamá**: 6 mi. above Goofy Lake on road to Cerro Jefe, *Croat 15208* (CAS, MO); El Llano-Cartí road, km 7–12, 360–400 m, *Croat 25088* (MO); km 9.8, 1100–1200 ft., *Mori et al. 4162a* (MO); Campo Tres, 3 mi. NE of Altos de Pacora, 500–850 m, *Croat 22705* (MO), *Croat 22758* (MO). **San Blas**: Cerro Brewster, 9°18′N, 79°16′W, 850 m, *de Nevers et al. 5396* (MO); El Llano-Cartí road, km 18.3, 9°19′N, 78°55′W, 350 m, *de Nevers 5980* (CAS, NY, PMA), *de Nevers & Herrera 7858* (MO), *Henderson 88* (NY); trail to Cerro Habu from Río Urgandi, 9°23′N, 78°48′N, 100–300 m, *de Nevers et al. 8025* (MO).

DISTRIBUTION AND HABITAT. — Central Panama (Panamá, San Blas) and Colombia (Valle); lowland or premontane rainforest at 300–800 m elevation.

DISCUSSION. — This species is characterized by its large, orange fruits, and simple to pinnate, strongly plicate, leathery leaves. It is similar to *Bactris coloradonis*, but is distinguished by its strongly plicate, leathery leaves. *Bactris kunorum* shares the strongly plicate, leathery leaves of *B. grayumii*, but can be distinguished by its larger fruits and crenate fruiting corolla.

14. Bactris longiseta H. Wendl. ex Burret, Repert Spec. Nov. Regni Veg. 34:213. 1934.

TYPE. — COSTA RICA. **Heredia**: Pedregal, May 1857, *H. Wendland 81* (lectotype, GOET, here designated).

Stems cespitose and forming dense to loose colonies, 3–4.5 m tall, 2–2.5 cm diam, spiny on the internodes. **Leaves** 6–7; sheath 30–41 cm long, with a sparse to dense covering of black spines to 2 cm long; petiole 37–85 cm long, lacking spines or with a few spines to 6.5 cm long; rachis to 135 cm long, without spines or with a few spines to 4.5 cm long; pinnae 15–29 per side, regularly or irregularly arranged in distinct clusters and spreading in slightly different planes, linear to narrowly elliptic, caudate, with 1 prominent main vein, with spines 1–2 cm long on the margins, rarely lacking spines, the middle ones 30–72 cm long, 3.5–7 cm wide. **Inflorescences** interfoliar; peduncle ca. 10 cm long, strongly recurved; prophyll 7.5–15 cm long; peduncular bract 23–30 cm long, 3–5 cm wide, densely covered with erect, black or brown spines to 1 cm long; rachis 1.5–3 cm long; rachillae 20–30, 4.5–11 cm long, 1 mm diam at anthesis; triads irregularly arranged amongst paired or solitary staminate flowers proximally; **staminate flowers** 5 mm long, ± persistent after anthesis; sepals very briefly connate basally, free and spreading above, narrowly triangular, 1 mm long; petals 5 mm long, connate basally, free above, lanceolate, fleshy; **pistillate flowers** 5 mm long; calyx 1.5 mm long; corolla 4 mm long; staminodes absent; **fruits** obovoid, rostrate, purple-brown, 1.5–1.6 cm long, 1.5–1.6 cm diam; mesocarp juicy; endocarp turbinate, pitted apically; endocarp with numerous fibers, with juice sacs attached; endocarp pores equidistant; fruiting perianth with small calyx, 3–4 mm long, corolla crenate.

ADDITIONAL SPECIMENS EXAMINED. — COSTA RICA. **Province unknown**: Río Sarapiquí, *Wendland s.n.* 1857 (K). **Alajuela**: Río María Aguilar between Cariblanco and San Miguel, *Moore 6561* (BH); Cariblanco, *Moore 6627* (BH). **Heredia**: Parque Nacional Braulio Carrillo, sendero del transecto, 10°16′38″N, 84°04′57″ W, 1000 m, *Boyle 1283* (MO); between Río Peje and Río Sardinalito, 10°17′N,

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FIGURE 7. *Bactris kunorum* (*de Nevers et al. 5396*). A. Portion of leaf sheath and petiole. B. Leaf blade. C. Infructescence. D. Fruit in two views and seed (upper left). E. Apex of leaf blade showing crossveins. A, B, C and E same scale.

84°04′W, 700–750 m, *Grayum 6742* (MO); between Corazón de Jesús and La Virgen, 340 m, *Moore 6575* (BH); Puerto Viejo, Río Sarapiquí, 100 m, *Moore 6590* (BH), *Holdridge 5118* (BH), *Moore et al. 10130* (BH). **Limón**: Barra del Colorado, 10°38′N, 83°45′W, *Grayum et al. 8999* (MO).

DISTRIBUTION AND HABITAT. — COSTA RICA (Alajuela, Heredia, Limón); lowland rainforest, below 1000 m elevation.

LOCAL NAMES AND USES. — Costa Rica: *huiscoyol.*

DISCUSSION. — This species is distinguished by its usually broad pinnae with spiny margins, its purple-brown fruits with numerous endocarp fibers with juice sacs attached, and its equidistant endocarp pores.

15. **Bactris major** Jacq., Select. stirp. amer. hist. 134. 1780–81. *Bactris ovata* Stokes, Bot. mat. med. 4:394. 1812, nom. superfl. *Augustinea major* (Jacq.) Oerst., Linnaea 28:395. 1856. *Pyrenoglyphis major* (Jacq.) H. Karst., Fl.Columb. 2:141. 1866.
Fig. 8

TYPE. — Jacq., Select. stirp. amer. hist., t. 171, fig. 2. 1763 (lectotype designated by Glassman, 1972).

Augustinea ovata Oerst., Vidensk Meddel. Dansk Naturhist. Foren. Kjöbenhavn 1858:38. 1859. *Pyrenoglyphis ovata* (Oerst.) H. Karst., Fl. Columb. 2:142. 1866. *Bactris ovata* (Oerst.) H. Wendl. in Kerch., Palmiers 234. 1878, non Stokes (1812). *Bactris augustinea* L. H. Bailey, Gentes Herb.3:95. 1933.

TYPE. — NICARAGUA. **State?**: Punto Poderoso, 1845–1848, *A. Oersted 6532* (holotype, C).

Augustinea balanoidea Oerst., Vidensk Meddel. Dansk Naturhist. Foren. Kjöbenhavn 1858:39. 1859. *Pyrenoglyphis balanoidea* (Oerst.) H. Karst., Fl. Columb. 2:142. 1866. *Bactris balanoidea* (Oerst.) H. Wendl. in Kerch., Palmiers 233. 1878.

TYPE. — COSTA RICA. **Puntarenas**: Puntarenas, *A. Oersted s.n.* (C?, n.v.).

Bactris superior L. H. Bailey, Gentes Herb. 3: 99. 1933. *Pyrenoglyphis superior* (L. H. Bailey) Burret, Repert. Spec. Nov. Regni Veg. 34:246. 1934.

TYPE. — PANAMA. **Canal Area**: Barro Colorado Island, 12 Jun 1931, *L. & E. Bailey 162* (lectotype, BH, excluding leaves [here designated]).

Stems cespitose, 2–10 m tall, 2–6 cm diam, forming dense or open colonies, internodes 13–26 cm long, spiny. **Leaves** 3–10; sheath 22–55 cm long, very fibrous on margins, sheath, petiole and rachis moderately to densely covered with short black spines, these intermingled with longer, brown or black, ± terete spines to 11 cm long; petiole 0.1–1.5 m long; rachis 0.8–1.8 m long; pinnae 28–46 per side, more or less regularly arranged, spreading in the same plane, linear, aristate, middle pinnae 25–60 cm long, 1–3.5 cm wide, minutely spiny on margins, somewhat metallic when dry. **Inflorescences** interfoliar; peduncle 17–40 cm long, densely spiny, recurved; prophyll 13–30 cm long; peduncular bract 28–60 cm long, densely to moderately covered with black spines to 1 (–2) cm long; rachis 2–4 cm long; rachillae (3–) 5–10 (–17), 15–23 cm long, 2 mm diam at anthesis, 3–4 mm thick in fruit; triads irregularly arranged amongst paired or solitary staminate flowers; **staminate flowers** 3–8 mm long, somewhat persistent; sepals 1.5–2 mm long, briefly connate below, narrowly triangular; petals connate below for ca. one third their length, free and valvate distally, 3–7 mm long; **pistillate flowers** 4–8 mm long; calyx 4–6 mm long, minutely spinulose; corolla 3–5 mm long, minutely and densely spinulose; staminodial ring adnate to corolla, to 1 mm long; **fruits** irregularly ellipsoid to widely obovoid, 3.3–4.5 cm long, 2.3–3.5 cm diam, brown or purple-black, with minute spinules or small brown scales, glabrescent; mesocarp juicy; endocarp ellipsoid; endocarp fibers numerous, free; endocarp pores equatorial, equidistant, but fertile one displaced proximally; fruiting perianth with regularly lobed calyx shorter than the regularly lobed corolla, staminodial ring adnate to corolla.

ADDITIONAL SPECIMENS EXAMINED. — MEXICO. **Chiapas**: Mpio. Ocosingo, Río Usumacinta, ruins of Yaxchilán, limestone ridges, 300 m, *Breedlove 33902* (CAS). **Oaxaca**: between Collantes and Minizo, *Conzatti 4412* (US); Lagoon of Tonomeca, *Reko 3461* (US). **Tabasco**: *Matuda 3192* (US); San Juan Bautista, Río Grijalva, *Doyle 265* (US); 22 km W of H. Cárdenas, Colegio Superior de Agricultura, *Iltis 27260* (WIS). **Veracruz**: Mpio. Las Choapas, Rancho Gavilán, 3 km before Las Choapas, 17°54′N, 94°06′W, *Calzada 6049* (F).

BELIZE. "fruit in market," *Maxon & Hay 2049* (US). **Belize**: Belize River near Belize, *Lundell 4334* (MICH). **Cayo**: Belize River, Ridge Lagoon River ca

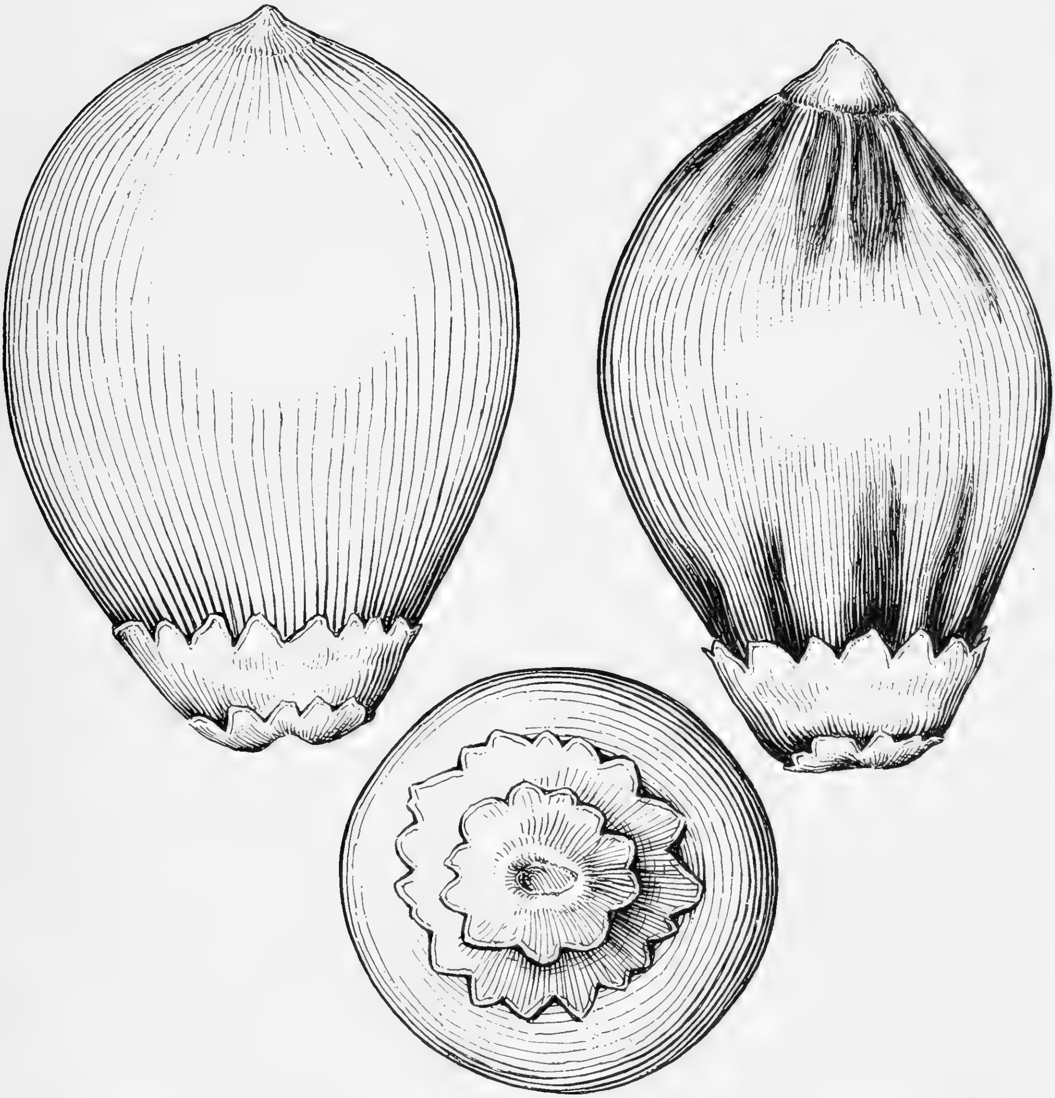


FIGURE 8. *Bactris major* (*Bailey 162*). Fruit in three views (life size). Courtesy of the L. H. Bailey Hortorium, Cornell University.

12 mi. NW of Belize, *Croat 23437* (MO). **Corozal:** *Gentle 256* (MICH), *Gentle 429* (MICH). **Stann Creek:** Prospecto-Maskall road, *Gentle 900* (MICH); San Andrés, *Lundell 4842* (MICH).

GUATEMALA. **Alta Vera Paz:** banks of Río Polochic, below Panzós, *Maxon & Hay 3096* (US); **Escuintla:** Escuintla, 335 m, *Smith 2060* (US). **Izabal:** shore of Lake Izabal, *Blake 7857* (US); vicinity of Quiriguá, 75–225 m, *Standley 24458* (US); Río Polochic, *Cook & Doyle 6* (US), *7* (US), *8* (US); Sepacuité, *Cook & Doyle 16* (US). **Petén:** El Paso, *Lundell 1522* (MICH); along Río Chinajá, N of Chinajá on trail to Zacatal, 50–70 m, *Steyermark 39211* (F). **Retalhuleu:** between Nueva Linda and Champerico, ca. 120 m, *Standley 87626* (F).

EL SALVADOR. **Ahuachapan:** El Imposible, 13°39′N, 89°56′W, *Sandoval 302* (MO). **La Libertad:** Finca Santa Emilia, W of La Libertad, *Carlson 562* (F); Hacienda Sol y Mar, km 45, Tamanique, 20 m, *Flores 30* (PMA). **La Unión:** Laguna de Maquigue, *Standley 20900* (US). **San Miguel:** Laguna de Olomega, *Standley 20992* (US); ca 50 mi. NW of San Miguel on road CA-1, *Croat 32793* (MO). **San Salvador:** near San Salvador, *Calderón 1185* (US); **San**

Vicente: 2 mi. W of Puente de Cuscatlán, 250 ft, *Allen 7270* (US). **Sonsonate**: vicinity of Sonsonate, 220–300 m, *Standley 22351* (US).

HONDURAS. **Atlántida**: Bel Aire, 10 km S of Jutiapa along road to Trujillo from La Ceiba, 15°45′N, 86°30′W, *Balick et al. 1713* (NY, US); Triunfo, near Tela, *Standley 53842* (US), *54714* (US). **Colón**: Río Guaimoreto, 15°57′N, 85°54′W, *Saunders 611* (F, US). **Comayagua**: Agua Caliente, 220 m, *Nelson et al. 6291* (MO). **Cortés**: San Pedro Sula, *Thieme 5536* (US). **Islas de la Bahía**: Isla de Roatán, French Harbour, 50 m, *Nelson & Romero 4418* (MO). **Yoro**: 3 km NW of Santa Rita on road to Negrita, *Harmon & Dwyer 3863* (MO).

NICARAGUA. **Chontales**: between Santo Tomás and Villa Somoza, *Bunting & Licht 1103* (F, NY). **Rivas**: Islas Ometepe-Mérida, 11°27′N, 85°32′W, 700–800 m, *Robleto 354* (MO). **Río San Juan**: Managua, *Garnier 778* (US); along road to San Carlos, 5 km SE of Río Oyate, 11°42′N, 84°57′W, 40 m, *Miller & Nee 1369* (MO); Bocas de Sábalo, 11°03′N, 84°27′W, 70–100 m, *Moreno 26729* (MO). **Zelaya**: Yauya, ca 18 km SE of La Luz, 150–200 m, *Bunting & Licht 598* (F).

COSTA RICA. **Alajuela**: Cantón de Upala, Llano de Achiote, 10°53′N, 84°59′W, 35 m, *Grayum et al. 9074* (MO, NY). **Puntarenas**: west of Manuel Antonio National Park, *Grant 91-01565* (US); Cabo Blanco Nature Reserve, 9°35′N, 85°06′W, 0–200 m, *Burger & Liesner 6681* (F, MO, NY); Isla del Caño, *Gómez 19989* (MO); Isla San Lucas, Golfo de Nicoya, 9°57′N, 84°54′W, 5–40 m, *Grayum 4283* (MO); Reserva Biológica Carara, 9°48′N, 84°36′W, 20 m, *Grayum & Warner 8365* (MO); Lagartos Bay, Gulf of Nicoya, *Barclay 2773* (BM); Nicoya Penninsula, Colonía Macio, *Cook & Doyle 740* (US).

PANAMA. **Province unknown**: La Jagua, *Bartlett 17020* (MICH). **Canal Area**: Summit, *Bartlett & Lasser 16791* (MICH), *16793* (MICH), *16795* (MICH); Juan Mina, Chagres River, *Bartlett & Lasser 16317* (MICH); vicinity of Albrook Tower, *Blum 838* (SCZ); Panama City, Curundu, 50 m, *Churchill 6028* (CAS, MO); Barro Colorado Island, *Bartlett 16747* (MICH), *Croat 5510* (SCZ), *Croat 5650* (SCZ), *Croat 5740* (MO), *Croat 7142* (MO), *Croat 7284* (MO), *Croat 7289* (MO), *Croat 8567* (MO), *Croat 8742* (MO), *Croat 9045* (MO, SCZ), *Croat 9553* (MO), *Croat 10735* (MO), *Croat 10740* (MO, SCZ), *Croat 11003* (MO), *Croat 11954* (MO), *Croat 11980* (MO, SCZ), *Kenoyer 162* (US), *Maxon et al. 6829* (US); Gamboa, *Nee 7532* (PMA), *Schmalzel 925* (MO), *Shattuck 938* (MO); Balboa, *Cook & Martin 15* (US); Madden Forest, *Croat 8954* (MO), *11055* (MO), *10786* (MO); road C2F, 0.5 mi. NW of Summit Naval Radio Station, *Croat 11034* (MO), *11036* (MO); forest across from Summit Golf Course, *Croat 11202* (MO, SCZ); Margarita Swamp, *Cook & Martin 2* (US); Ft. Sherman, 8 April 1925, *Cook s.n.* (US); near beach at Ft. Kobbe, *Duke 4714* (MO); 8 km W from Balboa in Rodman Tank Farm, *Garber 153* (MO); Coco Solo, *Gentry 6479* (MO); NW edge of Gamboa, near Chagres airport, *Mori & Kallunki 4722* (MO); Río Indio de Gatún, *Pittier 2780* (US). **Chiriquí**: Burica Peninsua, Quebrada Mérida, 6 km S of Puerto Armuelles, *Busey 704* (MO, PMA); Burica Peninsula, Quebrada Tuco, 9 mi. S of Puerto Armuelles, 0–150 m, *Croat 22114* (MO). **Coclé**: Cerro Mangote, *McPherson 10046* (MO); near Capellanía, *McPherson 10048* (MO); Tonosí, Río Tonosí, Quebrada Ocho Paso, *Stern et al. 1832* (US); Penonomé, *Williams 52* (NY, US). **Darién**: El Real, 8°07′N, 77°44′W, *de Nevers & Herrera 8240* (CAS, MO); Río Tuira ca. 4 mi. above Chepigana, *Duke 5487* (MO); La Palma, 0-50 m, *Pittier 6620* (US). **Los Santos**: 5 mi. S of Pocri, *Croat 9743* (MO). **Panamá**: Lago Sororia, NE of Nueva Gorgona, 8°33′N, 79°51′W, 5 m, *de Nevers & Piperno 10549* (CAS, PMA); Río La Maestra, 0–25 m, *Allen 42* (MO); Río Pacora, Panama National Highway, *Bartlett 16479* (MICH), *Bartlett & Lasser 16951* (MICH), *Nee & Mori 3615* (WIS); Río Tapia, *Bartlett 16945* (MICH), *Maxon & Harvey 6765* (US); vicinity of El Llano, *Duke 5868* (MO); San José Island, 8′15″N, 79′08″W, sea level, *Harlow 45* (US), *Erlanson 510* (US), *Johnston 816* (US); Taboga Island, *Maxon 6909* (US), 4 mi. W of Chepo near Inter American Highway, *Tyson 6737* (MO, PMA); Matías Hernández, *Pittier 6756* (US).

Distribution and Habitat. — Southern Mexico throughout Central America, and also in northern Colombia and Venezuela, as far east as Trinidad; drier areas where ground water is present, often in disturbed or seasonally inundated places.

Local Names and Uses. — Belize: *hone*, *pork-and-dough boy*. Guatemala: *coconut-boy*, *match*. Panama: *caña brava*.

Discussion. — This species is distinguished by its regularly arranged, linear pinnae which have a somewhat metallic sheen when dry, its few, thickened rachillae, its large ellipsoid, purple-black fruits, and its fruiting corolla with staminodial ring. It is closely related to a small group of species (or subspecies) that occur in South America. Burret (1934) cites a type specimen of Jacquin, but did not see it nor give its location.

The leaves of the type specimen of *Bactris superior* are excluded because they appear to belong to a different species, possibly *B. coloniata*.

16. Bactris maraja Mart., Hist. nat. palm. 2:93. 1826.
Fig. 9

Pyrenoglyphis maraja (Mart.) Burret, Repert. Spec. Nov. Regni Veg. 34:252. 1934.
TYPE. — Tab. 71, fig. 1 in Mart., Hist. nat. palm. 2, 1826 (lectotype [designated by Burret, 1933–1934]).

Bactris divisicupula L. H. Bailey, Gentes Herb. 6:230. 1943.
TYPE. — PANAMA. **Coclé**: El Valle de Antón, 21 May 1939, *P. Allen 1817* (lectotype, MO [designated by de Nevers, 1988]; isolectotypes, BH, GH).

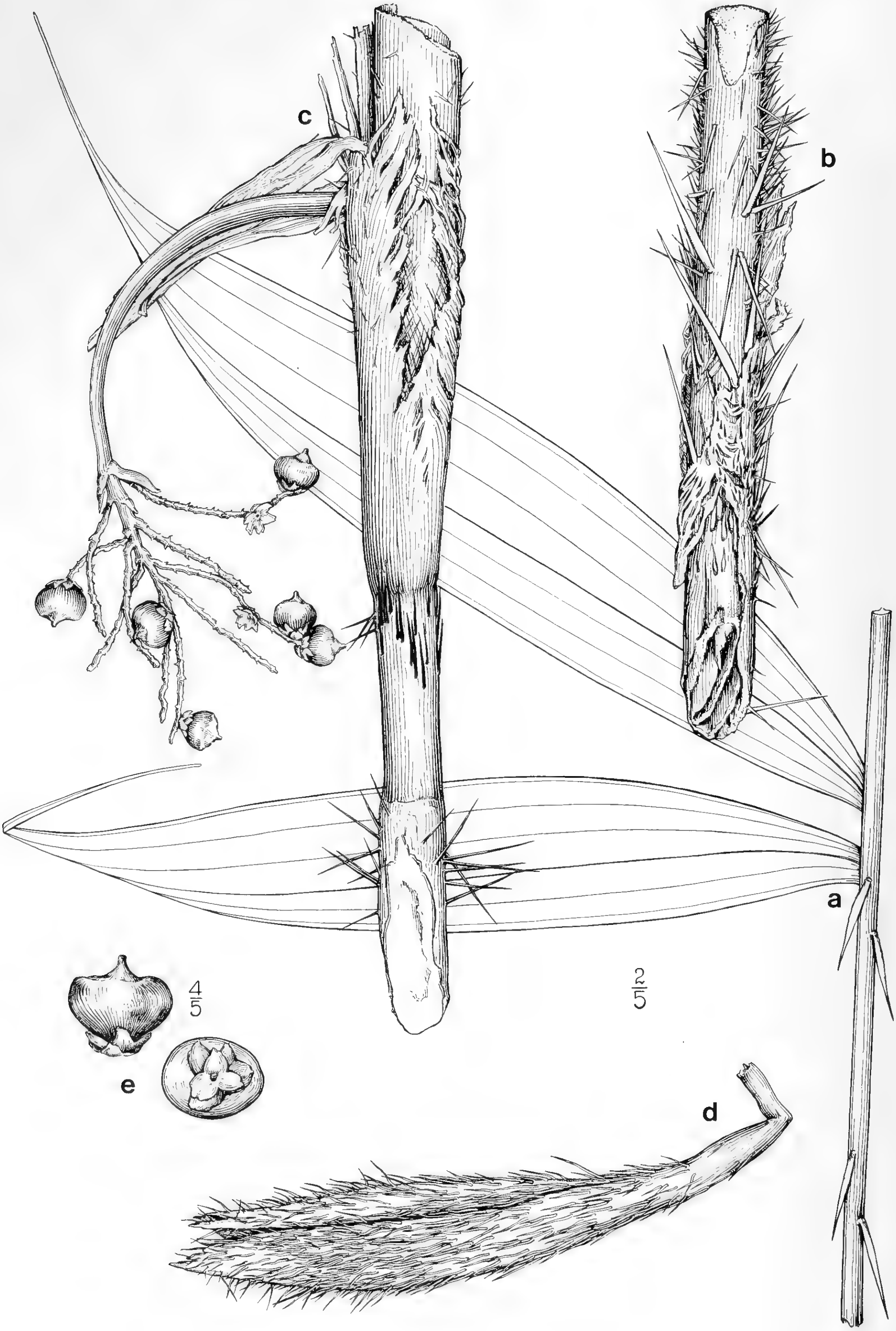
Bactris fuscospina L. H. Bailey, Gentes Herb. 6:228. 1943.
TYPE. — PANAMA. **Panamá**: Cerro Campana, 31 Dec 1939, *P. Allen 2086* (lectotype, MO [designated by de Nevers, 1988]; isolectotype, BH).

Stems cespitose, in open clusters of 2–15 stems, 3–7 (–10) m tall, 2–4 cm diam, with black spines on internodes. **Leaves** 3–10, horizontally spreading; sheath 20–35 cm long, sheath, petiole and rachis with moderate to dense covering of flattened, yellowish (occasionally brown or black) spines, when yellowish with black base and apex, to 5 (–10) cm long; petiole 13–60 cm long; rachis 78–130 cm long; pinnae 15–22 per side, irregularly arranged in clusters of 2–5 and spreading in several planes, or regularly arranged and spreading in one plane, sigmoid, middle pinnae 20–48 cm long, 3–6 cm wide. **Inflorescences** interfoliar; peduncle 16–18 cm long, spiny, curved; prophyll 10–26 cm long; peduncular bract 22–38 cm long, typically brown-velvety-tomentose, occasionally with flattened spines to 4 mm long or glabrous; rachis 3–5 cm long; rachillae 8–15, 6–15 cm long; triads irregularly arranged amongst paired or solitary staminate flowers; **staminate flowers** to 3.5 mm long, deciduous; sepals briefly connate below, free above, narrowly triangular, 1 mm long; petals connate below for ca. half their length, free and valvate above, obovate, 3 mm long; **pistillate flowers** 2.5 mm long (pre-anthesis); calyx 2.5 mm long, exceeding the corolla; corolla 1 mm long; staminodes absent; **fruits** widely depressed obovoid, rostrate, 1.3–2 cm diam, purple-black at maturity, rarely minutely spinulose; mesocarp juicy; endocarp turbinate; endocarp fibers numerous, terete, black, with juice sacs attached; endocarp pores displaced; fruiting perianth with deeply 3-lobed calyx half as long as the deeply 3-lobed corolla.

ADDITIONAL SPECIMENS EXAMINED. — COSTA RICA. **Limón**: Sixaola region, between headwaters of Quebrada Mata de Limón and Q. Quiebra Caña, Finca Anai, 9°34′N, 82°40′W, 20–40 m, *Grayum et al. 8003* (CAS); woodlands S of La Lola on the railroad, 120 m, *Moore 6711* (BH). **Puntarenas**: Palmar, *Schubert 1184* (A).

PANAMA. **Canal Area**: Barro Colorado Island, *Bailey 505* (BH); Skunk Hollow, Carribean side, *Blum 1496* (MO); Agua Salud, *Cook & Martin 63* (US); Pavón road W of Gatún Locks, *Johnston 1538* (BH); near Marú Towers W of Gatún Locks, *Johnston 1552* (BH); along Río Petitpie from road to Ft. Sherman from Gatún Locks, *Mori & Kallunki 2704* (MO); Pipeline road near Gamboa, 50 m, *Nee 7846* (MO, PMA, NY); Frijoles, *Stevens 1185* (US). **Colón**: Santa Rita Ridge, *Croat 14182* (MO). **Darién**: N base of Cerro Pirre, along Quebrada Perisenico, 8°01′N, 77°44′W, 70–270 m, *de Nevers et al. 8263* (MO); Parque Nacional del Darién, ridge between Río Topalisa & Río Pucuro, ca. 13 km E of Pucuro, 500 m, 8°03′N, 77°20′W, *de Nevers et al. 8331* (CAS); Río Urutí, *Duke & Bristan 220* (MO, US); Mamey, *Whitefoord & Eddy 348* (PMA). **Panamá**: Cerro Jefe, *Allen 3440* (BH, MO); Cerro Azul, *Croat 11551* (MO); 3 mi. NE of Alto Pacora, 500–800 m, *Croat 22767* (MO); Cerro Campana, *Dwyer et al. 4859* (BH, MO); El Llano-Cartí road, km 8.5, *Nee & Warmbrodt 10400* (MO). **San Blas**: El Llano-Cartí road km 19, 350 m, 9°19′N, 78°55′W, *de Nevers et al. 6127* (MO, PMA), *de Nevers & Hammel 8550* (CAS), *Galdames et al. 1350* (PMA); Cangandí, 9°24′N, 79°24′W, 0–30 m, *de Nevers et al. 6444* (MO), *7121* (MO), *7697* (MO), *Herrera 243* (CAS); opposite Isla Miria Ubigandup, Río Ailigandi, 9°26′N, 78°54′W, 0–20 m, *Herrera & Harris 556* (MO); Aila Tiwar, 8°48′N, 77°40′W, 25–100 m, *Sugden 430* (MO).

DISTRIBUTION AND HABITAT. — Costa Rica (Limón, Puntarenas), Panama (Canal Area, Coclé, Colon, Darién, Panamá, San Blas) and throughout northern South America in Colombia (Amazonas, Antioquia, Choco, Vaupés, Vichada), Venezuela (Amazonas), the Guianas, Ecuador (Napo), Peru (Amazonas, Loreto, Madre de Dios, Ucayali), Brazil (Acre, Amapá, Amazonas, Pará, Rondônia, Roraima), and Bolivia (Beni, La Paz); tropical moist forest, tropical wet forest, premontane wet forest, and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premontane rain forest, usually on terra firme but occasionally in inundated areas, at low elevations but occasionally reaching 1000 m elevation. It is remarkable that L. H. Bailey collected *B. maraja* on Barro Colorado Islnad in the 1930s, but when Tom Croat did intensive field work there in the 1970s he did not find it.

LOCAL NAMES AND USES. — Panama: *alar*, *gui*, *gui wala* (Kuna), *uvita*. The fruits are sucked by the Kuna for their flavor.

DISCUSSION. — This species is characterized by its flattened whitish or yellowish spines, glabrous leaves with grouped, sigmoid pinnae with a prominent drip-tip, and obovoid, purple fruits.

Bactris maraja Mart. is one of the few names validly lectotypified by Burret. His reference to the "von Martius veschriebenen und abgebildeten Fruchtkolben der als Typus der Art anzusehen" (Burret, 1933–34:253) satisfies the requirement of the Code (Greuter et al., 1988, art. 8.3) that the word "type" or its equivalent appear. According to Burret (1933–34:252), fruits and a rachilla from the infructescence illustrated by Martius, labeled in Martius's hand, were deposited at B. We cannot confirm the existence of this material; in any case, Burret clearly intended the illustration of the entire infructescence ("fruchtkolben," "spadicem fructiferum") for typification, rather than the preserved fragments.

17. **Bactris mexicana** Mart. in A. D. Orb., Voy. Amér. mér. 7(3), Palmiers 65. 1844.

TYPE. — MEXICO. **Veracruz:** Misantla, Mar 1827, *C. Schiede s.n.* (holotype, M, n.v.).

Stems cespitose, 2–3 m tall, 2–3.5 cm diam, usually spiny on internodes. **Leaves** 5–7; sheath 20–37 cm long, moderately to densely covered with black spines to 3 cm long; petiole 35–100 cm long, occasionally with black spines to 7 cm long, these white-bulbous-based and tending to be clustered; rachis 0.8–1.5 m long, occasionally with black spines to 6.5 cm long; pinnae 8–26 per side, irregularly arranged in clusters and spreading in different planes, or regularly arranged (but with gaps) and spreading in the same plane, linear to sigmoid, narrowed at base, aristate, the middle ones (30–) 45–60 cm long, 2–5 cm wide, glabrous or scarcely to densely pubescent abaxially, the margins often minutely spiny with 3 mm long, straight spines. **Inflorescences** interfoliar; peduncle 6–15 cm long, 0.8–1.3 cm wide, recurved, densely covered with short spines; prophyll 9–14 cm long, 2–4 cm wide; peduncular bract 19–25 (–30) cm long, 3–5 cm wide, densely covered with short black spines to 1 cm long; rachis 1.2–6.5 cm long; rachillae 12–36, 8–16 cm long, 1 mm diam at anthesis; triads irregularly arranged amongst paired or solitary staminate flowers; **staminate flowers** 2–3 mm long; sepals very briefly connate below, lanceolate, 1 mm long; petals 3 mm long; **pistillate flowers** 3 mm long; calyx 1 mm long; corolla minutely 3-lobed apically, 3 mm long; staminodes minute; **fruits** obovoid, stigmatic residue prominent, occasionally rostrate, 0.8–1.2 cm long, 0.9–1.2 cm diam, orange; mesocarp mealy, fibrous; endocarp turbinate, not pitted; endocarp fibers very few; endocarp pores equidistant; fruiting perianth with a minutely 3-lobed, 1 mm long calyx and truncate to crenate, corolla 3 mm long.

DISTRIBUTION AND HABITAT. — Mexico (Chiapas, Oaxaca, Tabasco, Veracruz), Guatemala (Alta Verapaz, Izabal, Petén), Belize (Cayo, Stann Creek, Toledo), Honduras (Atlántida), and Nicaragua (Zelaya); lowland rainforest below 600 m elevation.

DISCUSSION. — We have not seen the types of *Bactris mexicana*, *B. baculifera* or *B. trichophylla*, but judging from their descriptions, and the fact that *B. mexicana* is the only species of *Bactris* in Mexico and Belize with orange fruits, the latter two names belong here. On the Atlantic slope of Nicaragua and Costa Rica, a few specimens (*Robles 1668*, *Grijalva 1535*) have leaves which overlap in characters between *B. mexicana* and *B. gracilior* (under which see discussion).

Two taxa are recognizable amongst the specimens examined, each with a more or less discrete

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FIGURE 9. *Bactris maraja* (*Allen 1817*). A. Midsection of leaf. B. Stem, showing flattened spines. C. Infructescence, with recurved peduncle. D. Peduncular bract. E. fruit in two views. All × 2/5 except E (4/5). Courtesy of the L. H. Bailey Hortorium, Cornell University.

geographic range. There is, however, overlap of character states in specimens from Chiapas and northern Guatemala, and so we recognize the two as varieties.

Key to the varieties of *Bactris mexicana*

1. Pinnae sigmoid, irregularly arranged in clusters and spreading in different planes, glabrous abaxially; petiole and rachis with scattered, black spines............... 17a. *B. mexicana* var. *mexicana*.

1. Pinnae linear, regularly arranged (but with gaps) and spreading in the same plane, pubescent abaxially; petiole and rachis usually without spines.......................... 17b. *B. mexicana* var. *trichophylla*.

17a. Bactris mexicana var. mexicana

Bactris acuminata Liebm. ex Mart., Hist. nat. palm. 3:321. 1853.
TYPE. — Mexico. **Oaxaca**: Chinantla, Oct 1842, *F. Liebmann 10797* (holotype, C; isotypes, MO, P, US).

Bactris baculifera Karw. ex Mart., Hist. nat. palm. 3:322. 1853.
TYPE. — Mexico. **Veracruz**: Jicaltepec, *W. Karwinsky s.n.* (holotype, BR?, n.v.).

ADDITIONAL SPECIMENS EXAMINED. — MEXICO. **Chiapas**: Mpio. Ocozocoautla, 46 km N of Ocozocoautla on road to Mal Paso, 700 m, *Breedlove 38304* (CAS, MO); Mun. Palenque, 50 km SW of Palenque on road to Ocosingo, near Colonia Ursulo Galvano, 370 m, *Breedlove 47360* (CAS); 80 km SW of Palenque on road to Ocosingo, 760 m, *Breedlove & Almeda 57205* (CAS, NY). **Oaxaca**: "in sylvis densis," *Liebmann 10796* (US); Mpio. Santa María Chimalapa, Arroyo Margo, 16°55′N, 94°39′W, 250 m, *Hernández 390* (CAS, MO); Loma Bonita, *Hernández 600* (NY), *Hernández 694* (MO); Mpio. Sta. María Chimalapa, Paso Napajoa del Río Negro, 16°51′N, 94°40′W, 300 m, *Hernández 694* (MO); 37 mi. from Empalme Balboa beyond Mathias Romero, *Moore 6353* (NY, US). **Tabasco**: 8.2 km from Fco. Rueda, *Cowan et al. 3985* (NY); Retiro, Tenosique, *Matuda 3478* (MO, US). **Veracruz**: Mpio. Hidalgotitlán, Río Soloxuchil, 100 m, *Aguilar 151* (NY); Mpio. Choapas, Las Cruces, *Gómez-Pompa 1516* (F); Los Tuxtlas, 18°34′N, 95°04′W, 160 m, *Aguilar 144* (NY), *Calderón 2130* (F), *Gentry et al. 32307* (MO), *Ibarra M. & Sinaca C. 1967* (MO), *Ibarra s.n.* (NY); Maloapam, *Liebmann 10792* (MO); Pital, *Liebmann s.n.* (NY); 4 km beyond Nanchitla on road to Villahermosa, *Moore 8065* (BH); Agustín Melgar, 17°15′N, 94°33′W, 100 m, *Nee 29759* (F, NY).

LOCAL NAMES AND USES. — Mexico: *chischi*, *junco*.

17b. Bactris mexicana var. trichophylla

(Burret) A. Henderson, stat. nov., *Bactris trichophylla* Burret, Repert. Spec. Nov. Regni Veg. 32:113. 1933.

TYPE. — BELIZE. **Stann Creek**: 19 mile, Stann Creek Valley, *W. Schipp S368* (holotype, B, destroyed).
NEOTYPE. — BELIZE. **Toledo**: Río Grande, ca. 80 m, *W. Schipp S520* (B, here designated).

ADDITIONAL SPECIMENS EXAMINED. — MEXICO. **Chiapas**: Mun. La Trinitaria, 15 km ENE of Dos Lagos, above Santa Elena, 1000 m, *Breedlove 56585* (CAS); Mun. Ocosingo, Bonampak, 1200 ft., *Breedlove 15721* (CAS); Mun. Palenque, 6–12 km S of Palenque, 300 m, *Breedlove & Dressler 29771* (CAS).

BELIZE. **Belize**: 42.5 mi. NW of Belize along Northern Highway, *Croat 23972* (MO); along Western Highway at mi. 35, *Croat 24788* (MO). **Cayo**: near Vaca, *Gentle 2575* (MICH), *2586* (MICH); Valentin, *Lundell 6284* (MICH); Mollejon Cr., on Raspa road 10 km S of Augustine, 500 m, *Meave & Howe 1361* (MO); north boundary of Roaring River Estates, 50 m, *Spellman & Newey 1686* (MO); Cotton Tree Creek, 0.5 km W of Guacamallo Bridge, 500 m, *Sutton et al. 50* (MO). **Stann Creek**: Prospects, Maskall road, *Gentle 900* (MICH); Maskall-Bakers road, *Gentle 1373* (MICH, MO); Stann Creek Railway, 15 mi., *Gentle 2105* (MICH); Middlesex, *Gentle 2901* (MICH); between Rancho Chico and Cockscomb, Monkey River, *Gentle 4313* (NY); Humming Bird Highway, *Gentle 9225* (CAS, MO, NY). **Toledo**: Bladen Watershed, 16°35′N, 88°45′W, 140 m, *N. Brokaw 136* (NY); ca. 5 mi. W of Columbia Forest Station, *Croat 24340* (MO); Solomon Camp, junction of Richardson Creek and Bladen Branch, 16°32′N, 88°45′W, 80–420 m, *Davidse & Brant 32059* (MO); trail to Esperanza, beginning 1 mi. N of Columbia Forest Station, *Dwyer 11101* (MO); Maya Mts., Columbia Forest Reserve, 16°22′N, 89°10′W, *Holst 4501* (MO, NY).

GUATEMALA. **Alta Verapaz**: Trece Aguas, *Cook & Doyle 1* (US); Secangunin, *Cook & Doyle 47* (US), *48* (US); Sepacuite, *Cook & Doyle 16* (US); Cubilgüitz, 300–350 m, *Steyermark 44418* (F, MO, NY). **Izabal**: ca. 7 mi. S of Puerto Barrios, 50 m, *Croat 41807* (MO); Puerto Barrios, *Standley 24984* (NY, US). **Petén**: Tikal, *Bartlett 12605* (MICH), *Contreras 66* (CAS, MO, NY); 5 mi. S of entrance to Tikal National Park, *Croat 24752* (MO); Santa Teresa, Río

Subin, *Lundell 2655* (MICH); Hiltun, *Lundell 3588* (MICH); NW of Chinajá, *Steyermark 45494* (F).

HONDURAS. **Atlantidá**: Lancetilla, 15°41′N, 87°28′W, 450–590 m, *MacDougal et al. 3386* (NY), *Standley 56776* (US), 300 ft., *Yuncker 4991a* (MO, NY), *Yuncker 4991b* (MO). **Colón**: lower slopes of Puerto Arturo, along trail to Río Negro Dam, ca. 200 ft., *Saunders 614* (MO).

NICARAGUA. **Zelaya**: costado SW de Cerro El Hormiguero, 13°44′10″N, 84°59′50″W, 900–1000 m, *Grijalva 502* (MO); 84 5 km SE of Siuna, ca. 13°40′N, 84°45′W, *Grijalva & Burgos 1535* (MO); near Río Okanwas, 12 mi. E of Rosita, *Neill 4480* (MO); Comarca del Cabo, Miguel Bikou, *Robbins 5875* (MO); road to Alamikamba, 13°32′N, 84°30′W, 25 m, *Stevens 21746* (MO, NY).

LOCAL NAMES AND USES. — Belize: *hone*. Guatemala: *huiscoyol*.

18. Bactris militaris H. E. Moore, Gentes Herb. 8:229. 1951.
Fig. 10

TYPE. — COSTA RICA. **Puntarenas**: Cantón de Osa, near Tinoco Station, 30 April 1949, *P. Allen 5276* (holotype, BH; isotype; US).

Stems cespitose, 1–5 m tall, 2.5–4 cm diam, in tight clumps of 5–20 stems. **Leaves** 5–8, simple and bifid, erect, arching at the tips, strongly plicate; sheath to 37 cm long, sparsely to densely covered with black spines to 8.5 cm long; petiole to 43 cm long, usually without spines; rachis to 2.8 m, without spines or with a few spines to 7 cm long; blade to 3.1 m long, to 25 cm wide at apex of rachis, elongate cuneate-oblanceolate in outline, very gradually expanded from a narrowly cuneate base to the bifid apex, without cross-veins. **Inflorescences** interfoliar; peduncle 20–38.5 cm, straight and erect in fruit, not spiny; prophyll 13–19 cm long; peduncular bract 30–49 cm long, densely tomentose, sparsely covered with slender brown spines to 4 mm long; rachis to 10 cm; rachillae 7–23, 1.5–6 cm long; triads scattered amongst paired or solitary staminate flowers; **staminate flowers** 4 mm long; sepals connate below, free and spreading above, 1 mm long; petals connate below for ca. half their length, free and valvate above, 4 mm long; **pistillate flowers** 3 mm long; calyx 0.5 mm long; corolla 3 mm long; staminodes minute or absent; **fruits** very widely obovoid, indistinctly rostrate, 1.5–1.7 cm diam, red or orange, glabrous; mesocarp mealy; endocarp turbinate, pitted or smooth; endocarp fibers few, broad or terete, without juice sacs; endocarp pores equidistant; fruiting calyx minute, corolla 2 mm.

ADDITIONAL SPECIMENS EXAMINED. — COSTA RICA. **Limón**: Sixaola region, Finca Anai, 9°34′N, 82°40′W, 25–30 m, *Grayum et al. 4476* (MO); Refugio Barra del Colorado, between Río Chirripocito and Río Sardina, *Grayum et al. 8984* (MO); between the Río Madre and Blanco, shore at Moín, Atlantic coast, sea level, *Pittier 16715* (US). **Puntarenas**: near Tinoco Station, sea level, *Allen 6264* (BH), *6296* (BH), *Hodel et al. 1353* (BH, MO).

PANAMA. **Colón**: Santa Rita ridge, km 10, 350 m, *de Nevers et al. 10648* (CAS, COL, MO, NY, PMA).

DISTRIBUTION AND HABITAT. — Atlantic coast of Costa Rica (Limón) and Panama (Colón), and probably into adjacent Nicaragua, rarely on the Pacific side of Costa Rica (Puntarenas); low, wet, swampy sites near the sea, or on slopes, to 400 m elevation.

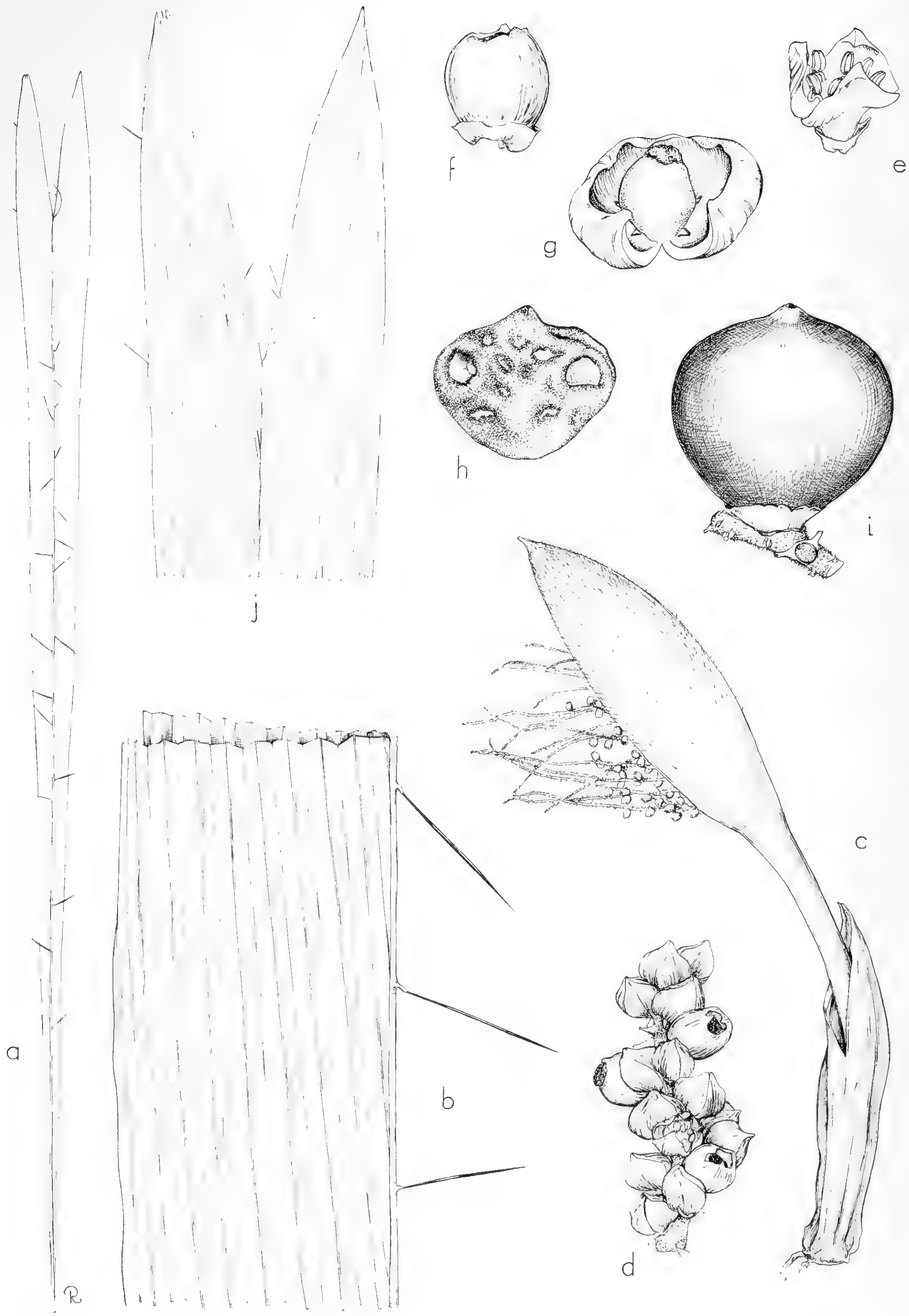
DISCUSSION. — This species is distinct by its long, narrow, simple leaves. It shares a straight, erect fruiting peduncle only with *B. hondurensis*, *B. charnleyae* and *B. panamensis*.

The fruits of *Bactris militaris* are variable. Those from the Pacific side of Costa Rica (*Allen 6264*, *6296*) are red and have pitted endocarps with few, flattened endocarp fibers; those from the Atlantic coast of Costa Rica and Panama (*de Nevers et al. 10648*, *Grayum 8984*, *Pittier 16715*) have orange fruits and smooth endocarps with numerous terete fibers which appear to have juice sacs attached and appear to originate in tubercules. More specimens are needed to decide if two taxa exist.

19. Bactris panamensis de Nevers & Grayum, sp. nov.
Fig. 11

TYPE. — Panama. **Panamá**: Cerro Jefe, 9°15′N, 79°30′W, 650 m, 27 Aug 1986, *G. McPherson 9992* (holotype, MO).

Statura parva *Bactris hondurensi* similis sed foliis pinnatis pinnis subtus concavis apice prominenter caudatis fructibus parvioribusque.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Stems cespitose, 1.5–3 m tall, 0.7–0.9 cm diam. **Leaves** number unknown; sheath 13–22 cm long, sheath and petiole sparsely to densely black-spiny, the spines to 2.8 cm long; petiole 18–28 cm long; rachis 31–62 cm long, without spines or rarely with occasional spines to 2.5 cm long; pinnae 15–19 (–25) per side, irregularly arranged in clusters of 2–3 in proximal half of leaf, more regularly arranged distally, the middle ones 10–19 cm long, 1.6–3.6 cm wide, narrowly to broadly elliptical or oblanceolate, often sigmoid, without obvious cross-veins, marginally setose with the setae to 2 mm long. **Inflorescences** interfoliar; peduncle 3.5–6 cm long, erect to arching, with appressed, blackish spines to 1.5 mm long; prophyll not seen; peduncular bract ca. 8.5–12.5 cm long, covered with blackish spines to 1.2 cm long; rachis 1.5–2 cm long; rachillae 8–12, 2–3.4 cm long, 0.5 mm diam; triads irregularly arranged and scattered amongst paired or solitary staminate flowers; **staminate flowers** not seen; **pistillate flowers** 3 mm long; calyx 0.5 mm long, shallowly cupuliform, hyaline, glabrous, not striate, with acute lobes; corolla 2.5 mm long, campanulate to urceolate, acutely 3-lobed to one-third to base, striate, glabrous; **fruits** obovoid, prominently rostrate, 0.7–1 cm long, 0.7–0.8 cm diam, orange, striate, glabrous; mesocarp very thin, mealy; endocarp turbinate; endocarp fibers lacking; endocarp pores equidistant; fruiting calyx minute, corolla 3–4 mm long, deeply 3-parted at apex by enlarging fruit, with 6 minute staminodia.

ADDITIONAL SPECIMENS EXAMINED. — PANAMA. **Chiriquí**: Gualaca-Chiriquí Grande road, near Continental Divide, 1075 m *de Nevers et al. 8765* (CAS, PMA). **Coclé**: El Copé, *Moore et al. 10535* (BH). **Colón**: Santa Rita Ridge, km 13.8, 9°20′N, 79°45′W, 350 m, *de Nevers 7204* (MO), km 20.7, 9°23′N, 79°40′W, 530 m, *Foster et al. 14082* (PMA). **Panamá**: Campo Tres, 3 mi. NE of Altos de Pacora, *Croat 22727* (MO); El Llano-Cartí road, km 12, *Croat 26072* (MO); Cerro Jefe, 1000 m, *Croat 17346* (MO), *Correa et al. 10623* (PMA), *Folsom & Page 5935* (MO), *Read et al. 81-5* (MO, US). **San Blas**: Cerro Brewster, 9°18′N, 79°16′W, 850 m, *de Nevers 4050* (MO), *5527* (MO, NY), *5555* (MO, NY).

DISTRIBUTION AND HABITAT. — Panama (Chiriquí, Coclé, San Blas, Panamá, Veraguas); tropical wet forest between 300 and 1200 m elevation.

DISCUSSION. — This species is known from scattered localities along the Atlantic coast of Panama. It is similar to *Bactris hondurensis* and *B. charnleyae* in its small stature. It can be separated from those by its pinnate leaves and concave pinnae with prominent drip-tips. The fruits are smaller than those of *B. hondurensis*. It can be distinguished from *B. charnleyae* by the lack of endocarp fibers and lack of long spines on the peduncle and peduncular bract.

20. Bactris pilosa H. Karst., Linnaea 28:405. 1856.

TYPE. — Venezuela. Zulia: Maracaibo, *H. Karsten s.n.* (W, n.v.; F neg. 31316).

Stems cespitose and forming large, dense clumps, or rarely solitary, 2–10 m tall, 2.5–4 cm diam, spiny. **Leaves** 4–8; sheath 20–80 cm long, sheath, petiole and rachis moderately to densely covered with brown or black spines to 5 cm long; petiole 28–60 cm long; rachis 1.2–2.2 m long; pinnae 59–68 per side, regularly or irregularly arranged, spreading in the same or different planes, linear, aristate, middle pinnae 27–47 cm long, 1.5–2.2 cm wide, slightly to densely pilose on adaxial and abaxial surface. **Inflorescences** interfoliar; peduncle 14–35 cm long, recurved, not spiny; prophyll 16–18 cm long; peduncular bract 27–47 cm long, densely covered with soft, appressed, brown spines, with longer, black spines intermixed; rachis 4–6 cm long; rachillae 6–26, 13–25 cm long; triads scattered amongst paired or solitary staminate flowers; **staminate flowers** 3.5 mm long; sepals very briefly connate below, free and spreading above, linear, 1 mm long; petals connate below for ca. one third their length, free and valvate above, 3.5 mm long;

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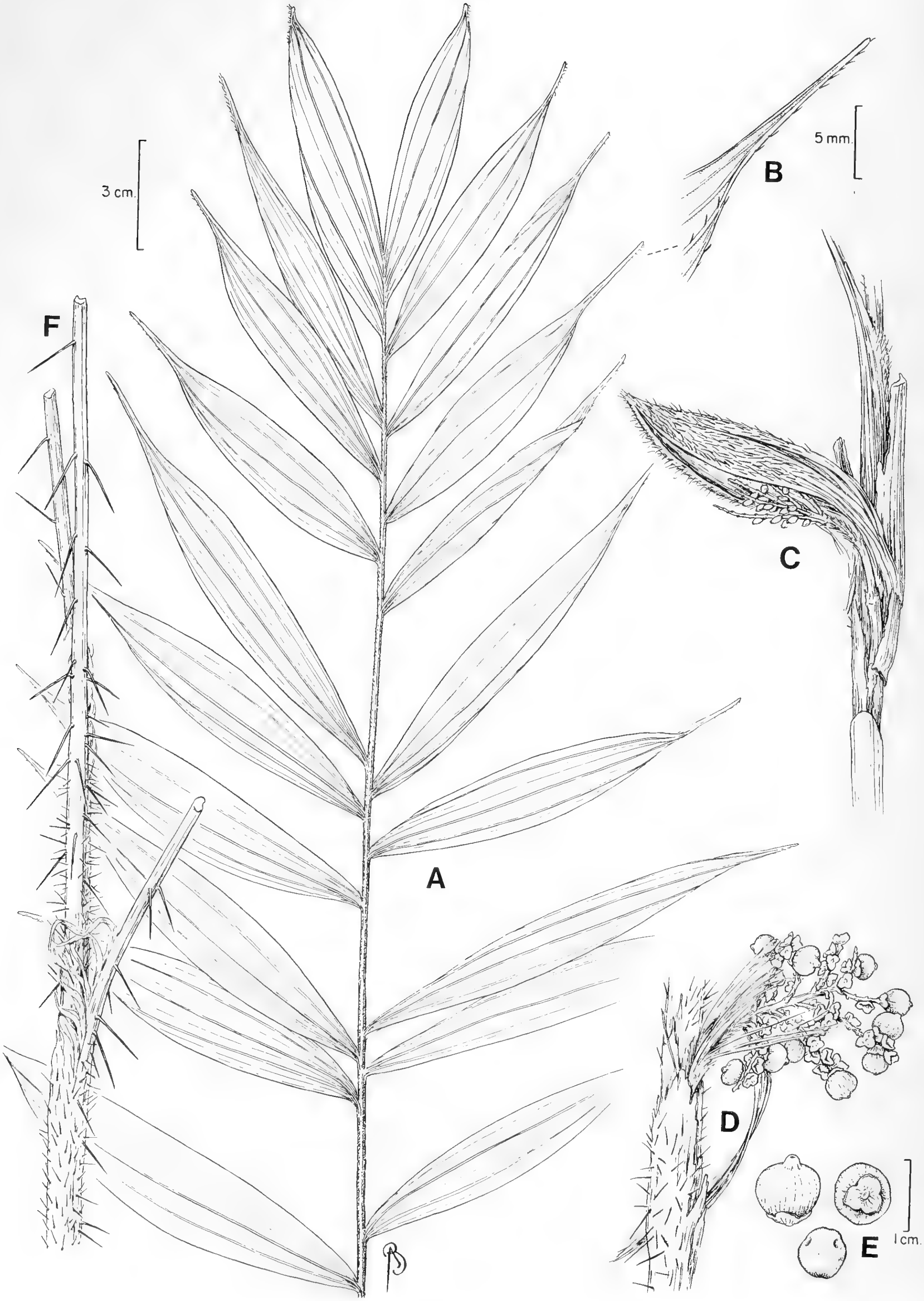
FIGURE 10. *Bactris militaris* (*Allen 5276*). A. Leaf shape × 1/21. B. Midsection of leaf × 1/3. C. Inflorescence × 1/3. D. Portion of flowering rachilla × 2. E. staminate flower × 4. F. and G. Pistillate flower, side view and expanded × 4. H. Pitted endocarp × 1.5. I. Fruit × 1.5. J. Leaf apex × 1/9. Courtesy of the L. H. Bailey Hortorium, Cornell University.


3 cm.
5 mm.
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pistillode absent; **pistillate flowers** (post-anthesis) 4 mm long; calyx 4 mm long, covered with very short bristles; corolla urceolate, 1.5 mm long, lepidote; staminodes absent; **fruits** depressed obovoid, rostrate, 2–2.5 cm long, 1.3–2 cm diam, purple-black, covered with very short bristles; mesocarp juicy; endocarp turbinate; endocarp fibers numerous, with juice sacs attached; endocarp pores equidistant; fruiting perianth with corolla shorter than the calyx.

ADDITIONAL SPECIMENS EXAMINED. — PANAMA. **Darién**: road to Pinogana near El Real, *Croat & Porter 15479* (MO); Cerro Pirre, 8°N, 77°47W, *Croat 68989* (MO), *de Nevers 8242* (CAS); Perrecenico River, *Duke & Bristan 244* (MO, US); Río Pirre, 2–5 mi. above El Real, *Duke 5076* (MO), *5467* (MO).

DISTRIBUTION AND HABITAT. — Eastern Panama (Darién), Colombia (Antioquia, Bolívar, Chocó, Sucre, Tolima) and Venezuela (Táchira, Zulia); lowland forest below 600 m elevation.

LOCAL NAMES AND USES. — Panama: *sansagarra* (Embera), *uvita*.

DISCUSSION. — This species is characterized by its pubescent, purple fruits, truncate fruiting corolla slightly shorter than the calyx, large inflorescence, and pubescent leaves. The pinna pubescence is identical to that of *B. glandulosa*. *Bactris glandulosa* differs from *B. pilosa* in its regularly arranged triads, smaller, glabrous fruits, and fruiting calyx much shorter than the corolla.

INVALIDLY PUBLISHED NAMES

Bactris longipetiolata H. Wendl., nomen nudum, in Hemsl., Biol.centr.-amer., Bot. 3:412. 1885.

Bactris polystachya H. Wendl., nomen nudum, in Hemsl., Biol.centr.-amer., Bot. 3:413. 1885.

Bactris subglobosa H. Wendl., nomen nudum, in Kerch., Palmiers 234. 1878.

Bactris villosa H. Wendl., nomen nudum, in Hemsl., Biol. centr.-amer., Bot. 3:413. 1885.

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FIGURE 11. *Bactris panamensis* (*McPherson 9992*). A. Leaf apex. B. Drip-tip, showing venation. C. Inflorescence, showing erect peduncle. D. Infructescence. E. Fruit in two views and endocarp (below). F. Stem and leaf bases. A, C, D and F same scale.

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PROCEEDINGS
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A REVIEW OF THE GENUS *EUDERCES* LECONTE (COLEOPTERA: CERAMBYCIDAE: TILLOMORPHINI)

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The genus *Euderces* LeConte is revised with 57 recognized species, 26 of which are new. All but two known species are illustrated, previously known species are redescribed, and a key is provided. *Cleozona* Bates is placed in synonymy with *Euderces*. New *Euderces* species described are *E. andersoni*, *E. auricaudus*, *E. basimaculatus*, *E. batesi*, *E. biplagiatus*, *E. brailovskyi*, *E. elvirae*, *E. grossistriatus*, *E. noguerai*, *E. obliquefasciatus*, *E. perplexus*, *E. postipallidus*, and *E. propinquus* from Mexico; *E. tibialis*, *E. turnbowi* and *E. wappesi* from Mexico and Guatemala; *E. azureus*, *E. proximus* and *E. succinus* from Guatemala; *E. guatemalenus* from Guatemala and Honduras; *E. bellus* and *E. disparicrus* from Mexico, Guatemala and Honduras; *E. pusillus* from Mexico, Guatemala, and Costa Rica; *E. linsleyi* from Panama and Costa Rica; *E. paraposticus* from Colombia, and *E. venezuelensis* from Venezuela. New synonymies in *Euderces* are *E. cribratus* Bates = *E. laevicauda* Bates; *E. fenyesi* Linsley = *E. cribripennis* Bates; *E. auricomis* Chemsak = *E. cleriformis* Bates; *E. picipes occidentalis* Linsley = *E. picipes* (Fabricius); and *E. reichei exilis* Casey = *E. reichei* LeConte. The subspecies *E. bicinctus peninsularis* (Linsley) is removed from synonymy. *Eplophorus guerinii* (Chevrolat), *E. posticus* (Pascoe) and *E. waltli* Chevrolat are transferred to *Euderces*.

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Euderces LeConte, with 57 known species, occurs from North America to South America, and distribution appears to be centered in southern Mexico and Guatemala. Only four species are presently known to occur north of Mexico, ten species to the south between Honduras and Panama, and six species in South America. None are known from the West Indies. Adults belonging to this genus appear to mimic ants in both appearance and movement, and are sometimes collected in company with foraging ants. Some species may be collected on flowers, some running on dead wood, and others by beating foliage. The typical elytral pattern of median eburneous fasciae and preapical pubescent fasciae together produce the illusion of a constriction resembling the narrow petiole characteristic among ants, and this, along with size, color, style and speed of movement, and an often forward-curved antennal posture (Fig. 1), contributes to the strong ant-like appearance. Little is known about the larval biology, and because of the scarcity of many of the species in collections, comprehensive knowledge of distributions is lacking.

MATERIALS AND METHODS

Over 1,900 adult specimens were examined in the course of this study, generously provided from the collections of a number of institutions and individuals. These are indicated in the text by codens, the key to which appears in the "Acknowledgments" section at the conclusion of the paper. Studies were based on examination of external structural features of adult specimens. No attempt has been made to draw further systematic or evolutionary conclusions by means of cladistic analysis or examination of internal morphology. "Length" of a specimen is taken to mean the length of the body from mandibles to elytral apex. Arrangement of species in the text is alphabetical. The partial habitus figures are intended to provide a clear illustration of important structural characters rather than a complete view. Figure 7 and following figures are shown at the same scale (except figures with scale bar added). In the case of several commonly collected and widespread species, the large number of specimens seen has necessitated mapping rather than enumerating individual specimen data. These maps (Figs. 2–6) reflect examined material only.

Tribe **Tillomorphini** Lacordaire

The tribe Tillomorphini is composed of a number of homogenous genera composed of species of small size, usually with eburneous elytral fasciae. Two of these genera are represented in North and Central America where most *Euderces* are found. Of these, *Tetranodus* Linell may be distinguished by the enlarged third to sixth antennal segments of the males, by the single, transverse eburneous fascia very narrowly divided at the sutural margin, and by the pointed inner apex of the upper eyelobe; and *Pentanodes* Schaeffer, which may be distinguished by the non-emarginate eyes and the somewhat inflated third to seventh antennal segments of the males.

Genus **Euderces** LeConte

Euderces LeConte, 1850:30; 1873:325; Thomson, 1860:217; 1864:428; Lacordaire, 1869:89; Provancher, 1877:604; Bates, 1880:59; 1885:304; LeConte & Horn, 1883:305; Leng, 1887:24, 195; Schaeffer, 1904:223; Linsley, 1935:87; 1964:180; Knull, 1946:225; Linsley, 1964:180; Chemsak, 1969:312; Hovore, 1988:15. (TYPE SPECIES: *Callidium picipes* Fabricius, monobasic)

Eplophorus Chevrolat, 1861:248; Linsley, 1935:87; Chemsak, 1969:307. (TYPE SPECIES: *Clytus spinicornis* Chevrolat, monobasic)

Apelocera Chevrolat, 1862:61; Thomson, 1864:195, 428; Aurivillius, 1912:420. (TYPE SPECIES: *Apelocera Waltli* Chevrolat (Thomson designation, 1864).)

Apilocera; Chevrolat, 1862:535; Pascoe, 1866:295; Bates, 1880:60; 1885:305.

Cleozona Bates, 1874:223; 1880:60; Linsley, 1935:87; Chemsak, 1969:304. (TYPE SPECIES: *Cleozona pulchra* Bates, monobasic) **NEW SYNONYMY.**

DESCRIPTION. — Form small, ant-like. Head with eyes divided, upper and lower lobes connected by a narrow, glabrous line, upper lobes small, rounded at inner apices, rarely lacking; antennae 11-segmented, filiform, third segment longest, segments three to five often spinose or dentate at apex. Pronotum elongate or globose, unarmed, usually impressed across base. Elytra basally gibbose or not, each elytron with one or two transverse or oblique, raised, eburneous fasciae not attaining suture; disk usually with median area densely cribrate-punctate. Abdomen with first sternite longer than second and third together. Male prosternum usually bearing scattered distinct, coarse punctures at base, female prosternum lacking distinct punctures.

REMARKS. — The genus *Euderces* was proposed by LeConte (1850) to accomodate *Callidium picipes* Fabricius. One of the characters given at that time was the presence of a very small spine at the apex of the third antennal segment. In 1861, Chevrolat described the genus *Eplophorus* to include species with distinctly spinose third antennal segments. Lacordaire (1869) then synonymized *Apelocera* with *Eplophorus*. Linsley (1964) synonymized *Eplophorus* under *Euderces*, having noted wide variation in antennal spines among what otherwise appears to be a compact and monophyletic group of species. The most recent treatment of the genus was by Chemsak (1969), in which several new species were characterized.

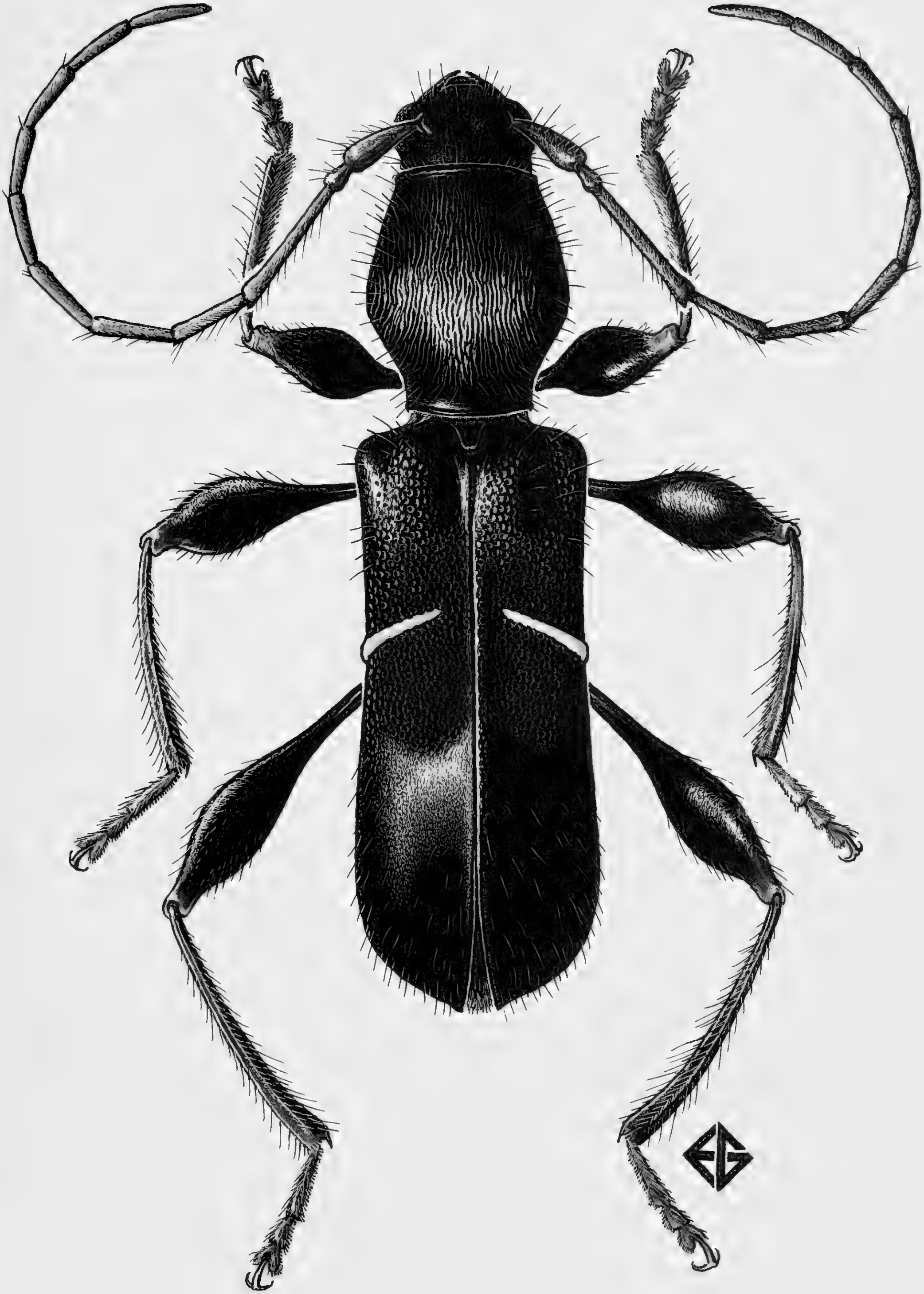

FIGURE 1. *Euderces picipes* (Fabricius), male.

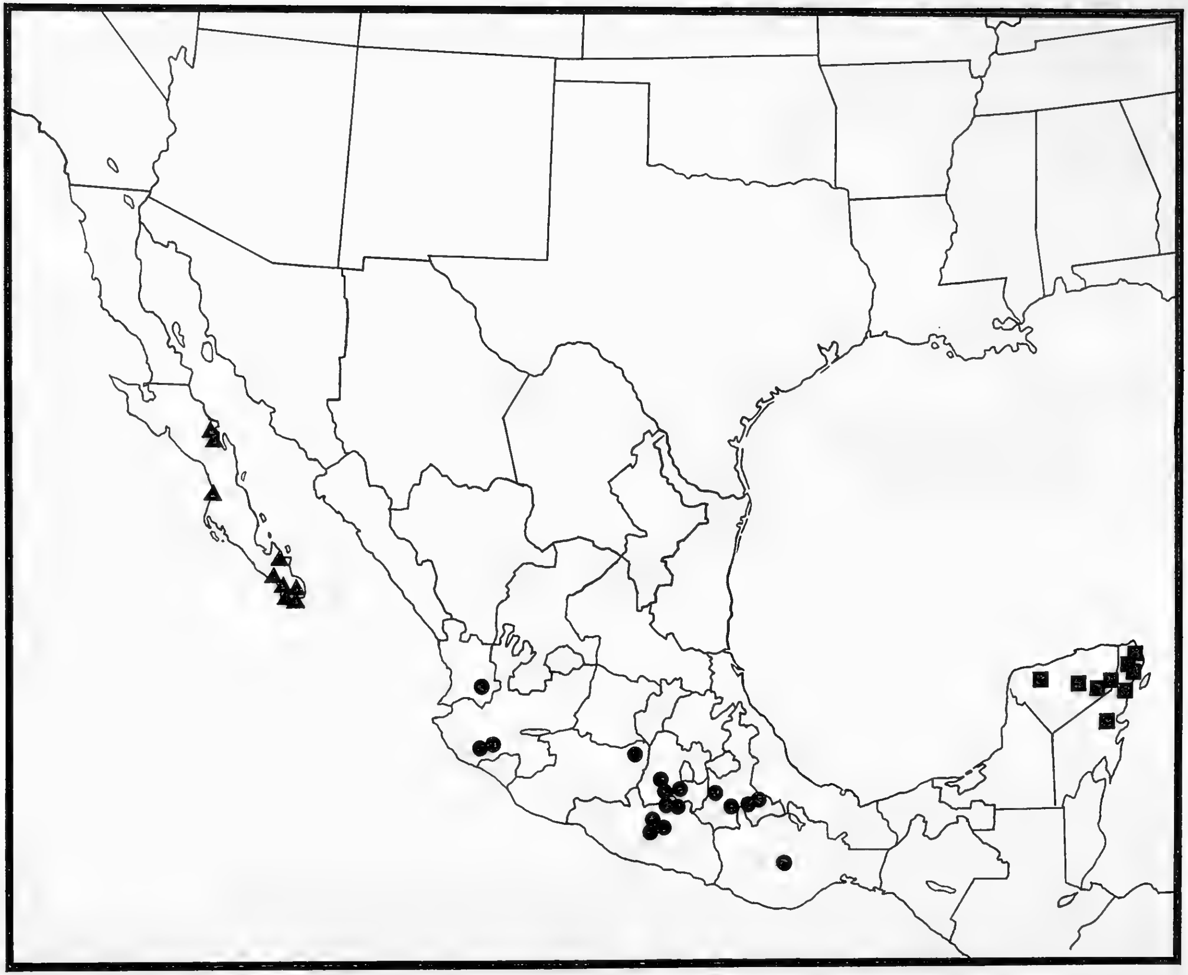

FIGURE 2. Known distribution of *Euderces cleriformis* (Bates) [open circles]; *E. boucardi* (Chevrolat) [closed circles]; *E. dimidiatipennis* (Melzer) [open squares]; *E. posticus* (Pascoe) [closed squares]; *E. paraposticus*, new species [triangle]; and *E. venezuelensis*, new species [cross].

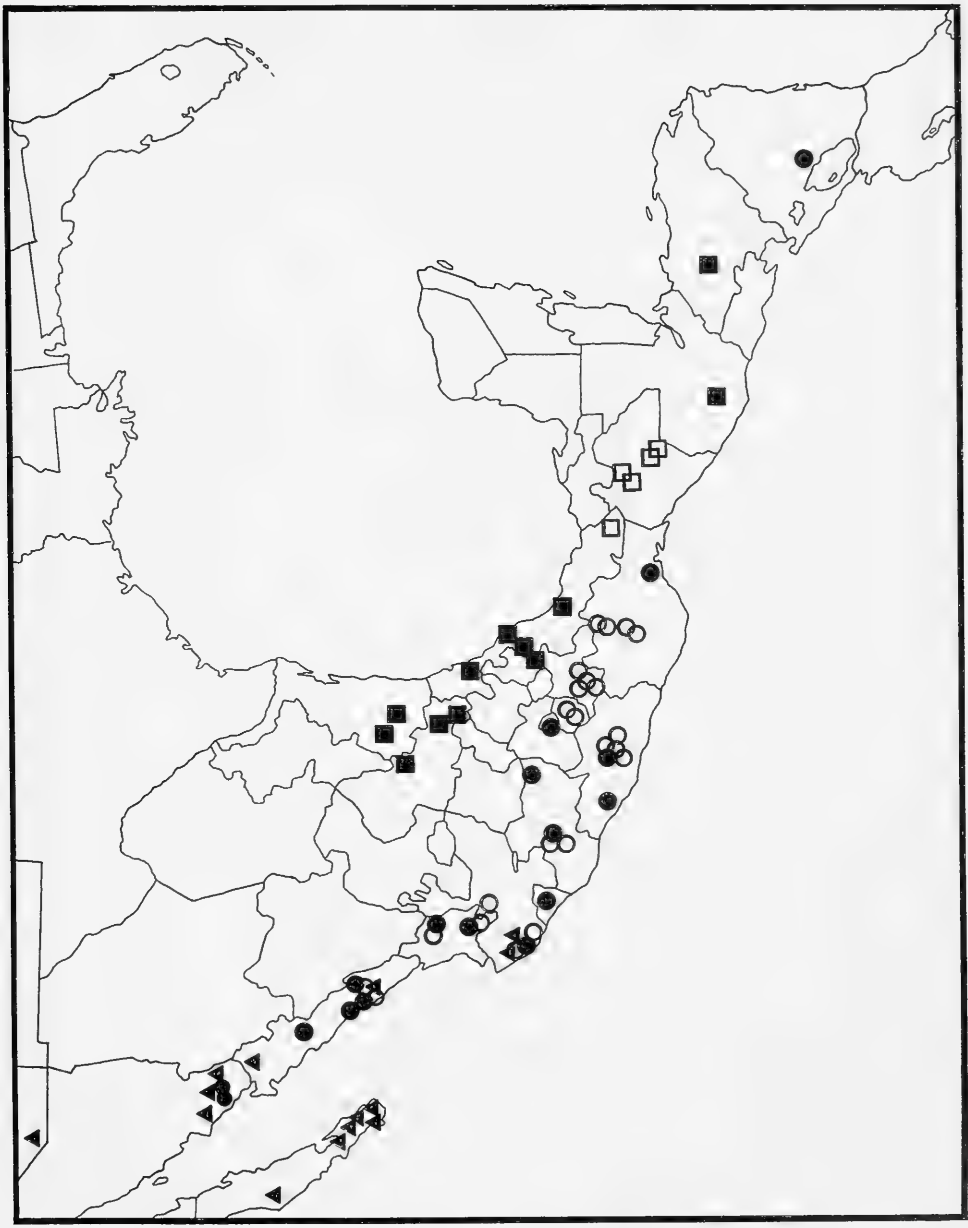

FIGURE 3. Known distribution of *Euderces cribripennis* Bates [circles]; *E. parallelus* LeConte [triangles]; and *E. yucatecus* (Bates) [squares].

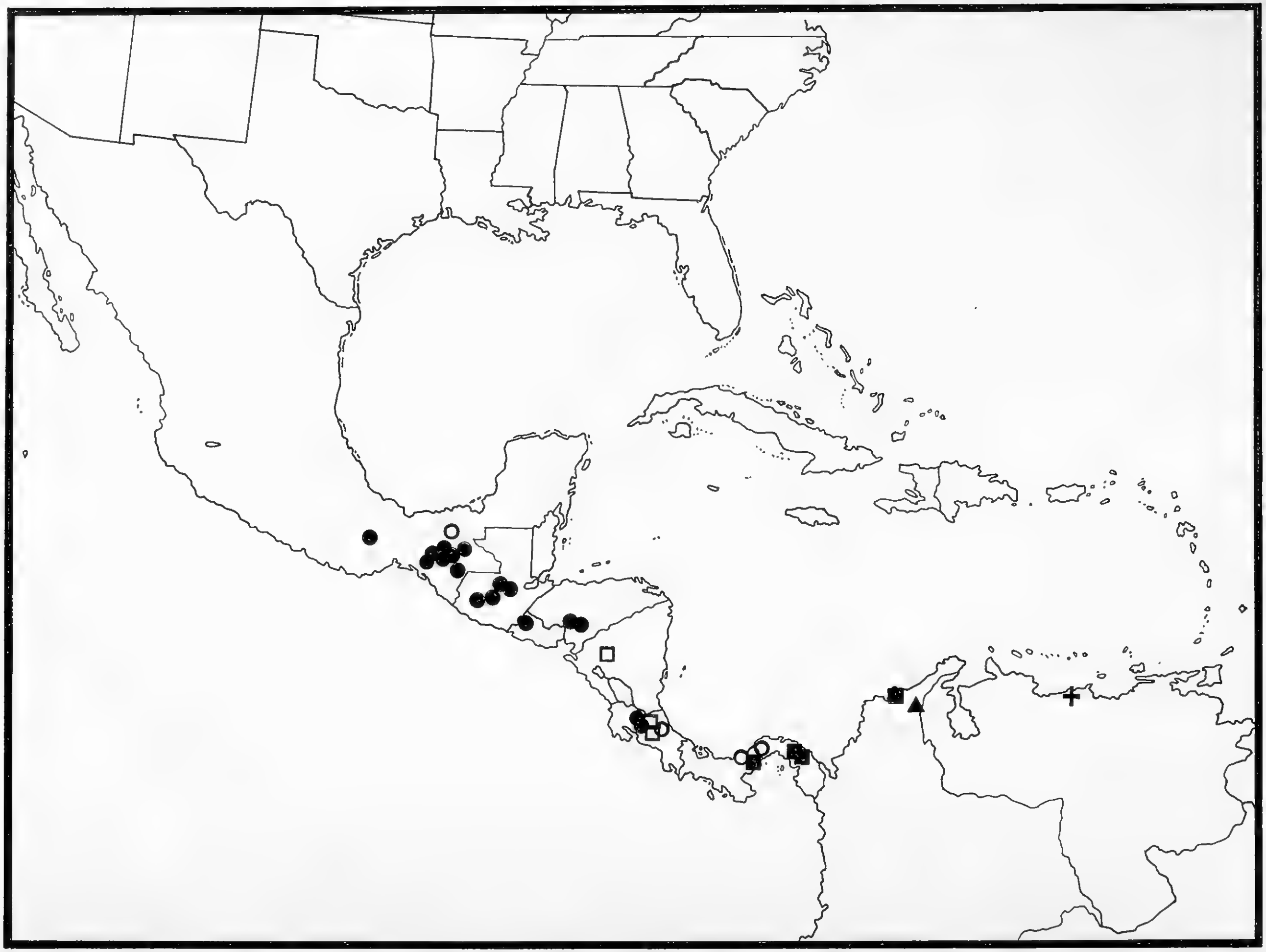

FIGURE 4. Known distribution of *Euderces longicollis* (Linsley) [open circles]; *E. pulcher* (Bates) [solid circles]; *E. bicinctus* (Linsley) [triangles]; *E. spinicornis* (Chevrolat) [solid squares]; and *E. hoegei* (Bates) [open squares].

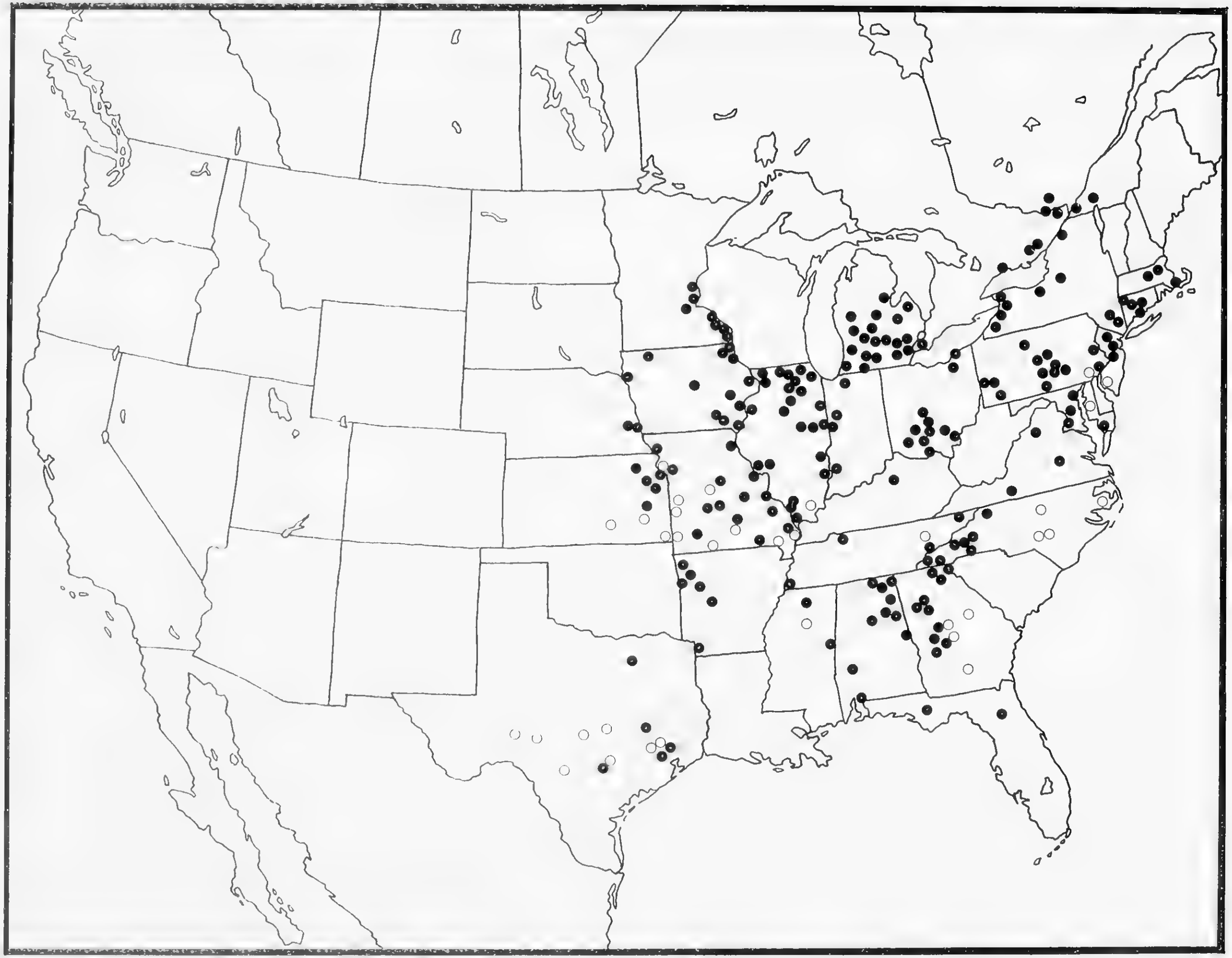

FIGURE 5. Known distibution of *Euderces pini* (Olivier)(open circles); and *E. picipes* (Fabricius) [closed circles].

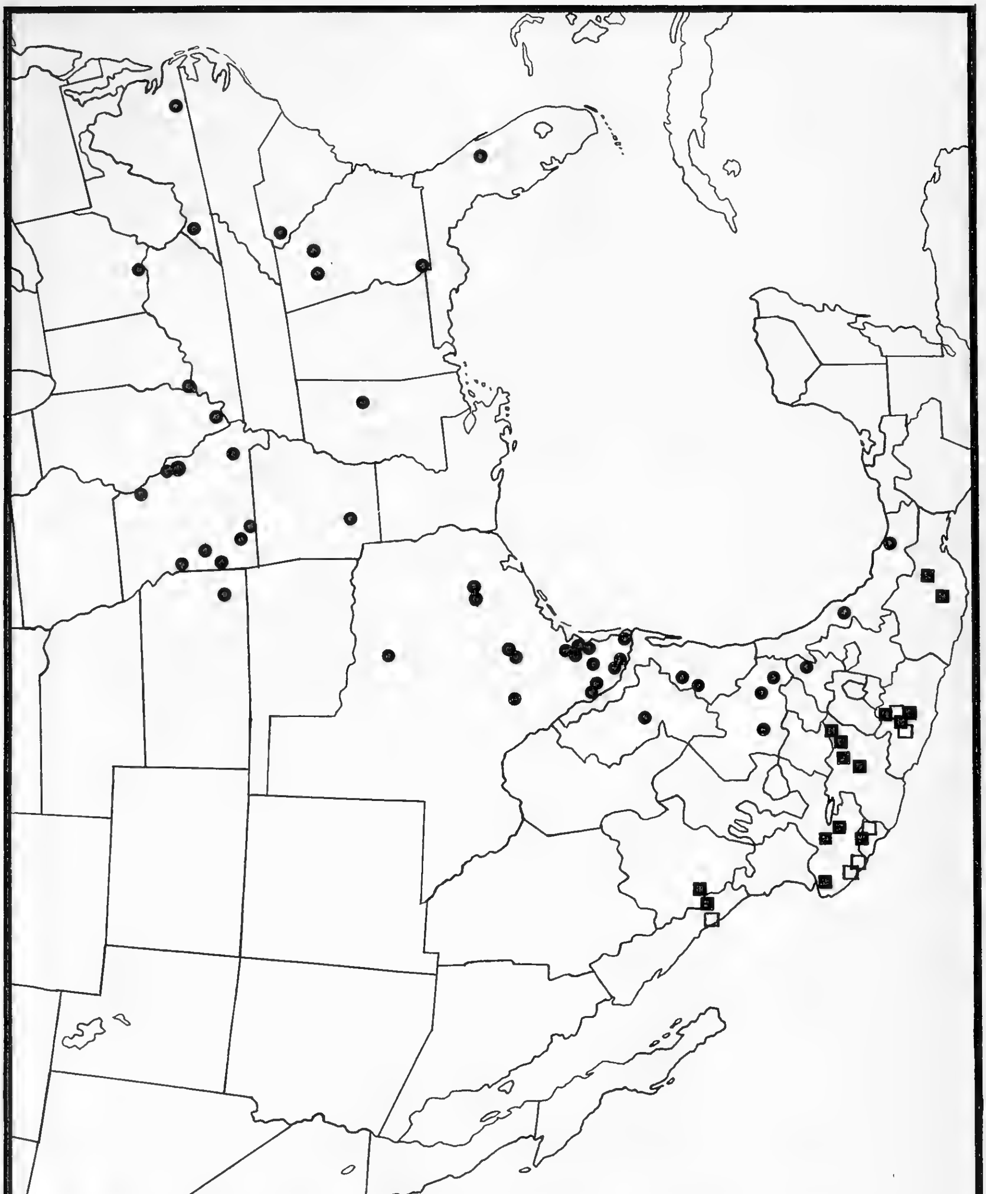

FIGURE 6. Known distribution of *Euderces reichei* LeConte [circles]; *E. nelsoni* Chemsak [open squares]; and *E. aspericollis* (Chemsak) [closed squares].

KEY TO THE SPECIES OF EUDERCES LECONTE

(NOTE. — *E. guerinii* and *E. waltli*, South American species not seen in the course of this study, have not been included in the following key.)

1. Antennae with third segment spined, spiculate, or dentate at apex 15
Antennae with apex of third segment unarmed, rounded at apex 2
2.(1) Elytra with two pairs of eburneous markings (anterior pair sometimes indistinct) 3
Elytra with single pair of eburneous fasciae 8
3.(2) Abdomen with patch of fine, appressed pubescence on each side of first sternite 4
Abdomen shining, lacking appressed pubescent patches on first sternite 5
4.(3) Pronotal disk with long, distinct, fine, longitudinal striae. Elytra with posterior eburneous fasciae transverse. Length 3.5–4 mm. (Fig. 31) Mexico (Chiapas), Guatemala .... *laevicauda* Bates
Pronotal disk moderately finely, longitudinally rugose. Elytra with posterior eburneous fasciae strongly oblique. Length 6 mm. (Fig. 37) Mexico (Guerrero)................ .... *obliquefasciatus*, new species
5.(3) Elytra with eburneous fasciae transverse, subparallel, close to and equidistant from suture. Length 3–5 mm. (Figs. 3, 38) Mexico (Baja California) .... *parallelus* LeConte
Elytra with eburneous markings not parallel nor equidistant from suture 6
6.(5) Elytra with anterior pair of eburneous markings obliquely linear; basal gibbosities moderately well developed. Pronotum as wide as long. Length 4–5 mm. (Fig. 59) Mexico (Baja California) .... *westcotti* Hovore
Elytra with anterior markings ovoid or indistinct; basal gibbosities not developed 7
7.(6) Integument bicolored, elytral base and most of suture orange-red. Anterior pair of elytral markings small, evanescent (sometimes absent); humeri transverse. Length 4.5–5.5 mm. (Fig. 44) Mexico (Oaxaca) .... *propinquus*, new species
Integument usually piceous (rarely reddish at base of elytra). Anterior pair of elytral eburneous markings distinct, raised, linear; humeri somewhat narrow, sloping. Length 3–5.5 mm. (Fig. 40) Mexico (Guerrero, Oaxaca, Morelos) .... *perplexus*, new species
8.(2) Elytral apices somewhat produced and acuminate; each side at base with small, distinct gibbosity. Length 3.75 mm. (Fig. 7) Guatemala.................. *acutipennis* Bates
Elytral apices not acuminate; basal gibbosities reduced or absent 9
9.(8) Pronotum with discal surface reticulate. Antennae of males about as long as body 10
Pronotum with discal surface striolate and medially asperate. Antennae of males shorter than body 11
10.(9) Integument piceous, usually with indistinct paler areas near elytral basal gibbosities. Pronotum with base moderately densely whitish pubescent. Length 5.5–7.5 mm. (Fig. 13) Western Mexico (Colima, Nayarit, Michoacán, Oaxaca, Guerrero, Durango) .... *basimaculatus*, new species
Integument piceous, apical 1/3 of elytra dull yellowish. Pronotum without distinct whitish pubescence at base. Length 5.5–7.5 mm. (Fig. 43) Mexico (Oaxaca) .... *postipallidus*, new species
11.(9) Elytra shining, lacking densely cribrate-punctate area near middle. Integument brown and orange-brown. Length 6 mm. (Fig. 26) Mexico (Oaxaca) .... *elvirae*, new species
Elytra partially opaque, with densely cribrate-punctate median area 12
12.(11) Abdominal first sternite lacking silky, recumbent pubescence, very sparsely clothed throughout with long, erect, pale hairs 13
Abdomen with first sternite partially clothed wth fine, pale, recumbent, silky pubescence 14

13.(12) Legs with femora carinate on both sides near apex. Elytral integument piceous (head, pronotum and basal 1/3 of elytra sometimes red); eburneous fasciae transverse. Length 3.5–5 mm. (Figs. 3, 22) Mexico (Nayarit to Oaxaca), Costa Rica (?) *cribripennis* Bates.

Legs with femora lacking carinae. Length 3–5 mm. [Aberrant specimens lacking anterior pair of eburneous fasciae]. Mexico (Baja California) .... *parallelus* LeConte

14.(12) Elytra black at apex, usually orange from base to about apical 1/3 along suture; eburneous fasciae usually somewhat arcuate; elytra nearly three times as long as humeral width. Length 3.5–5.75 mm. (Fig. 14) Mexico (Puebla, Oaxaca) .... *batesi*, new species.

Elytra with large, ill-defined, median,blackish macula on each side, with apex, base, and suture pale orange or yellowish; eburneous fasciae transverse; elytra about 2 2/3 times as long as humeral width. Length 3.75–5 mm. (Fig. 17) Mexico (Puebla, Oaxaca) .... *biplagiatus*, new species.

15.(1) Antennae with apex of third segment dentate .... 16.

Antennae with apex of third segment distinctly spined or acutely spiculate .... 21.

16.(15) Elytra with coarse, white, appressed pubescence which is denser along suture; sides unimpressed. Abdomen and legs rather densely, coarsely white pubescent. Length 7 mm. (Fig. 30) Mexico (Durango) .... *howdeni* Chemsak.

Elytra without coarse, white sutural pubescence. Abdomen not densely pubescent .... 17.

17.(16) Pronotal disk asperate. Elytra without distinct basal gibbosities. Integument reddish orange, abdomen and apical 1/3 of elytra piceous. Length 3.5–5 mm. (Figs. 6, 48) Central to southern USA (Ohio, Illinois to Florida, Texas) .... *reichei* LeConte.

Pronotal disk reticulate or striate. Elytra with basal gibbosities present .... 18.

18.(17) Pronotal disk reticulate and longitudinally rugose, side margins abruptly angled downward. Integument piceous, appendages and mouthparts orange-brown. Length 4.5 mm. (Fig. 8) Mexico (Guerrero) .... *andersoni*, new species.

Pronotal disk with distinct, longitudinal striae, side margins rounded .... 19.

19.(18) Integument dark orange-brown. Elytra slightly more than 2 1/2 times as long as width across humeri; preapical pubescent fascia lacking. Length 4.5–5 mm. (Figs. 2, 57) Venezuela .... *venezuelensis*, new species.

Integument bicolored reddish and piceous or all piceous. Elytra slightly less than 2 1/2 times as long as width across humeri; preapical pubescent fascia at least indistinctly present. Length 5–9 mm. North America ....20.

20.(19) Elytra with distinct white pubescent postmedian fascia which is impressed near suture; integument of basal 1/2 usually reddish. Abdominal first sternite with scattered, erect, inconspicuous hairs. (Figs. 5, 41) Eastern USA to Texas .... *pini* (Olivier).

Elytra without a distinct postmedian pubescent fascia or impression, integument usually piceous throughout. Abdominal first sternite densely white pubescent. (Figs. 1, 5) Eastern North America to Oklahoma and Texas .... *picipes* (Fabricius).

21.(15) Elytra with two pairs of eburneous markings .... 22.

Elytra with single pair of eburneous fasciae .... 26.

22.(21) Antennal third segment longitudinally sulcate. Elytra with basal gibbosities low, not strongly produced .... 23.

Antennal third segment not sulcate. Elytra with basal gibbosities strongly produced. Integument shining, black. Length 6–9 mm. (Fig. 32) Panama, Costa Rica .... *linsleyi*, new species.

23.(22) Elytral fasciae unequal, anterior pair much shorter .... 24.

Elytral fasciae equal, anterior and posterior pairs long, subparallel .... 25.

24.(23) Antennae with spine of third segment short, not as long as second segment. Pronotal sides rounded. Elytral anterior markings linear or sinuate. (Fig. 36) Mexico (Yucatán, Quintana Roo), Belize .... *noguerai*, new species.

Antennae with spine of third segment longer than second segment. Pronotum elongate, subcylindrical. Elytral anterior markings small, oval. (Figs. 4, 33) Western Mexico (Sinaloa to Guerrero) .... *longicollis* (Linsley).

25.(23) Elytra with eburneous fasciae strongly oblique, linear, widely separated. Antennae of males exceeding elytral apices by about three segments. Length 8.5–14 mm. (Figs. 4, 46, 12c) Western Mexico (Sonora to Oaxaca), Nicaragua .... *pulcher* (Bates).

Elytral markings more or less transverse, separated by less than width of metafemur. Antennae of males reaching elytral apices. Length 4.5–7.5 mm. (Figs. 4, 33) Arizona, western Mexico (Sonora, Sinaloa, Baja California) .... *bicinctus* (Linsley).

26.(21) Antennae with apical spine of third segment sharply spiculate or short to moderately long, but always less than 2/3 as long as entire fourth segment .... 27.

Antennae with apical spine of third segment long, 2/3 or more as long as entire fourth segment, often curved and blunt at apex .... 40.

27.(26) Legs with meso- and metafemora slender, incrassate. Integument dark metallic blue. Elytral apices strongly, obliquely emarginate, outer angle stoutly dentate. Length 10.5–11 mm. (Fig. 11, 12a) Guatemala .... *azureus*, new species.

Legs with femora clavate. Integument not metallic. Elytral apices rounded, truncate, or slightly emarginate .... 28.

28.(27) Metafemora gradually clavate, underside nearly straight, surface moderately coarsely scabrous. Length 4–6.5 mm. (Fig. 25, 12e) Mexico (Oaxaca, Chiapas) to Honduras........ .... *disparicrus*, new species.

Metafemora moderately abruptly clavate, surface smooth, shining .... 29.

29.(28) Elytral disk moderately sparsely punctate, lacking median cribrate-punctate area. Integument piceous, mouthparts, antennae, parts of legs, and tarsi orange-brown. Length 6–8 mm. (Fig. 55) Mexico (Chiapas), Guatemala .... *turnbowi*, new species.

Elytral disk with portion of the median area densely cribrate-punctate .... 30.

30.(29) Pronotal disk with long, longitudinal striations. Antennae of males short, reaching to about middle of elytra. Elytra with basal gibbosities close to suture. Length 4.5–6.5 mm. (Fig. 15) Southern Mexico (Chiapas) to Honduras .... *bellus*, new species.

Pronotal disk asperate, longitudinally rugose, or with shorter, finer striae. Elytral gibbosities, if present, located near middle of base on each side .... 31.

31.(30) Elytra without basal gibbosities .... 32.

Elytra with low to prominent basal gibbosities .... 33.

32.(31) Pronotum moderately sparsely asperate, lacking recumbent pubescence. Integument reddish orange, abdomen and apical 1/2 of elytra black (southern Mexico populations often all black) (Figs. 6, 48). Eastern U. S.(Ohio to Florida and Texas) to Mexico (Nuevo León, Tamaulipas, San Luis Potosí, Veracruz) .... *reichei* LeConte.

Pronotum moderately densely asperate, clothed at base and apex with fine, recumbent pubescence. Integument reddish, legs, abdomen, and apical 1/2 of elytra brown. (Fig. 50) Guatemala .... *rubellus* (Bates).

33.(31) Integument of pronotum reddish; elytra reddish, apical 1/2 often infuscated. Elytral gibbosities low, moderately small. Length 5–6 mm. (Figs. 6, 35) Western Mexico (Sinaloa, Jalisco, Guerrero, Chiapas) .... *nelsoni* Chemsak.

Integument of pronotum dark brown, piceous or black. Elytral gibbosities broad or strongly produced .... 34.

34.(33) Elytra with basal gibbosities strongly produced. Antennae with spine of third segment slightly more than 1/2 as long as entire fourth segment .... 35.

Elytra with basal gibbosities broad, not strongly produced. Antennae with spine of third segment at most 1/2 as long as entire fourth segment .... 36.

35.(34) Elytra with basal 1/3 of disk nearly glabrous; eburneous fasciae located slightly before basal third. Abdomen lacking oblique, lateral pubescent markings. Length 5.5–7 mm. (Fig. 58) Mexico (Chiapas), Guatemala .... *wappesi*, new species.

Elytral disk with basal 1/3 moderately pubescent near gibbosities; eburneous fasciae located slightly behind basal 1/3. Abdominal first segment with oblique, lateral pubescent markings. Length 4.5–55 mm. (Fig. 51) Guatemala .... *sculpticollis* (Bates).

36.(34) Pronotal disk moderately coarsely, longitudinally rugose-striate. Elytral apices somewhat obliquely truncate. Length 8.5–10.5 mm. (Fig. 45) Guatemala . *proximus*, new species.

Pronotal disk moderately densely asperate or finely striate. Elytral apices transversely subtruncate. Length 4.5–7.5 mm .... 37.

37.(36) Abdomen with each side of first sternite bearing oblique, pale pubescent marking. Length 4.5–7.5 mm. (Figs. 6, 28) Western Mexico (Sinaloa, Durango, Jalisco, Guerrero, Michoacán, Oaxaca), Guatemala .... *aspericollis* (Chemsak).

Abdomen with first sternite lacking pubescent markings .... 38.

38.(37) Elytra with transverse, glabrous fascia before apical pubescent patch distinct, narrow. Males with antennae longer than body. Length 5–8.25 mm. (Fig. 19) Mexico (Hidalgo, San Luis Potosí) .... *brailovskyi*, new species.

Elytra with apical pubescent patch preceded by wider or ill-defined glabrous fascia. Males with antennae not exceeding elytral apices .... 39.

39.(38) Elytral integument deep yellowish on apical 1/2. Pronotal disk with surface moderately finely, longitudinally reticulate and asperate. (Fig. 10) Mexico (Oaxaca, Guerrero) .... *auricaudus*, new species.

Elytral integument dark to apices. Pronotal disk with surface finely, densely asperate and striate. (Fig. 23) Bolivia .... *dilutus* Martins.

40.(26) Pronotum bicolored, orange at base, broadly black on disk. Elytra bicolored .... 41.

Pronotal integument unicolorous. Elytra variably colored .... 42.

41.(40) Elytra less than 2 1/2 times as long as width across humeri. Antennae with apical spine of third segment longer than fourth segment. Appendages orange-testaceous (Figs. 4, 52). Mexico (Tamaulipas, San Luis Potosí, Puebla, Veracruz), Guatemala, Honduras .... *spinicornis* (Chevrolat).

Elytra nearly three times as long as width across humeri. Antennae with spine of third segment about 3/4 length of fourth segment (Fig. 28). Guatemala and Honduras .... *guatemalenus*, new species.

42.(40) Integument yellow-brown, pronotum pale orange-brown. Elytra lacking cribrate-punctate areas. Length 5 mm. (Fig. 53) Guatemala .... *succinus*, new species.

Integument all or partly black, dark brown, or reddish. Elytra with median cribrate-punctate areas .... 43.

43.(42) Meso- and metatibiae strongly compressed. Elytra with opaque, cribrate-punctate area extensive, lacking impunctate area anterior to preapical pubescence .... 44.

Meso- and metatibiae not strongly compressed. Elytra with distinct impunctate area between cribrate-punctate area and preapical pubescence .... 45.

44.(43) Pronotum slightly longer than wide, sides broadly rounded. Form moderately robust, elytra slightly more than twice as long as width across humeri. Length 8.25–10 mm. (Fig. 56) Honduras, Guatemala .... *velutinus* (Fisher).

Pronotum about 1 1/2 times as long as wide, sides slightly rounded. Form less robust, elytra about 2 1/3 times as long as width across humeri. Length 7.25–8 mm. (Figs. 54, 12d) Mexico (Veracruz, Chiapas), Guatemala .... *tibialis*, new species.

45.(43) Antennae with third segment about 1 1/2 times as long as fourth segment .... 46.

Antennae with third segment distinctly more than 1 1/2 times as long as fourth ...... 47.

46.(45) Elytra with basal gibbosities well developed. Integument variable, pronotum and basal 1/2 of elytra usually reddish, piceous behind eburneous fasciae; sometimes all piceous, or with prothorax piceous. Antennae slightly thickened distally. (Figs. 2, 24) Nicaragua, Costa Rica .... *dimidiatipennis* (Melzer).

Elytra with basal gibbosities low; small impunctate spot present on suture between basal gibbosities and eburneous fasciae. Integument black. Antennae slender throughout. (Fig. 21) Costa Rica, Panama .... *cribellatus* (Bates).

47.(45) Integument reddish, apical portion of elytra infuscated .... 48.

Integument black, brown, or bicolored (black with reddish or orange areas) .... 49.

48.(47) Antennae of males slightly exceeding elytral apices. Pronotal discal surface longitudinally striate. Elytral basal gibbosities moderately produced. (Figs. 3, 60) Mexico (Yucatán, Quintana Roo) .... *yucatecus* (Bates).

Antennae of males reaching about middle of elytra. Pronotal surface moderately finely rugulose and asperate. Elytral basal gibbosities strongly produced. (Fig. 49) Mexico (Veracruz, Chiapas), Guatemala, Belize .... *reticulatus* (Bates).

49.(47) Elytral integument bicolored: black with reddish or orange areas .... 50.

Elytral integument dark brown or black .... 51.

50.(49) Elytral integument black, with orange areas at sides of disk on basal 1/2. (Figs. 2, 20) Mexico to Panama .... *cleriformis* (Bates).

Elytral integument with dark reddish orange area at middle surrounding eburneous fasciae, remainder of integument black. (Figs. 4, 29) Mexico (Veracruz, Chiapas)........ .... *hoegei* (Bates).

51.(49) Pronotum shining; disk with deep, long, longitudinal striations for most of length. Antennae with fourth segment short, about 1/3 as long as third, 1/2 as long as fifth, and shorter than spine of third segment. Appendages pale testaceous. Length 6–7 mm. (Fig. 27) Mexico (Veracruz) .... *grossistriatus*, new species.

Pronotum with striations, if present, not deep or long. Antennal fourth segment more than 1/2 as long as 5th segment. Appendages orange-brown to piceous or black .... 52.

52.(51) Larger species, length 7.5–12 mm .... 53.

Smaller species, length 3.5–6.5 mm .... 54.

53.(52) Pronotum not striate nor asperate. Elytral apices broadly subtruncate. Length 12 mm. (Fig. 34) Guatemala .... *magnus* (Bates).

Pronotum with discal surface striate. Elytral apices truncate. Length 7.5–10 mm. (Figs. 2, 18, 12b) Mexico (Chiapas) to Costa Rica .... *boucardi* (Chevrolat).

54.(52) Elytra with gibbosities moderately produced, apices narrowly subtruncate, outer angles dentate .... 55.

Elytra with basal gibbosities feeble, apices broadly rounded. Integument brown to black. Length 3.5–6 mm. (Fig. 47) Mexico (Chiapas) to Costa Rica .... *pusillus*, new species.

55.(54) Antennal third segment with spine about 2/3 as long as fourth segment. Pronotum slightly less than 1 1/2 times as long as wide, sides moderately rounded. Elytral glabrous fascia across apical 1/3 wide, shining. (Figs. 2, 39) Colombia.... *paraposticus*, new species.

Antennal third segment with spine at least as long as fourth segment. Pronotum 1 1/4 times as long as wide, sides rounded. Elytral glabrous fascia across apical 1/3 narrow. (Figs. 2, 42) Panama, Colombia .... *posticus* (Pascoe).

VARIATION. — Character states which in other groups could be considered as generic, such as the absence or length of antennal spines, the form and surface sculpture of the pronotum, the absence or size of basal elytral gibbosities, and the shape of the femora, are all highly variable within the genus *Euderces*.

In the case of the basal gibbosities which are often present to one degree or another, the following observations may be made: Eleven species have these gibbosities strongly developed and nearly vertical, namely *E. cleriformis*, *E. dimidiatipennis*, *E. guatemalenus*, *E. hoegei*, *E. linsleyi*, *E. magnus*, *E. pini*, *E. reticulatus*, *E. sculpticollis*, *E. spinicornis*, and *E.wappesi*. Thirteen species lack distinct basal gibbosities: *E. batesi*, *E. biplagiatus*, *E. cribripennis*, *E. laevicauda*, *E. longicollis*, *E. obliquefasciatus*, *E. parallelus*, *E. perplexus*, *E. propinquus*, *E. pulcher*, *E. pusillus*, *E. reichei*, and *E. rubellus*. The remaining species have the gibbosities distinctly present, but less well-developed, often only as moderately broad or arcuate tumidities. A similar set of four loosely formed groups appears when the antennae are examined. A small group of four apparently related species have the third and fourth segments longitudinally grooved, with a sharp spine shorter than the fourth segment at the apex of the third segment. These are *E. bicinctus*, *E. longicollis*, *E. noguerai*, and *E. pulcher*. The remaining species do not have grooved antennal segments. Seventeen of these species bear no spine at the apex of the third segment, or at most bear a small apical tooth. These are *E. andersoni*, *E. basimaculatus*, *E. batesi*, *E. biplagiatus*, *E. cribripennis*, *E. elvirae*, *E. laevicauda*, *E. obliquefasciatus*, *E. parallelus*, *E. perplexus*, *E. picipes*, *E. pini*, *E. postipallidus*, *E. propinquus*, *E. reichei*, *E. venezuelensis*, and *E. westcotti*. An equal number of species have this segment bearing a long, sometimes blunt, apical spine, 2/3 or more as long as the fourth segment: *E. boucardi*, *E. cleriformis*, *E. cribellatus*, *E. dimidiatipennis*, *E. grossistriatus*, *E. guatemalenus*, *E. hoegei*, *E. linsleyi*, *E. magnus*, *E. paraposticus*, *E. posticus*, *E. pusillus*, *E. reticulatus*, *E. spinicornis*, *E. succinus*, *E. tibialis*, and *E. yucatecus*. The remaining species have the apex of the third segment distinctly more than dentate, but with the spine less than 2/3 as long as the fourth segment. Although the hind legs of most *Euderces* have smooth, fairly abruptly clavate femora and somewhat flattened, longitudinally carinate tibiae (Fig. 12b), a few species show considerable structural variation from this norm. The most distinct of these occur in *E. disparicrus*, with gradually clavate, scabrous femora (Fig. 12e); *E. azureus*, with gradually incrassate femora and non-carinate tibiae (Fig. 12a); and *E. velutinus* and *E. tibialis*, with flattened meso- and metatibiae which are about as broad as the femoral club (Fig. 12d). In addition, the hind femora of the following species are briefly carinate on each lateral face just behind the apex: *E. batesi*, *E. biplagiatus*, *E. boucardi*, *E. cribripennis*, *E. disparicrus*, *E. noguerai*, *E. proximus*, *E. pusillus*, *E. reichei*, *E. succinus*, *E. tibialis*, *E. velutinus*, and *E. wappesi*.

Euderces acutipennis Bates
(Fig. 7)

Euderces acutipennis Bates, 1885:305; Aurivillius, 1912:419; Chemsak, 1969:313; Chemsak & Linsley, 1975:87. (TYPE LOCALITY: Panajachel, Sololá, Guatemala.)

REDESCRIPTION. — *Female*: Length 3.75 mm. Integument piceous, tarsi slightly paler; elytra with a single pair of eburneous fasciae. Head somewhat retracted into pronotum; eyes moderately prominent, lobes divided, upper lobe not visible; antennae reaching to about basal 1/3 of elytra, third segment subequal to scape and to fifth segment, about 1 1/2 times as long as fourth, segments unarmed and slightly swollen apically. Pronotum slightly longer than wide, sides broadly rounded, basal 1/6 impressed and narrowed, apex somewhat narrowed; discal surface moderately shining, finely, longitudinally striate, with pale pubescence at base, entire surface sparsely clothed with long, erect, pale hairs; prosternum without coarse punctures or pubescence; lateral and hind margins of mesepimera and metasternum densely pale pubescent. Scutellum small, apex subtruncate, surface indistinctly pale pubescent. Elytra about 2 1/2 times as long as width across humeri, sides slightly wider behind middle; apices strongly acuminate at suture; each side near base with a small, moderately distinct gibbosity; a narrow, transverse, raised, eburneous fascia present from margin to middle of disk on each side at about basal 1/3; surface of basal 1/5 shining, indistinctly punctate, median 1/4 densely cribrate-punctate on both sides of eburneous markings, remainder of elytra impunctate, alutaceous, with an indistinct, arcuate, transverse fascia of very short, fine, appressed, pale pubescence across apical 2/5; entire disk very sparsely clothed with erect hairs. Abdomen shining; terminal sternite as long as fourth, apex broadly rounded. Legs with femora moderately abruptly clavate; surface smooth, shining, partially clothed with appressed pale hairs.

Male: Unknown.

REMARKS. — As noted by Chemsak (1969), this species is somewhat anomalous in the genus due to the attenuated form of the elytral apices and the apparently retractile head. The holotype [BMNH] was the only specimen seen in this study.

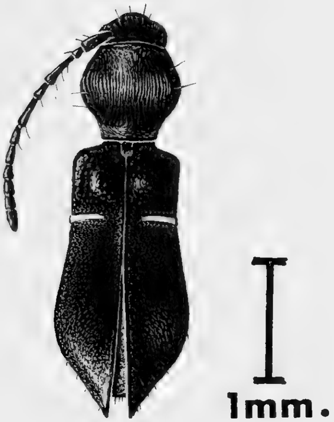

FIGURE 7. *Euderces acutipennis* Bates, Holotype female. Scale = 1 mm.

Euderces andersoni, new species
(Fig. 8)

TYPE. — Holotype female [CNMN] from MEXICO, Guerrero, 7.2 km NW El Ocotito, 853 m, July 7, 1987 (R. Anderson).

DESCRIPTION. — *Female*: Length 4.5 mm. Integument piceous, antennae and mouthparts orange-brown, legs dark reddish brown, elytra with a single pair of eburneous fasciae. Head with eyes divided, upper lobes very small; antennae reaching to about apical 1/3 of elytra, third segment nearly twice as long as scape, twice as long as fourth segment, dentate at apex, fourth segment minutely dentate at apex. Pronotum about 1 1/4 times as long as broad, sides rounded, somewhat impressed at base, less strongly narrowed at apex; disk with side margins abrupt; surface longitudinally reticulate-striolate, sparsely clothed at base with short, appressed pale pubescence; entire surface with sparse, long, erect, pale hairs; prosternum nearly smooth, with sparse, fine, pale pubescence near base; lateral margins of mesepimera and sides of hind margin of metasternum densely whitish pubescent. Scutellum small, rounded, surface very finely pubescent. Elytra slightly more than twice as long as width across humeri, sides feebly impressed before middle, slightly wider before apex; apices broadly rounded; each side near base with a fairly distinct, narrow, somewhat elevated gibbosity, apices of gibbosities asperate; a moderately wide, transverse, raised, eburneous fascia present on each side at about basal 1/3 extending from lateral margin nearly to suture; discal surface with basal 1/4 moderately coarsely punctate, somewhat shining, median 1/4 densely cribrate-punctate before and behind eburneous fasciae, apical 1/2 nearly impunctate, alutaceous, with a wide, transverse fascia of fine, appressed, pale pubescence across apical 1/4; entire disk clothed with long, erect, pale hairs. Abdomen shining, sparsely pubescent; last sternite slightly longer than fourth, apex rounded. Legs with femora moderately abruptly clavate; surface smooth, shining, sometimes with longitudinal bands of short, pale pubescence.

Male: Unknown.

REMARKS. — This species somewhat resembles a melanic form of *E. nelsoni*. In addition to

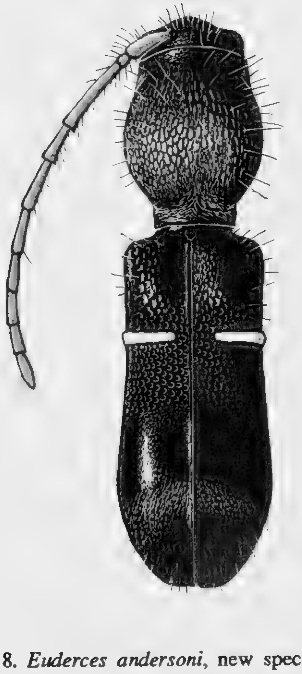

FIGURE 8. *Euderces andersoni*, new species, Holotype female.

integumental color, however, it differs from that species in having dentate antennal segments and a somewhat more strongly gibbose elytral base. It is a pleasure to name this species for Robert S. Anderson of the Canadian Museum of Nature in Ottawa.

Euderces aspericollis (Chemsak)
(Figs. 6, 9)

Eplophorus aspericollis Chemsak, 1969:311. (TYPE LOCALITY: Tuxpan, Michoacán, Mexico.)
Euderces aspericollis; Chemsak & Linsley, 1975:88.

REDESCRIPTION. — *Male*: Length 5–8 mm. Integument piceous to dark reddish brown, sometimes with pronotum and basal 1/2 of elytra reddish brown, elytra with a single pair of eburneous fasciae. Head with eyes moderately small, lobes divided, upper lobes small; antennae reaching to about apical 1/4 of elytra, third segment 2 1/2 times as long as fourth, armed at apex with a sharp spine which is about 1/2 as long as fourth segment, apex of fourth segment with a small spine. Pronotum about 1 2/5 times as long as broad, sides somewhat rounded, somewhat impressed toward base; discal surface longitudinally reticulate and moderately densely asperate, finely, moderately sparsely clothed with short, appressed, pale pubescence near base and apex; entire surface moderately sparsely clothed with long, erect, pale hairs; prosternum with posterior 3/5 bearing coarse punctures and moderately dense, subdepressed, whitish pubescence; lateral margins of mesepimera and hind margins of meso- and metasternum clothed with dense, whitish pubescence. Scutellum with apex rounded, moderately sparsely clothed with appressed, pale pubescence. Elytra slightly less than 2 1/2 times as long as width across humeri, sides slightly impressed before middle; apices truncate, hind angles not produced; each side near base moderately strongly, narrowly gibbose; a narrow, transverse, raised, eburneous fascia present on each side at about basal 2/5 from lateral margin to past middle of disk; discal surface with basal 1/3 coarsely, densely punctate, with appressed, pale pubescence surrounding basal gibbosities, extreme base and gibbosities less densely punctate with tops of gibbosities asperate-punctate, median 1/3 opaque, densely cribrate-punctate, apical 1/3 alutaceous, impunctate, with a moderately distinct, transverse fascia of appressed, pale pubescence across apical 1/4, moderately pubescent behind fascia; entire disk clothed with long, erect, pale hairs. Abdomen with first sternite indistinctly, obliquely marked at sides with whitish pubescence; terminal sternite nearly as long as fourth, apex broadly rounded. Legs with femora moderately abruptly clavate, surface smooth, shining, with longitudinal bands of short, pale pubescence.

Female: Similar to male. Length 4.5–8 mm. Antennae shorter, reaching to about middle of elytra. Prosternum lacking coarse punctures. Abdomen with terminal sternite slightly longer than fourth, apex rounded.

REMARKS. — Although most specimens are piceous to dark brown throughout, occasional

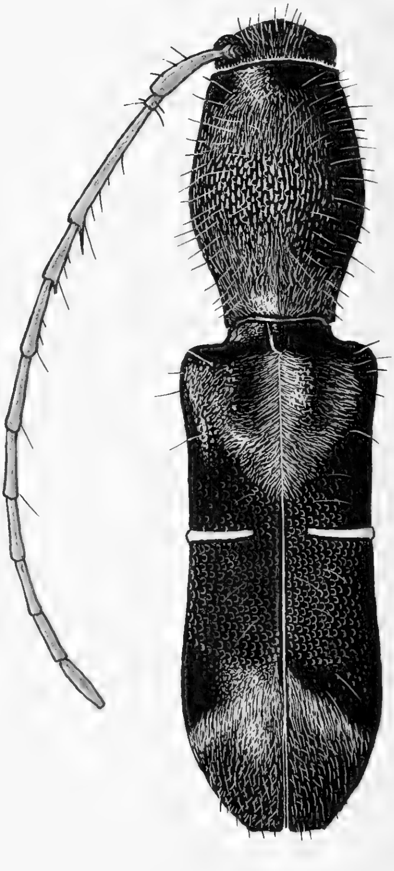

FIGURE 9. *Euderces aspericollis* (Chemsak), male.

specimens have been seen with the head, pronotum, and basal half of the elytra reddish brown, and a very few specimens all reddish brown. Flight period appears to be June to September. Although not otherwise known from outside of southwestern Mexico (see Fig. 6), a single female specimen has been seen bearing the label: "Tegucigalpa, Honduras, Aug. 11, 1919 (F. J. Dyer)," which is tentatively assigned to *aspericollis* being structurally very similar, but of a lighter reddish brown color.

Euderces auricaudus, new species
(Fig. 10)

TYPES. — Holotype male [EMEC], allotype and 127 paratypes (78 males, 49 females) from MEXICO, OAXACA, 7–8 mi. E Mitla, 6200 ft., beaten from *Quercus* sp., July 3–9, 1994 (Giesbert). 74 additional paratypes from MEXICO as follows: OAXACA: 1 female, 20.5 mi. NW Oaxaca, 5500 ft., "dry oak savannah," August 6, 1983 (R. Anderson, W. Maddison); 1 female, 11.1 km NW Diaz Ordaz, 2400 m., July 4, 1989 (Barchet); 1 female, 14 km NW Diaz Ordaz, 2600 m., June 15, 1979 (H. & A. Howden); 1 male, 1 female, N of Hwy #190, 7 km N Diaz Ordaz, July 17, 1992 (G. H. Nelson, D. S. Verity); 1 female, Hwy #190, 37 km NW Jct. with Hwy 131, July 18, 1992 (Nelson & Verity); 9 males, 5 females, Hwy #175, 14.1 km N int. Hwy. #191, 2100 m., "dry pine/oak forest," July 2, 1989 (E. Barchet); 1 male, Zempoaltepetl, 2 km S Diaz Ordaz, 2075 m., July 4, 1989 (Barchet); 1 male, 8 mi. N Telixlahuaca, 7100 ft., August 31, 1982 (O'Brien); 1 male, 1 female, 6 km E Miahuatlan, Tamazulapan, 1800 m., July 5, 1989 (Barchet); 1 female, 3 km NW Sola de Vega, 1400 m., July 7, 1989 (Barchet); 1 male, 12 km S Benito Juarez, 2100 m., July 1, 1989 (Barchet); 1 male, 6.7 km N El Punto, 2100 m., June 29, 1989 (Barchet); 13 males, 2 females, 3 mi. N El Punto, 7300 ft., July 4–7, 1994 (E. Giesbert);1 male, 10.8 km N Jct. #175/#195, 1859 m., "oak-Acacia woodland," July 19, 1987 (R. Anderson); 1 male, 19.8 km N Macuitlxochitl, 1900 m., July 1, 1989 (Barchet); 1 male, 3 females, 6–9 mi. NE Mitla, July 20, 1985 (Jones, Schaffner); 4 males, 5 females, 13–14 km E Mitla, 2100 m., August 5–11, 1986 (Howdens); 1 female, Hwy. #175, 4 km W Capulalpan, 2000 m., June 13, 1979 (Howdens); 1 male, 19 mi. NW Totolapan, July 28, 1963; 1 male, 1 female, Hwy. #131, 70 km S Oaxaca, Rio de la Y, 2150 m., June 17, 1979 (Howdens); 1 male, 3 mi. SE Matatlan (Microondas road), 6650 ft., July 17, 1987 (Kovarik, Schaffner); 1 male, 8 mi. E Nochixtlan, July 5, 1975 (Triplehorn); 1 male, 1 female, 12–13 km S Miahuatlan, August 10, 1986 (Howdens); 3 females, 2 males, El Cerezal, 36 km NE Oaxaca, 2300 m., June 12, 1979 (Howdens); 1 male, 1 female, 5 km N Oaxaca, 1700 m., June 14, 1979 (Howdens); GUERRERO: 1 male, 6.2 mi. SW Xochipala, July 13, 1985 (Jones, Schaffner); 1 female, 23.6 km W Hwy #95, Xochipala rd., July 24, 1992 (Nelson, Verity). Paratypes are deposited with CNMN, EMEC, TAMU, MAIC, HAHC, JEBC, EFGC, JEWC.

DESCRIPTION. — *Male*: Length 5–8 mm. Integument piceous, apical 1/2 of elytra deep yellowish, elytra with a single pair of eburneous fasciae (elytra rarely all piceous). Head with eyes moderately small, lobes divided, upper lobes small; antennae nearly reaching apices of elytra, third segment 2 1/2 times as long as fourth, armed at apex with a sharp spine which is about 1/2 as long as fourth segment, apex of fourth segment with a small spine, apex of fifth segment sometimes dentate. Pronotum about 1 1/3 times as

FIGURE 10. *Euderces auricaudus*, new species, male.

long as broad, sides somewhat rounded, somewhat impressed toward base; discal surface longitudinally reticulate and moderately densely asperate, finely, moderately sparsely clothed with short, appressed, golden pubescence near base and apex; entire surface moderately sparsely clothed with long, erect, pale hairs; prosternum with posterior 3/5 bearing coarse punctures and moderately dense, subdepressed, whitish pubescence; lateral margins of mesepimera and hind margins of meso- and metasternum clothed with dense, whitish pubescence. Scutellum with apex rounded, moderately densely clothed with appressed, golden pubescence. Elytra slightly less than 2 1/2 times as long as width across humeri, sides slightly impressed before middle; apices rounded to subtruncate, hind angles not produced; each side near base moderately strongly, narrowly gibbose; a narrow, transverse, raised, eburneous fascia present on each side at about basal 2/5 from lateral margin to past middle of disk; discal surface with basal 1/3 coarsely, densely punctate, with appressed, pale pubescence surrounding basal gibbosities, tops of gibbosities asperate-punctate, median 1/3 opaque, densely cribrate-punctate and finely golden pubescent, apical 1/3 alutaceous, impunctate, with a moderately distinct, transverse fascia of appressed, pale pubescence across apical 1/4, moderately densely golden pubescent behind fascia; entire disk clothed with long, erect, pale hairs. Abdomen moderately sparsely golden pubescent; terminal sternite nearly as long as fourth, apex broadly rounded. Legs with femora moderately abruptly clavate, surface smooth, shining, with longitudinal bands of short, pale pubescence.

Female: Similar to male. Length 4.5–8 mm. Antennae shorter, reaching to about apical 1/3 of elytra. Prosternum lacking coarse punctures. Abdomen with terminal sternite slightly longer than fourth, apex rounded.

REMARKS. — This species is very close to *E. aspericollis*, differing from the latter only in having the dark yellowish integument and golden pubescence of the apical 1/2 of the elytra, the slightly more robust pronotum, and the lack of an oblique pubescent marking on each side of the first abdominal sternite. A large series of specimens was beaten from dry foliage and twigs of recently fire-killed *Quercus* sp. The species name refers to the elytral color pattern: *aurum* = gold (L.) + *cauda* = tail (L.).

Euderces azureus, new species
(Figs. 11, 12a)

TYPES. — Holotype male [EMEC] and allotype from GUATEMALA, Baja Verapaz, 6–9 km E Purulhá, 5000 ft., April 15–24, 1990 (E. Giesbert). One additional male paratype from GUATEMALA, El Progreso, Sierra de las Minas, 19 km N Estancia de la Virgen, 6000 ft., April 18–20, 1990 (Giesbert) [EFGC].

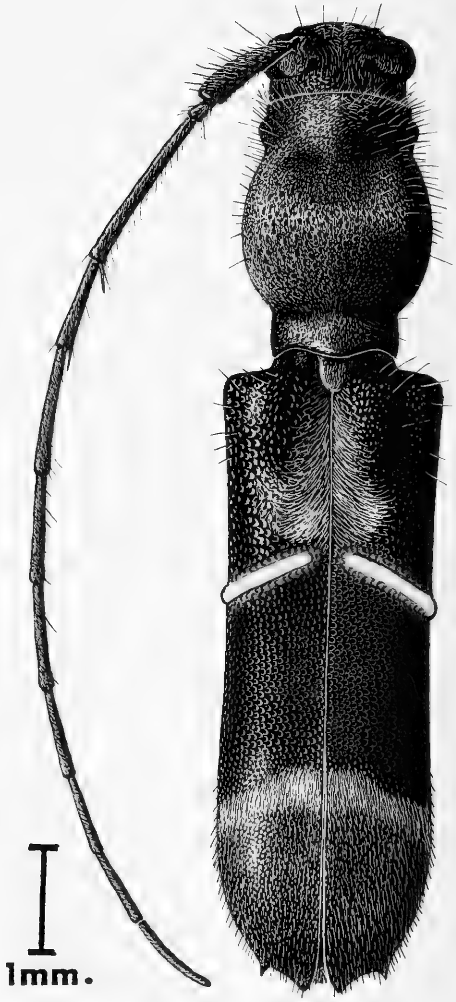

FIGURE 11. *Euderces azureus*, new species, male.

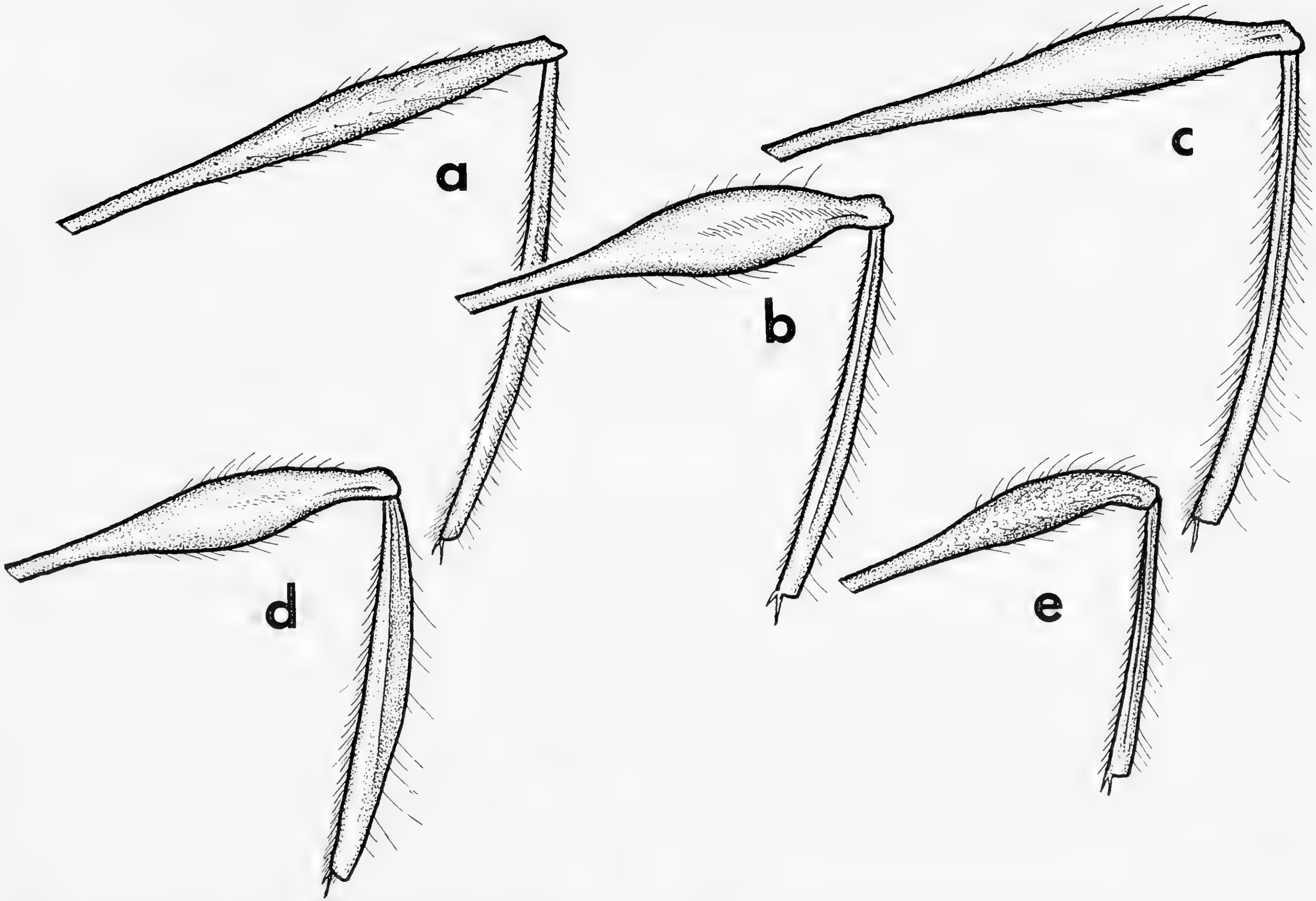

FIGURE 12. Hind femora and tibiae of (a) *Euderces azureus*; (b) *E. boucardi*; (c) *E. pulcher*; (d) *E. tibialis*; and (e) *E. disparicrus*. (Not to scale.)

DESCRIPTION. — *Male*: Length 10.5–11 mm, form moderately slender. Integument piceous with distinct dark metallic blue reflections; elytra with a single pair of eburneous fasciae. Head with eyes moderately prominent, lobes divided; antennae reaching to about elytral apices, third segment nearly twice as long as fourth, armed at apex with sharp spine which is about as long as second segment, apex of fourth segment with a somewhat shorter spine. Pronotum about 1 1/2 times as long as broad, sides sinuate, rounded at middle, basal 1/5 and apex strongly, transversely impressed; disk with middle strongly convex, surface finely, densely asperate at middle; sparsely clothed with short, pale, subdepressed pubescence laterally and at base and apex; entire surface moderately sparsely clothed with long, erect, pale hairs which are denser near apex; prosternum with posterior 1/2 bearing coarse punctures and subdepressed, pale pubescence; lateral and hind margins of mesepimera and metasternum clothed with dense, whitish pubescence. Scutellum rounded at apex, moderately sparsely clothed with short, pale pubescence. Elytra nearly three times as long as width across humeri, sides feebly impressed before middle; apices strongly oblique, subemarginate, outer angle stoutly dentate; each side near base moderately strongly gibbose; a somewhat broad, oblique, strongly raised, eburneous fascia present on each side at about basal 1/3 from lateral margin nearly to suture; discal surface with basal 1/3 shining, coarsely, densely punctate, with pale, appressed pubescence between and behind basal gibbosities, median 1/3 densely cribrate-punctate, opaque behind eburneous fasciae; apical 1/3 finely, shallowly, densely punctate, with a slightly angulate fascia of appressed whitish pubescence across apical 1/3; entire disk clothed with long, erect, pale hairs. Abdomen moderately sparsely clothed with suberect, pale pubescence; terminal sternite nearly as long as fourth, apex broadly rounded. Legs with femora incrassate, apices obtusely dentate; tibiae broadly, shallowly grooved, not carinate (see Fig. 12a).

Female: Similar to male. Length 11 mm. Antennae shorter, slightly exceeding middle of elytra. Prosternum lacking coarse punctures. Abdomen with terminal sternite slightly longer than fourth, apex feebly subtruncate.

REMARKS. — This large, handsome species may be immediately distinguished from all others by the dark metallic-blue integument, the slender, incrassate femora, and lack of tibial carinae. The name refers to the integumental color: *azur* = blue (F.).

Euderces basimaculatus, new species
(Fig. 13)

TYPES. — Holotype male [EMEC] from MEXICO, Colima, vic. El Terrero, 5100 ft., July 18, 1990 (J. Wappes). Allotype and 2 paratypes (1 male, 1 female) from MEXICO, Nayarit, Volcan Ceboruco, July 15–16, 1993 (Wappes, Morris, Huether). Additional 13 paratypes from MEXICO as follows: 1 male, holotype locality and date, 5500 ft. (E. Giesbert); 1 female, Oaxaca, near Chasumba, July 26, 1932 (H. Smith); 1 male, Michoacán, Pedregal near Tancitaro, 6000 ft., "sweeping herbs," June 23, 1941 (H. Hoogstraal); 1 male, 1 female, Oaxaca, 13–14 km E Mitla, 2100 m, August 8, 1986 (H. Howden); 1 female, Michoacán, 18.5 km E Morelia, 2220 m., "oak-pine-Acacia forest," July 28, 1988 (R. S. Anderson); 1 female, Durango, 24 mi. W La Ciudad, 7000 ft., July 21, 1964 (L. A. Kelton); 1 female, Puebla, 4.4 mi. SW Acatepec, July 9, 1977 (J. C. Schaffner); 1 female, Oaxaca, 5.5 mi. NE Huajuapan de Leon, July 14, 1974 (Clark, Murray, Ashe, Schaffner); 2 females, Guerrero, 6 km W Taxco, July 21–24, 1983 (J. Chemsak, A. & M. Michelbacher); 1 female, Guerrero, 4 mi. W Chilpancingo, 4000 ft., July 15, 1984 (J. B. Woolley); 1 female, Guerrero, 6 km NW Ixcateopan, September 20, 1989 (R. Turnbow). Paratypes are deposited with CNMN, CASC, EMEC, MAIC, JEWC, EFGC, RHTC.

DESCRIPTION. — *Male*: Length 6–6.5 mm. Integument piceous, elytra with outer side of feeble basal gibbosities usually marked with moderately large, oblique, indistinct maculae of orange-brown, which may be enlarged to occupy the entire basal gibbose area; mouthparts, antennae, femoral bases and apices, and tarsi often orange-brown, elytra with a single pair of eburneous fasciae. Head with eyes moderately small, lobes divided; antennae reaching to about elytral apex, third segment nearly twice as long as fourth, segments unarmed apically. Pronotum about 1 1/3 times as long as broad, sides moderately rounded, base impressed, apex somewhat narrowed; discal surface moderately finely reticulate, base and apex indistinctly, finely, sparsely, whitish pubescent; entire surface sparsely clothed with long, erect, pale hairs; prosternum with posterior 2/3 bearing coarse

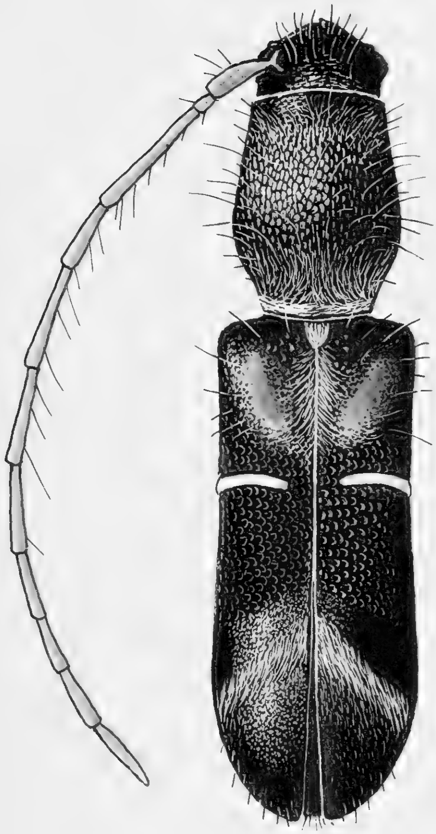

FIGURE 13. *Euderces basimaculatus*, new species, male.

punctures and moderately dense, subdepressed, whitish pubescence; hind-lateral margins of mesepimera and metasternum whitish pubescent. Scutellum with apex broadly rounded, surface densely white pubescent. Elytra about 2 1/2 times as long as width across humeri, sides subparallel, slightly wider behind middle, apices rounded; each side near base feebly gibbose; a narrow, transverse, raised, somewhat arcuate eburneous fascia present from margin to middle of disk on each side at about basal 1/3; surface of basal 1/4 somewhat shining, moderately densely punctate, asperate-punctate on gibbosities, with pale, subrecumbent pubescence surrounding basal gibbosities, premedian 1/3 of elytra densely cribrate-punctate around and mostly behind eburneous fasciae, remainder of elytra impunctate, alutaceous, with apical 1/3 covered with pale, subdepressed pubescence, the front margin of which is somewhat oblique on each side and more dense; entire disk sparsely clothed with long, erect hairs. Abdomen shining, first sternite with oblique lateral markings of whitish pubescence, remaining sternites sparsely pubescent; terminal sternite nearly as long as fourth, apex broadly rounded. Legs with femora moderately abruptly clavate, surface smooth, shining, with longitudinal bands of pale pubescence, and sparsely clothed with long, erect, pale hairs.

Female: Similar to male. Length 5.5–7.5 mm. Antennae slightly shorter, slightly exceeding middle of elytra. Prosternum lacking coarse punctures. Abdomen with terminal sternite slightly longer than fourth, apex rounded.

REMARKS. — Structurally similar to *E. postipallidus*, but differing from the latter in the color of the elytral integument and in having coarser, more distinct whitish pubescence at the pronotal base. The specific name refers to the integumental markings of the elytra: *basis* = base (L.) + *macula* = spot (L.).

Euderces batesi, new species
(Fig. 14)

TYPES. — Holotype male [EMEC], allotype and 2 paratypes (1 male, 1 female) from MEXICO, Oaxaca, N of Oaxaca City on Hwy #175, 6.7 km S La Cumbre, 1625m, July 3, 1989 (E. Barchet). Additional 41 paratypes from OAXACA, MEXICO as follows: 2 females, Mitla (A. Fenyes); 2 females, 10 mi. NE Huajuapan de León, June 27, 1965 (Burke, Meyer, Schaffner); 1 male, 2 females, 5 mi. SW Oaxaca, 4700 ft. "*Acacia* thorn scrub," August 4, 1983 (R. Anderson, W. Maddison); 1 male, 18 mi. W Totolapan, July 29, 1963 (J. Doyen); 1 female, Monte Alban, July 2, 1969 (H. Hespenheide); 1 male, 13–14 km E Mitla, 2100 m, "beating *Acacia* spp.," August 8, 1986 (H. & A. Howden); 1 female, 11 km E Mitla, 1800 m, August 3, 1986 (Howdens); 3 females, 10 mi. E Totolapan, 4000 ft., July 20, 1987 (P. Kovarik, J. Schaffner); 1 female, 3 mi. SE Matatlan, Microondas road, 6650 ft., July 17, 1987 (Kovarik, Schaffner); 1 female, 7.1 km NW Diaz Ordaz, 6400 ft., "beating Oak," July 4, 1989 (J. Beierl); 1 male, 3.5 mi. N Diaz Ordaz, 6400 ft., "reared from *Acacia* twig girdled by *Oncideres* sp.," emerged January 4, 1995 (Giesbert); 1 male, 1 female, Hwy #175 10 km NE Oaxaca, 1800 m, June 11, 1979 (Howdens); 1 male, 2 females, 1.1 mi. W El Tule, 5400 ft., July 17, 1987 (Kovarik, Schaffner); 1 female, 7 km NNW Diaz Ordaz, 2200 m, July 11, 1992 (C. L. Bellamy); 1 male, 11 km NE Oaxaca, 1800 m, "oak-acacia woodland," July 27, 1992

FIGURE 14. *Euderces batesi*, new species, male.

(R. S. Anderson); 2 males, 2 females, S of Oaxaca City, 3 km NW Sola de Vega on Rio Mahuatlan, 1400 m, July 7, 1989 (Barchet); 1 male, 1 female, S of Oaxaca City, 2.5–5 km SW Ayocuesco, 1350–1500 m, July 7, 1989 (Barchet); 3 females, 38 km SE Oaxaca, 2–3 km S Diaz Ordaz, 1600–2075 m, July 4, 1989 (Barchet); 2 males, 1 female, N of Oaxaca City, 14.1 km N intersection Hwys #175 & #191, 2100 m, "dry pine/oak forest," July 2, 1989 (Barchet); 1 female, E of Oaxaca City, Sierra de Zempoaltepetl, 19.8 km N Macuitlxochitl, 1900 m, August 1, 1989 (Barchet); 1 male, 1 female, 7–8 mi. E Mitla, 6200 ft., July 3–9, 1994 (E. Giesbert). Additional 7 paratypes from PUEBLA, MEXICO as follows: 1 female, Hwy #131, 14 mi. SE Altepexi, 3000 ft., August 31, 1982 (O'Brien); 1 male, 1 female, 5 mi. W Tepeaca, July 6, 1962 (J. M. Campbell); 1 male, 4.3 mi. SW Acatepec, July 16, 1971 (Clark, Murray, Hart, Schaffner); 1 female, 2 km S Acatepec, August 19, 1982 (Clark & Cave); 1 female, 5 km SSE Chila, 1830 m, July 7, 1992 (R. L. Westcott); 1 female, 2 km E Tecamachalco, July 4, 1974 (J. Chemsak, J. Powell); 1 male, 1 female, 5 km SSE Chila, 1830 m, July 7, 1992 (R. L. Westcott). Paratypes are deposited with EMEC, CASC, CNMN, TAMU, MAIC, JEBC, HAHC, EFGC, JEWC.

DESCRIPTION. — *Male*: Length 3.5–5.5 mm, moderately slender. Integument orange-brown (rarely all black), front and vertex, prothorax except basal portions, apical 1/3 (usually) and along each side of disk to basal 1/3 of elytra, often a small humeral spot, abdomen, and parts of legs infuscated; elytra with a single pair of eburneous markings. Head with eyes moderate-sized, lobes divided, upper lobe small; antennae short, not reaching middle of elytra, third segment slightly longer than scape, about 1 1/3 times as long as fourth, segments unarmed and feebly swollen apically. Pronotum about 1 1/3 times as long as broad, sides rounded, base narrowed and deeply compressed, apex somewhat narrowed, and slightly impressed; discal surface moderately finely striolate, asperate in median area, very sparsely clothed with short pale pubescence near base; entire surface with sparse, long, erect, pale hairs; prosternum with posterior 2/3 bearing coarse punctures and moderately sparse, short, silvery pubescence; lateral margins of mesepimera and hind margin of metasternum indistinctly pale pubescent. Scutellum with apex subtruncate, surface pale pubescent. Elytra nearly three times as long as width across moderately narrow, slightly sloping humeri; sides somewhat impressed slightly before middle, widest at apical 1/3; apices narrowly rounded; a narrow, transverse, raised, somewhat arcuate eburneous fascia present from margin to middle of disk on each side at about basal 2/5; surface with basal 3/5 densely cribrate-punctate, apical 2/5 alutaceous, with an indistinct, strongly oblique fascia of short, fine, appressed, pale pubescence across apical 1/3; entire disk sparsely clothed with long, pale, erect hairs. Abdomen shining; first sternite with fine, pale pubescence on each side, remaining sternites sparsely pubescent; terminal sternite nearly as long as fourth, apex broadly rounded. Legs with femora abruptly clavate, apical carinae short; surface smooth, shining, very sparsely clothed with long, erect, pale hairs.

Female: Similar to male. Length 4–5.75 mm. Antennae slightly shorter, not reaching middle of elytra. Prosternum lacking coarse punctures. Abdomen with terminal sternite slightly longer than fourth, apex rounded.

REMARKS. — *Euderces batesi* may be recognized by the small, slender form, moderately short striae of the pronotal disk, moderately narrow and slightly sloping elytral humeri, the single pair of usually somewhat arcuate elytral eburneous fasciae, the fine, appressed, pale pubescence on the first abdominal sternite, and usually bicolored pattern of the body integument. A very few individuals are found with all black integument, greatly resembling specimens of *E. perplexus*, but *E. batesi* may be recognized by the arcuate eburneous fasciae and the presence of fine, appressed pubescence on the first abdominal sternite. This species matches Bates' original description of *E. laevicauda* quite well and it has usually been erroneously determined as such. Examination of the type specimen of *laevicauda*, however, reveals that species to bear 2 distinct pairs of eburneous markings, a character the description failed to mention. The species name honors H. W. Bates, undoubtedly the single most important pioneer in the study of Neotropical Cerambycidae.

Euderces bellus, new species
(Fig. 15)

TYPES. — Holotype male [EMEC], allotype and 41 paratypes (20 males, 21 females) from GUATEMALA, Baja Verapaz, 19–24 km N Salamá,, 4500 ft., May 25–31, 1989 (E. Giesbert, J. Wappes). Eight additional paratypes as follows: 1 female, MEXICO, Chiapas, Chincultic, nr. El Rincon, June 14, 1969 (Bright & Campbell); 1 female, MEXICO, Chiapas, 35 km N Comitan, June 15, 1987 (Wappes); 1 female, GUATEMALA, Baja Verapaz, 16 km N Salamá on Pantín rd., 1550 m, June 1, 1991 (H. & A. Howden); 2 females, GUATEMALA, Zacapa, 12–14 km S San Lorenzo (Sierra de las Minas), 1000–2000 ft., June 3–6, 1989 (Giesbert); 2 females, HONDURAS, Francisco Morazan, El Aguacate, Tatumbla, August 13, 1988 (R. D. Cave); 1 male, HONDURAS, Francisco Morazan, Tegucigalpa, El Rincon. July 13, 1989 (Cave). Paratypes are deposited with EMEC, EFGC, JEWC, HAHC.

DESCRIPTION. — *Male*: Length 4.5–6.5 mm. Integument black, mouthparts, antennal scape and second segment, bases of antennal segments three to seven, mesosternum and mesepisterna, apex of metasternum, metacoxae, and bases of femora reddish, apical 3/5 of elytra black, scutellum and elytral gibbosities infuscated or piceous, elytra with single pair of eburneous fasciae. Head with eyes moderately small, lobes divided; antennae reaching basal 1/3 of elytra, third segment twice as long as fourth, apices of segments three to five apically armed with stout spines of decreasing length, sixth segment feebly dentate. Pronotum somewhat longer than broad, sides rounded, base and apex somewhat impressed and narrowed; disk slightly flattened, surface moderately finely, distinctly, longitudinally striate, finely asperate, base and apex indistinctly, finely, moderately sparsely pale pubescent; entire surface sparsely clothed with long, erect, pale hairs; prosternum with posterior 1/2 bearing coarse


FIGURE 15. *Euderces bellus*, new species, male.

punctures and subdepressed, pale pubescence; hind margins of meso- and metasternum clothed with pale pubescence. Scutellum with apex broadly rounded, surface moderately densely pale pubescent. Elytra nearly three times as long as width across humeri, sides feebly impressed at basal 1/2, slightly wider behind middle, apices subtruncate, slightly emarginate; each side near base with a distinct, low gibbosity near suture; a narrow, transverse or feebly oblique, raised, eburneous fascia present from margin to past middle of disk on each side at about basal 2/5; discal surface moderately shining, base moderately densely punctate, tops of basal gibbosities punctate, dull, densely cribrate-punctate anterior to eburneous fasciae, punctures reduced behind fasciae, apical 1/2 shining, nearly impunctate, finely alutaceous; fine, pale, moderately sparse pubescence present on each side of basal gibbosities, a chevron-like fascia present across apical 3/8 which extends forward on suture past middle; entire disk very sparsely clothed with long, erect hairs. Abdomen shining, first sternite clothed at sides with an oblique patch of white hairs, remaining sternites sparsely pubescent; terminal sternite nearly as long as fourth, apex broadly rounded. Legs with femora somewhat abruptly clavate; surface smooth, shining, sparsely clothed with fine, pale golden pubescence.

Female: Similar to male. Length 5–8 mm. Antennae slightly shorter, reaching to about basal 1/4 of elytra. Prosternum lacking coarse punctures. Abdomen with terminal sternite slightly longer than fourth, apex more narrowly rounded.

REMARKS. — The type series was taken on the yellow, ball-like blossoms of a low growing leguminous plant (*Acacia* sp. ?) in central Guatemala. The specific name refers to the taxon's attractive appearance: *bellus* = beautiful (L.).

Euderces bicinctus bicinctus (Linsley)
(Figs. 4, 16)

Eplophorus bicinctus Linsley, 1935:88; 1942:56; Chemsak, 1969:308. (TYPE LOCALITY: Los Mochis, Sinaloa, Mexico)
Euderces bicinctus Chemsak & Linsley, 1975:87.
Euderces balli Knull, 1935:192; Linsley, 1964:191. (TYPE LOCALITY: Baboquivari Mts., Arizona.)

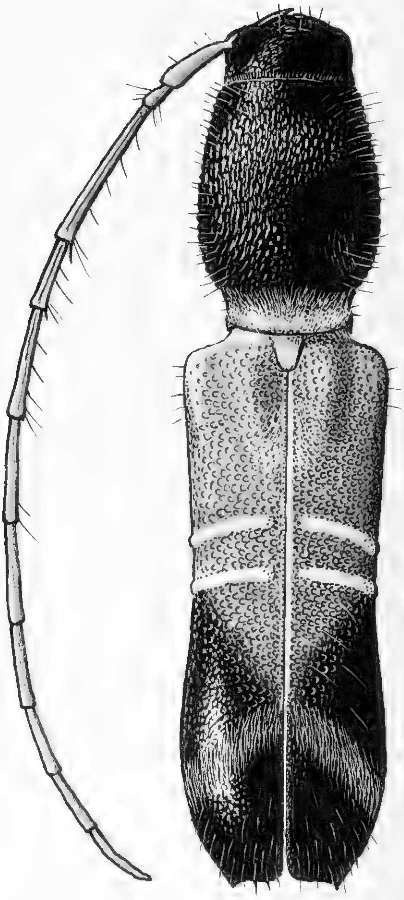

FIGURE 16. *Euderces bicinctus bicinctus* (Linsley), male.

REDESCRIPTION. — *Male*: Length 5–7.5 mm. Integument piceous, marked with reddish orange as follows: mouthparts and genae, base of prothorax, meso- and metasternum, scutellum, elytral humeri with variable marking down suture, often with basal half or more orange, legs and antennae; elytra with two pairs of eburneous fasciae. Head with eyes rather small, lobes divided; antennae reaching apex of elytra, third and fourth segments longitudinally grooved, third segment nearly twice as long as fourth, armed at apex with a sharp spine which is about 1/4 as long as fourth segment, apex of fourth segment with a small spine, apex of fifth segment with a small spicule. Pronotum with sides rounded, base narrowed and somewhat impressed; disk with surface longitudinally striate and rugulose, white pubescent fascia present across base; entire surface clothed with long, erect, pale hairs; prosternum with posterior 3/5 bearing coarse punctures and moderately dense, erect, white pubescence; hind margins of mesepimera and metasternum clothed with dense, white pubescence. Scutellum subtriangular, clothed with appressed white pubescence. Elytra about 2 1/2 times as long as width across humeri, sides slightly impressed at middle, apices truncate and bidentate; each side near base feebly gibbose; a pair of subequal and subparallel, narrow, transverse, raised, eburneous fasciae present on each side slightly before middle; discal surface with basal 2/3 densely cribrate-punctate, with an indistinct patch of subrecumbent whitish hairs behind basal gibbosities, apical 1/3 impunctate, alutaceous, with an inverted chevron of appressed whitish pubescence at apical 1/4; entire disk sparsely clothed with long, erect, pale hairs. Abdomen with first sternite densely pubescent, remaining sternites very sparsely, finely pale pubescent; terminal sternite about as long as fourth, apex very broadly rounded. Legs with femora moderately abruptly clavate; surface smooth, shining.

Female: Similar to male. Length 5–7 mm. Antennae slightly shorter. Prosternum lacking coarse punctures, pubescence less dense, subdepressed. Abdomen with terminal sternite slightly longer than fourth, apex somewhat more narrowly rounded.

REMARKS. — The orange markings of the prothorax, elytra, and underside are quite variable, but always present to some degree. The grooves on the basal antennal segments are variable and most distinct on larger male specimens. A few individuals have been seen in which the paler portions of the integument are dark reddish rather than orange. The known flight period is July to September; the range is southern Arizona and northwestern Mexico (see Fig. 4).

Euderces bicinctus peninsularis (Linsley), revalidated
(Fig. 4)

Eplophorus bicinctus peninsularis Linsley, 1942:56; Hovore, 1988:15. (TYPE LOCALITY: San Domingo, Baja California.

DIAGNOSIS. — Differs from *E. bicinctus bicinctus* (Linsley) by the black integumental color, with only a very small area immediately surrounding each elytral eburneous fascia brownish orange. The femoral apices, tibiae, tarsi, and antennae are brownish orange. Average size slightly smaller: 4.5–7 mm.

REMARKS. — Examination of a large number of specimens reveals little variation in the characteristic integumental color which distinguishes this population. Flight period: July to September in Baja California del Sur (see Fig. 4).

Euderces biplagiatus, new species
(Fig. 17)

TYPES. — Holotype male [EMEC], allotype and 2 female paratypes from MEXICO, Oaxaca, 5.7 mi. SE Quiotepec, 2100 ft., July 21, 1987 (Kovarik, Schaffner).Three additional paratypes from MEXICO as follows: 1 female, Oaxaca, Gen. Juan de los Cues, June 14, 1984 (H. Garcia); 1 male, Puebla, 6 mi. SW Tehuacan, July 8, 1981 (Bogar, Schaffner, Friedlander); 1 male, Puebla, 6 mi. N Tehuacan, August 22, 1987 (J. Doyen). Paratypes are deposited with EMEC, TAMU.

FIGURE 17. *Euderces biplagiatus*, new species, male.

DESCRIPTION. — *Male*: Length 3.75–5 mm, moderately slender. Integument blackish, with elytral base, suture, and apex dull yellow-orange, apex usually somewhat paler yellowish, leaving a large, median, oblong blackish plaga on each side of disk, humeri lightly infuscated; mesosternum, sometimes metasternum and sides of prosternum, mouthparts and tarsi orange; elytra with a single pair of eburneous markings. Head with eyes moderate-sized, lobes divided, upper lobe small; antennae moderately short, reaching to about middle of elytra, third segment slightly longer than scape, about 1 1/2 times as long as fourth, segments unarmed and feebly swollen apically. Pronotum slightly longer than broad, sides rounded, base narrowed and deeply impressed, apex somewhat narrowed, and slightly impressed; discal surface moderately finely striolate, finely asperate in median area, clothed with short, appressed pale pubescence near base; entire surface with sparse, long, erect, pale hairs; prosternum with posterior 2/3 bearing coarse punctures and moderately sparse, short, erect pubescence; lateral margins of mesepimera and hind margin of metasternum clothed with fine, silvery pubescence. Scutellum with apex subtruncate, surface pale pubescent. Elytra about 2 2/3 times as long as width across slightly sloping humeri; sides feebly impressed near middle, widest at apical 1/3; apices narrowly rounded; a narrow, transverse, raised, transverse, eburneous fascia present from margin to near suture on each side at about basal 1/3; surface with basal 2/3 densely cribrate-punctate, apical 1/3 alutaceous, clothed with short, fine, subdepressed, pale golden pubescence; entire disk sparsely clothed with long, pale, erect hairs. Abdomen shining; first sternite moderately sparsely clothed with fine, pale pubescence on each side at base, remaining sternites very sparsely pubescent; terminal sternite nearly as long as fourth, apex broadly rounded. Legs with femora abruptly clavate, with short apical carinae; surface smooth, shining, very sparsely clothed with long, erect, pale hairs.

Female: Similar to male. Length 4–5 mm. Antennae slightly shorter, not reaching middle of elytra. Prosternum lacking coarse punctures. Abdomen with terminal sternite slightly longer than fourth, apex more narrowly rounded.

REMARKS. — This species is close to *E. batesi*, but may be distinguished by the pale yellowish elytral apices and suture, the longer, more transverse eburneous markings and slightly stouter form. The species name refers to the elytral pattern: *bi* = two (L.) + *plaga* = a large, longitudinal spot (L.)

Euderces boucardi (Chevrolat)
(Figs. 2, 12b, 18)

Apilocera boucardi Chevrolat, 1862:535; Bates, 1880:60. (TYPE LOCALITY: Coban, Vera Paz, Guatemala.)
Apelocera Boucardi Aurivillius, 1912:420.
Eplophorus boucardi Blackwelder, 1946:583; Chemsak, 1969:308; Chemsak, Linsley & Mankins, 1980:32.
Euderces boucardi Chemsak & Linsley, 1975:87.

REDESCRIPTION. — *Male*: Length 7.5–10 mm. Integument blackish, legs and antennae brown, elytra with a single pair of eburneous fasciae. Head with eyes moderately small, lobes divided; antennae reaching apical 1/8 of elytra, third segment about twice as long as fourth, armed at apex with a long, feebly sinuate spine nearly as long as fourth segment, apex of fourth segment with a small, sharp spine. Pronotum about 1 1/3 times as long as wide, sides moderately rounded, somewhat impressed at base and apex; disk with surface dull, longitudinally rugulose or striate except near apex, clothed with depressed golden pubescence which is interrupted at middle by an indistinct, transverse, somewhat arcuate, glabrous fascia; entire surface sparsely clothed with long, erect, golden hairs; prosternum with posterior 3/5 bearing coarse punctures and moderately dense, subdepressed, white pubescence; lateral and hind margins of mesepimera and metasternum with wide bands of dense, white pubescence. Scutellum small, parallel-sided, apex broadly rounded, moderately sparsely pubescent. Elytra about 2 1/2 times as long as width across humeri, sides very slightly impressed at middle; apices truncate, feebly emarginate, outer angle dentate; each side near base somewhat gibbose near suture, gibbosity developed into a low, obtuse tubercle on each side of scutellum; a narrow, transverse, raised, eburneous fascia present on each side at basal 1/3; surface shining, basal 1/3 very sparsely punctate, glabrous except for distinct posthumeral patch of golden pubescence covering basal gibbosities, median 1/3 densely cribrate-punctate and pubescent across middle behind

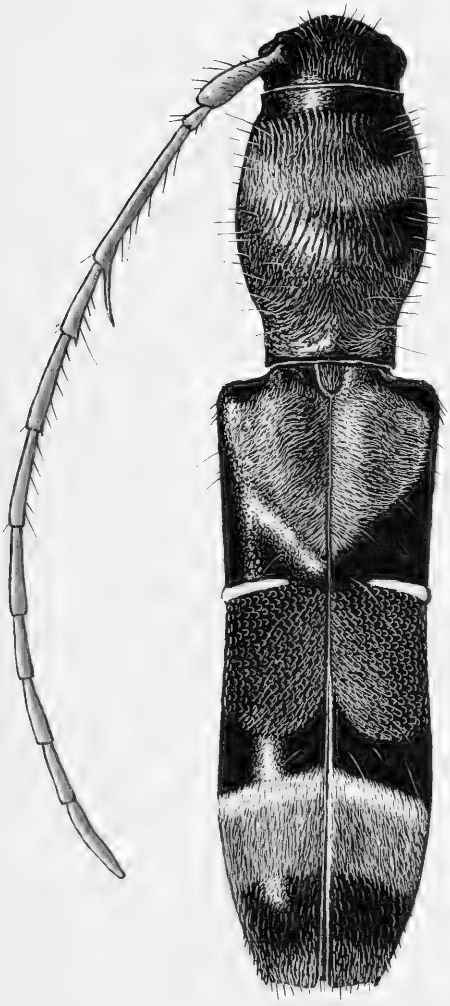

FIGURE 18. *Euderces boucardi* (Chevrolat), male.

eburneous fasciae, apical 1/3 nearly impunctate, with a well-defined, broad, arcuate fascia of golden pubescence across apical 1/3, front margin of pubescent fascia whitish, area behind fascia bearing scattered, short, erect, golden hairs; entire disk sparsely clothed with long, erect, golden hairs. Abdomen shining, first sternite clothed with white pubescence at sides, remaining sternites sparsely pubescent; terminal sternite nearly as long as fourth, apex broadly rounded. Legs with femora moderately abruptly clavate, indistinctly carinate at apices; surface smooth, shining, with longitudinal bands of short, pale pubescence.

Female: Similar to male. Length 7.5–10 mm. Antennae shorter, slightly exceeding middle of elytra. Prosternum lacking coarse punctures. Abdomen with terminal sternite slightly longer than fourth, apex rounded.

REMARKS. — This is one of the more commonly collected Central American *Euderces*, found from southern Mexico to Costa Rica (see Fig. 2), with a flight period from May to August.

Euderces brailovskyi, new species
(Fig. 19)

TYPES. — Holotype male [UNAM] from MEXICO, Hidalgo, km 30, Carr. Tasquillo-Huichapan, June 4, 1983 (H. Brailovsky). Allotype female and 2 male paratypes from MEXICO, San Luis Potosi, 4 km W Guadalcazar, July 18, 1988 (R. Turnbow) [RHTC].

DESCRIPTION. — *Male*: Length 5–8.25 mm. Integument blackish throughout or sometimes with the basal 1/4 of the elytra (infuscated on humeri and basal gibbosities), mesosternum, and apical portion of metasternum reddish, sometimes with apical 3/8 of elytra dull yellowish; elytra with a single pair of eburneous fasciae. Head with eyes rather small, lobes divided, upper lobes small; antennae slightly longer than elytra, third segment a little more than 1 1/2 times as long as fourth, armed at apex with a small, sharp spine, apex of fourth segment minutely spinose. Pronotum with sides moderately rounded, narrowed and impressed at base and apex, base narrower than apex; discal surface finely, longitudinally striate and rugulose, moderately clothed with appressed, pale golden pubescence which is densest at base, entire surface clothed with long, erect, pale hairs; prosternum with posterior 2/3 bearing coarse punctures and moderately dense, subdepressed, white pubescence; lateral and hind margins of mesosternum, and hind margin of metasternum with dense, whitish pubescence. Scutellum rounded, clothed with appressed golden pubescence. Elytra slightly more than twice as long as width across humeri, sides slightly impressed before middle; apices subtruncate; each side near base moderately gibbose; a narrow, raised, transverse eburneous fascia present on each side at basal 1/4 from lateral margin to beyond middle of disk; discal

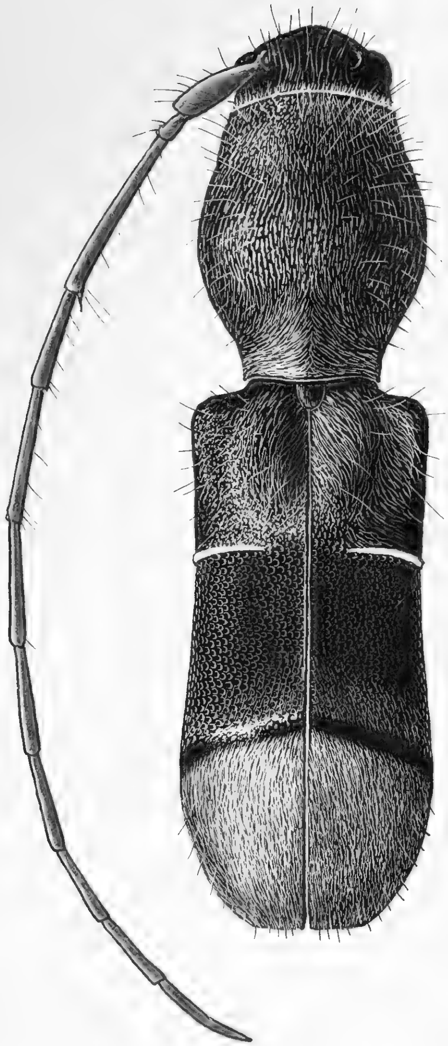

FIGURE 19. *Euderces brailovskyi*, new species, male.

surface with basal 1/4 coarsely, irregularly punctate, moderately sparsely clothed with moderately long, subdepressed, pale pubescence, median 3/8 densely cribrate-punctate, indistinctly clothed with subdepressed golden pubescence, apical 3/8 impunctate, densely clothed behind a narrow, slightly oblique, shining, glabrous line with appressed, pale to golden yellow pubescence; entire disk sparsely clothed with long, erect, pale hairs. Abdomen shining, sparsely pubescent; terminal sternite nearly as long as fourth, apex broadly rounded. Legs with femora moderately abruptly clavate; surface smooth, shining, with longitudinal bands of pale pubescence.

Female: Similar to male. Length 6.5 mm. Antennae slightly shorter, reaching apical 1/3 of elytra. Prosternum lacking coarse punctures. Abdomen with terminal sternite slightly longer than fourth, apex rounded.

REMARKS. — This species may be distinguished from all others by the narrow glabrous fascia immediately anterior to the apical pubescent patch of the elytra, as well as by the length of the pale hairs which make up the pubescence on the basal 1/4 of the elytra, and by the long male antennae. The holotype appears to be a particularly large and varicolored individual, with the basal 1/3 reddish and the apical 3/8 dark yellow. Integumental color is somewhat variable: two of the three specimens from San Luis Potosi are piceous, lacking reddish or yellowish areas, and one male has the basal 1/3 of the elytra reddish. It is a pleasure to name this species for Dr. Harry Brailovsky of UNAM, Mexico City, who collected the holotype and who has been a great help to the authors' work in Mexico.

Euderces cleriformis (Bates)
(Figs. 2, 20)

Apilocera cleriformis Bates, 1885:306; Chemsak, 1967:74 (lectotype). (TYPE LOCALITY: Bugaba, Panama)

Eplophorus cleriformis Blackwelder, 1946:583; Chemsak, 1967:74.

Euderces cleriformis Chemsak & Linsley, 1975:88.

Apilocera breviformis Bates, 1892:165. (TYPE LOCALITY: Teapa, Tabasco, Mexico)

Apelocera breviformis Aurivillius, 1912:420.

Eplophorus auricomis Chemsak, 1969:309. (TYPE LOCALITY: Turrialba, Costa Rica.) **NEW SYNONYMY**

REDESCRIPTION. — *Male*: Length 5–7 mm. Integument piceous, usually marked with dull orange as follows: mouthparts, an area on each side of the elytral disk just behind humerus, which is bordered on the inner side by the elytral gibbosity, and at the rear by the eburneous fascia, mesosternum, legs and antennae, elytra with a single pair of eburneous fasciae. Head with eyes moderately small, lobes divided; antennae reaching slightly beyond middle of elytra, third seg-

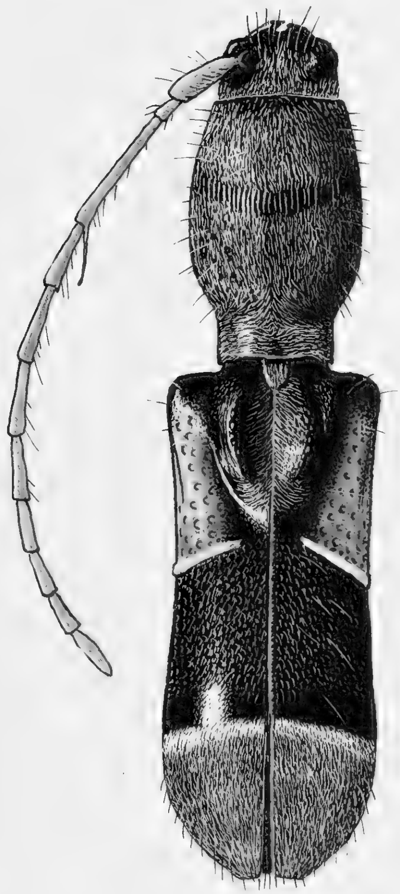

FIGURE 20. *Euderces cleriformis* (Bates), male.

ment nearly three times as long as fourth, apically armed with a long, feebly sinuate, blunt spine which is nearly as long as fourth segment, apex of fourth segment usually feebly dentate. Pronotum with sides rounded; basal 1/6 compressed and narrowed; disk with surface dull, longitudinally rugulose or striate, finely pale pubescent, pubescence interrupted slightly before middle by a moderately narrow, transverse, somewhat arcuate, finely longitudinally striate fascia; entire surface sparsely clothed with long, erect, pale hairs; prosternum with posterior 3/5 bearing coarse punctures and moderately dense white pubescence; hind margins of mesepimera and metasternum with wide markings of dense, silvery-white pubescence. Scutellum parallel-sided, apex broadly rounded, moderately clothed with pale, appressed pubescence. Elytra more than twice as long as width across humeri; sides slightly impressed at basal 1/2; apices narrowly and feebly subtruncate; each side near base with a highly elevated, arcuate gibbosity near suture, apices of gibbosities asperate-punctate; a narrow, transverse to slightly oblique, raised, eburneous fascia present on each side slightly before middle; surface shining, with a densely cribrate-punctate and finely pubescent area across middle behind eburneous fasciae, basal 2/5 sparsely, somewhat more coarsely punctate, with appressed pale pubescence on area inside basal gibbosities, apical 1/3 impunctate, with a well-defined pale pubescent patch covering apical 1/4; entire disk moderately sparsely clothed with long, erect, golden hairs. Abdomen with first sternite glabrous except at sides, remaining sternites moderately sparsely pale pubescent; terminal sternite about as long as fourth, apex broadly rounded. Legs with femora moderately abruptly clavate; surface smooth, shining, with longitudinal bands of short, pale pubescence.

Female: Similar to male. Length 5–7 mm. Antennae slightly shorter. Prosternum lacking coarse punctures. Abdomen with apex of terminal sternite somewhat more narrowly rounded.

REMARKS. — This species ranges from southern Mexico to Pamama (see Fig. 2). The apex of the fourth antennal segment is not distinctly dentate in the Costa Rican specimens seen, and this armature is also very feeble in specimens from the Panamanian population. The flight period extends from May to December. No significant differences were seen to support separating *E. auricomis*.

Euderces cribellatus (Bates)
(Fig. 21)

Apilocera cribellata Bates, 1885:306; Chemsak, 1967:74 (lectotype). (TYPE LOCALITY: Volcan de Chiriqui, Panama.)
Apelocera cribellata Aurivillius, 1912:420.
Eplophorus cribellatus Blackwelder, 1946:583; Chemsak, 1967:78.
Euderces cribellatus Chemsak & Linsley, 1975:87.

MATERIAL EXAMINED. — Lectotype female [BMNH], PANAMA, Volcan de Chiriqui; 1 male, 1 female, COSTA RICA, Guanacaste prov., 3 km SE Rio Naranjo, March 3–8, 1992 (F. D. Parker); 1 male,

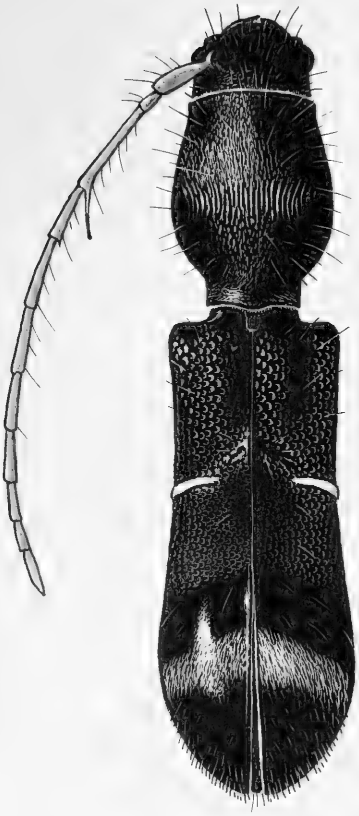

FIGURE 21. *Euderces cribellatus* (Bates), female.

COSTA RICA, Puntarenas, San Vito, Las Alturas, 1500 m., January, 1992 (Hanson & Godoy); 1 female, COSTA RICA, Guanacaste prov., Est. Maritza, 600 m lado Vol. Orosí, Malaise trap, 1989 [INBC]; 1 male, same locality, 1991 [INBC]; 1 male, 1 female, COSTA RICA, Puntarenas prov., vic. Las Alturas, January 23–24, 1996 (F. T. Hovore)[FTHC].

REDESCRIPTION. — *Male*: Length 4.5–6 mm, form slender. Integument blackish brown, mouthparts, vague area near elytral suture at basal 1/4, femoral bases, and sometimes antennae, tibial apices and tarsi dark orange-brown; elytra with a single pair of eburneous fasciae. Head with eyes moderately small, lobes divided; antennae reaching about to apical 1/3 of elytra, third segment slightly more than 1 1/2 times as long as fourth, armed at apex with a long, slender, blunted spine which is nearly as long as fourth segment, apex of fourth segment dentate. Pronotum about 1 1/2 times as long as wide, sides moderately rounded, narrowed and compressed across basal 1/8, slightly narrowed to apex; disk with surface shining, longitudinally striate and rugulose across middle, moderately sparsely clothed with fine, appressed golden pubescence across basal impression and on apical 1/3; entire surface sparsely clothed with long, erect, golden hairs; prosternum with posterior 3/5 bearing coarse punctures and subdepressed, pale pubescence; lateral and hind margins of mesepimera, metasternum, and metacoxae clothed with dense, whitish pubescence. Scutellum with apex broadly rounded, surface moderately clothed with fine, golden pubescence. Elytra slightly less than 2 1/2 times as long as width across humeri, sides very slightly impressed before middle, widest before rounded apices; each side behind base moderately gibbose near suture; a narrow, transverse, slightly oblique, raised, eburneous fascia present on each side at basal 2/5 from margin to about middle of disk; surface shining, basal 1/4 nearly glabrous, coarsely, densely punctate except for a moderately distinct impressed, oblique, nearly impunctate fascia near suture between basal gibbosities and eburneous fasciae (indistinct on some specimens), premedian 1/4 dull, densely cribrate-punctate, apical 1/2 shining, impunctate, with a moderately well-defined fascia of pale pubescence across apical 1/3, sometimes limited to a sutural spot, area behind fascia sparsely pubescent; entire disk sparsely clothed with long, erect, golden hairs. Abdomen shining, sparsely pubescent; terminal sternite nearly as long as fourth, apex broadly rounded. Legs with femora moderately abruptly clavate, surface smooth, shining, with indistinct, preapical patches of short, pale pubescence on each face.

Female: Similar to male. Length 7 mm. Antennae slightly shorter, barely reaching middle of elytra. Prosternum lacking coarse punctures. Abdomen with terminal sternite slightly longer than fourth, apex rounded.

REMARKS. — This rarely collected species from Costa Rica and Panama may be distinguished from all others by the combination of the blackish brown, slender form with a long spine on the third antennal segment, transmedially striate pronotal sculpture, and small, depressed, often impunctate and sometimes indistinct area near the suture at the basal 1/4 of elytra behind the moderately distinct postbasal gibbosities.

The lectotype and the Puntarenas specimen have the posterior pubescent elytral fascia reduced to a distinct, rounded sutural spot, while the Guanacaste specimens (figured) have this fascia complete and transverse. The lectotype also differs slightly in coloration, with the antennae and tarsi piceous. The flight period appears to be limited to the dryer months from January to March.

Euderces cribripennis Bates
(Figs. 3, 22)

Euderces cribripennis Bates, 1892:165; Aurivillius, 1912:419; Linsley, 1935:89; Chemsak, 1969:317; Chemsak & Linsley, 1975:87. (TYPE LOCALITY: Chilpancingo, Guerrero, Mexico)

Euderces fenyesi Linsley, 1957:37; Chemsak & Linsley, 1975:87. (TYPE LOCALITY: Cuernavaca, Mexico.) **NEW SYNONYMY**

REDESCRIPTION. — *Male*: Length 3.5–4.5 mm. Integument blackish (or sometimes with head, prothorax, and basal 1/3 of elytra reddish), femora dark brown, mouthparts, antennae, apices of tibiae, and tarsi orange-brown, elytra with a single pair of eburneous markings. Head with eyes small, moderately prominent, lobes divided, upper lobe small; antennae slightly exceeding middle of elytra, scape moderately robust, third segment slightly longer than scape, about 1 1/3 times as long as fourth, segments unarmed or feebly dentate and slightly swollen apically. Pronotum 1 1/3 times as long as broad, sides rounded, base narrow and deeply compressed, apex slightly narrowed; discal surface moderately finely striolate, finely asperate medially at basal 1/2, very sparsely clothed with long, erect, pale hairs; prosternum with posterior 1/2 bearing coarse punctures and pale pubescence; lateral portions of mesepimera and hind portion of metasternum indistinctly pale pubescent. Scutellum with apex subtruncate, surface finely pale pubescent. Elytra slightly more than 2 1/2 times as long as width across somewhat narrowed and sloping humeri; sides subparallel, slightly wider behind middle; apices rounded; base without distinct gibbosities; a narrow, transverse, raised, eburneous fascia present from margin nearly to suture on each side at about basal 1/3; surface of disk with basal 3/5 densely cribrate-punctate, apical 2/5 impunctate, alutaceous, sometimes with a very indistinct fascia of short, fine, appressed, pale pubescence across apical 1/3; entire disk sparsely clothed with long, erect hairs. Abdomen shining, very sparsely pubescent; terminal sternite nearly as long as fourth, apex broadly rounded. Legs with femora moderately abruptly clavate, usually with feeble apical carinae; surface smooth, shining, very sparsely clothed with long, erect, pale hairs.

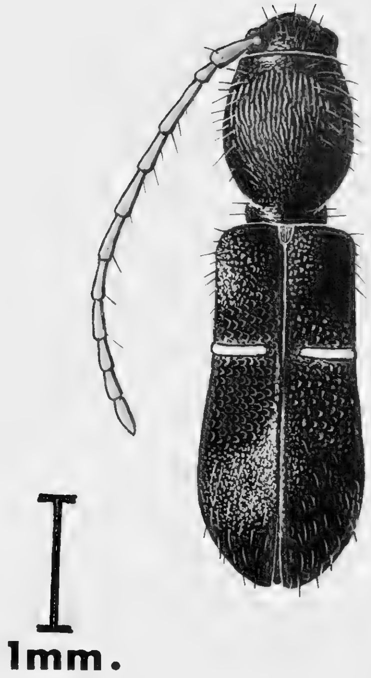

FIGURE 22. *Euderces cribripennis* Bates, male.

Female: Similar to male. Length 3.5–5 mm. Antennae shorter, reaching to about basal 1/3 of elytra. Prosternum lacking coarse punctures. Abdomen with terminal sternite slightly longer than fourth, apex rounded.

REMARKS. — A phenotype with partially reddish integument occurs sympatrically with the typical blackish form in the areas of Chilpancingo, Guerrero, and Cuernavaca, Morelos. Populations east of these points are primarily this bicolored form, but no structural differences are apparent. The flight period is from June to September. The range of *E. cribripennis* is in mainland southwestern Mexico (see Fig. 3). A single male specimen in rather bad condition but probably belonging to this species, was taken in a Malaise trap at Volcan Cacao, Guanacaste, Costa Rica [INBC]. Specimens appearing to belong to this species have been collected in Baja California, however on closer examination these proved to be individuals of *E. parallelus* with the anterior pair of eburneus markings missing. The present species may be distinguished by the more robust antennal scape, and more widely separated inner ends of the remaining eburneous fasciae.

Examination of the type of *E. fenyesi* Linsley [CASC] showed it to be synonymous with the present species.

Euderces dilutus Martins
(Fig. 23)

Euderces dilutus Martins, 1975:18. (TYPE LOCALITY: Santa Cruz, Bolivia.)

MATERIAL EXAMINED. — 1 female, Huachi, Rio Beni, Bolivia, September (W. M. Mann), "Mulford Bio Expl 1921–22" [NMNH].

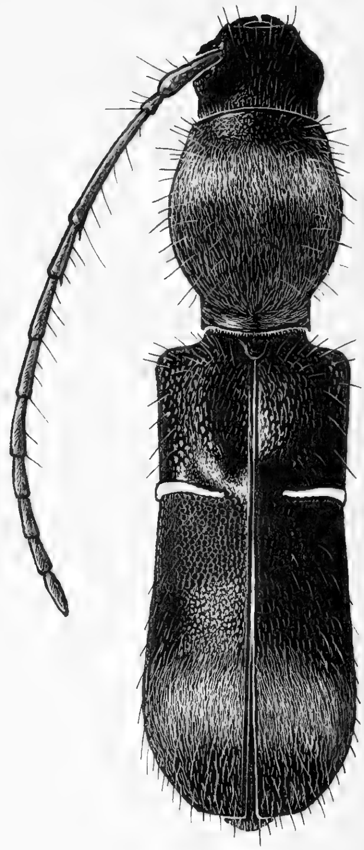

FIGURE 23. *Euderces dilutus* Martins, female.

REDESCRIPTION. — *Female*: Length 6–6.5 mm. Integument dark reddish brown to blackish, genae, front of head, antennae, and femora reddish brown; elytra with a single pair of eburneous fasciae. Head with eyes moderately small, lobes divided, upper lobes small; antennae reaching past middle of elytra, third segment more than 2 1/2 times as long as fourth, armed at apex with a short, sharp spine, apex of fourth segment with a short spine, apex of 5th segment minutely dentate. Pronotum about 1 1/4 times as long as broad, sides moderately rounded, somewhat impressed toward base; discal surface very finely, moderately densely asperate, with fine, short, irregular striations, moderately densely clothed with appressed, golden pubescence which does not obscure the surface; entire pronotum sparsely clothed with long, erect, pale hairs; prosternum shining, indistinctly rugose; lateral margins of mesepimera and hind margin of metasternum clothed with dense, whitish pubescence. Scutellum with apex rounded, surface shining, indistinctly pubescenct. Elytra about 2 1/2 times as long as width across humeri, sides slightly impressed before middle; apices subtruncate; each side near base moderately gibbose close to suture; a transverse, raised, eburneous fascia present on each side at about basal 1/3 from lateral margin to just past middle of disk, somewhat narrowed toward suture; discal surface with basal 1/3 moderately densely punctate, tops of gibbosities asperate-punctate, a shining, impunctate area present near suture immediately behind gibbosities, median 1/3 behind eburneous fasciae moderately densely cribrate-punctate with fine, sparse, golden pubescence, apical 1/3 moderately coarsely alutaceous, with a wide, moderately distinct, transverse fascia of appressed, pale golden pubescence across apical 1/4; entire disk clothed with long, erect, pale hairs which are densest near apices. Abdomen sparsely golden pubescent; terminal sternite about as long as fourth, apex rounded. Legs with femora moderately abruptly clavate, surface smooth, shining, with longitudinal bands of short, pale pubescence.

Male: Unknown.

REMARKS. — The single female specimen seen in this study, apparently assignable to this species, was not compared with the type. The above description and accompanying illustration are based on this specimen. Martins described the elytral apices of the type specimen as being suturally dentate, while the apices of the present specimen are subtruncate and unarmed. This species from the western Amazonian Llanos region of Bolivia has the most southern distribution known in the genus, but is structurally similar to the Mexican *E. aspericollis*, differing primarily by the more pubescent, less asperate pronotal surface, the lack of lateral pubescent markings on the first abdominal sternite, and the smooth area behind the elytral gibbosities. Flight occurs from September to November.

Euderces dimidiatipennis (Melzer)
(Figs. 2, 24)

Apelocera dimidiatipennis Melzer, 1932:216. (TYPE LOCALITY: San Jos, Costa Rica.)
Eplophorus dimidiatipennis Blackwelder, 1946:583.
Euderces dimidiatipennis Chemsak & Linsley, 1975:87.

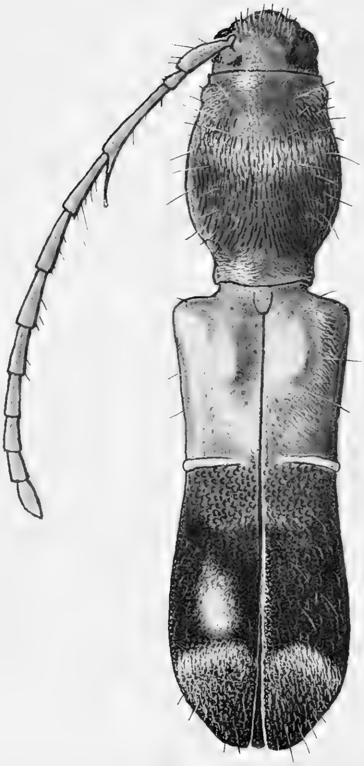

FIGURE 24. *Euderces dimidiatipennis* (Melzer), male.

REDESCRIPTION. — *Male*: Length 5–8 mm. Integument reddish or orange-brown, abdomen, often apical 1/2 of elytra, and prothorax rarely, blackish, or often entirely blackish with legs and antennae dark brown, elytra with a single pair of eburneous fasciae. Head with eyes moderately small, lobes divided; antennae reaching beyond middle of elytra, segments 3–11 feebly widened and flattened, third segment about 1 1/2 times as long as fourth, apically armed with a long, feebly sinuate, blunt spine which is about 4/5 as long as fourth segment, apex of fourth segment dentate. Pronotum with sides moderately rounded; base compressed and narrowed; apex somewhat narrowed; disk with surface indistinctly, shallowly, longitudinally rugulose or striate, finely pale pubescent, basal 1/2 minutely asperate; entire surface sparsely clothed with long, erect, pale hairs; prosternum with posterior 1/2 bearing coarse punctures and moderately dense, subdepressed, white pubescence; hind-lateral margins of mesepimera and metasternum clothed with dense, silvery-white pubescence. Scutellum with apex broadly rounded, surface glabrous. Elytra slightly more than 2 1/2 times as long as width across humeri, sides widely, shallowly impressed at basal 1/2, rounded and widest behind middle; apices somewhat narrowly rounded; each side near base with an elevated, arcuate gibbosity close to suture, apices of gibbosities asperate-punctate, surface somewhat depressed behind gibbosities; a narrow, transverse, raised, eburneous fascia present from margin nearly to suture on each side at basal 2/5; surface shining, indistinctly punctate anterior to eburneous fasciae, with pale golden, recumbent pubescence surrounding basal gibbosities, middle 1/5 of elytra behind eburneous fasciae with a moderately wide, transverse, densely cribrate-punctate and finely pubescent area, apical 2/5 impunctate, with a patch of moderately sparse golden pubescence on apical 1/4, the anterior portion being somewhat denser, and the anterior margin curved on each side and partially composed of whitish pubescence; entire disk sparsely clothed with long, erect hairs. Abdomen shining; sternites sparsely pale pubescent laterally; terminal sternite nearly as long as fourth, apex broadly rounded. Legs with femora moderately abruptly clavate; surface smooth, shining, sparsely clothed with fine, pale golden pubescence.

Female: Similar to male. Length 5–8 mm. Antennae slightly shorter, not reaching middle of elytra, segments 3–11 not noticeably widened. Prosternum lacking coarse punctures. Abdomen with terminal sternite slightly longer than fourth, apex rounded.

REMARKS. — Examination of the type [NMNH] shows that specimen to be an uncommon color variety, with the prothorax blackish and the basal 1/2 of the elytra reddish orange. Integumental color is quite variable in the large number of specimens examined. The flight period appears to be from December to February, from Nicaragua to the Cordillera Central of Costa Rica (see Fig. 2).

Euderces disparicrus, new species
(Figs. 12e, 25)

TYPES. — Holotype male [EMEC], allotype and 16 paratypes (13 males, 3 females) from GUATEMALA, Baja Verapaz, 19–24 km N Salamá, 4500 ft., May 25–31, 1989 (E. Giesbert, J. Wappes). Additional 42 paratypes as follows: from GUATEMALA: 2 males, Zacapa, 12–14 km S San Lorenzo, 1000–2000 ft., June 3–6, 1989 (Giesbert); 1 male, Zacapa, 12 km S San Lorenzo, 510 m, June 18, 1993 (H. & A. Howden); 1 female, Zacapa, 12–14 km S San Lorenzo, 1–2000 ft., June 3–6, 1989; 4 males, Zacapa, San Lorenzo rd., 1500–1800 ft., June 1–10, 1991 (Wappes); 1 male, Zacapa, nr. San Lorenzo, 4000–6000 ft., April 13, 1990 (Wappes); 1 female, Zacapa, 3 km W Teculután, 300 m, June 3, 1991(H. & A. Howden); 1 male, Zacapa, Sierra de las Minas, 6 km NW San Lorenzo, 6000 ft., April 13, 1990 (Giesbert); 1 female, El Progreso, Sierra de las Minas, 15 km N Estancia de la Virgen, 4400 ft., April 18, 1990 (Giesbert); from HONDURAS: 5 males, 9 females, Olancho, Parque Nac. La Muralla, May 24–27, 1995 (R. Turnbow, J. E. Wappes); from MEXICO: 1 male, 3 females, Chiapas, Parque Nacional Sumidero, 1000 m, May 29–June 4, 1990 (H. & A. Howden); 1 female, same locality, June 23–24, 1990 (J. Huether); 1 male, 1 female, same locality, June 9, 1991 (F. W. Skillman, Jr.); 1 female, Chiapas, 17 km W Tuxtla Gutierrez, 3300 ft., June 27–July 8, 1986 (Giesbert); 2 males, 1 female, same locality, June 21–25, 1987 (Giesbert); 3 males, 1 female, Chiapas, nr. Tuxtla Gutierrez, 500–600 m, ex. flowers, June 2, 1991 (J. S. Ashe); 1 female, Oaxaca, 19 mi. S Matias Romero, June 25, 1969 (D. E. Bright). Paratypes are deposited with EMEC, CNMN, SMUK, EFGC, JPHC, FWSC, RHTC, JEWC, HAHC.

DESCRIPTION. — *Male*: Length 4–6.5 mm. Integument black (sometimes with apex of head, and rarely with entire integument reddish), mouthparts, antennae, apices of tibiae, and tarsi orange-brown; elytra with a single pair of

FIGURE 25. *Euderces disparicrus*, new species, male.

eburneous fasciae. Head with eyes moderately small, upper lobes greatly reduced or absent; antennae reaching beyond middle of elytra, third segment about twice as long as fourth, apically armed with a moderately short, sharp spine, apices of fourth and fifth segments minutely spinose. Pronotum about 1 1/4 times as long as broad, sides rounded, basal 1/6 deeply impressed and narrowed; disk with surface finely alutaceous, moderately densely asperate, appressed pubescence limited to extreme base; entire surface moderately sparsely clothed with long, erect, pale hairs; prosternum with posterior 1/2 bearing moderately coarse punctures and subdepressed, white pubescence; lateral margins of mesepimera and posterior margin of metasternum clothed with dense, silvery-white pubescence. Scutellum small, apex broadly rounded; usually white pubescent. Elytra a little more than twice as long as width across humeri, sides slightly impressed at basal 1/2, widest just before broadly rounded apices; each side near base with a small, feeble gibbosity near suture; a narrow, transverse, raised, eburneous fascia present from near margin to middle of disk on each side at basal 1/4; surface shining and nearly impunctate at extreme base, densely cribrate-punctate anterior and posterior to eburneous fasciae for about 1/2 of the elytral length, apical 1/4 impunctate, alutaceous, with a moderately indistinct oblique fascia of whitish pubescence on each side; entire disk sparsely clothed with long, erect hairs. Abdomen shining, sternites very sparsely pale pubescent; terminal sternite nearly as long as fourth, apex broadly rounded. Legs with femora gradually clavate, upper side curved more than underside, surface moderately coarsely scabrous, with a variably distinct subapical carinae on mesofemora (sometimes on metafemora), sparsely pale pubescent (see Fig. 12e).

Female: Similar to male. Length 4.5–6.5 mm. Antennae slightly shorter, not reaching middle of elytra. Prosternum lacking coarse punctures. Abdomen with terminal sternite slightly longer than fourth, apex rounded.

REMARKS. — This species is distinct by the combination of the small size and gradually clavate and scabrous femora. Superficially, *E. disparicrus* resembles *E. reticulatus* and *E. pusillus*, but may easily be separated by the form of the femora, as well as by the eburneous fasciae not reaching the margins. The specific name refers to the form of the femora: *dispar* = different (L.) + *crus* = leg (L.).

Euderces elvirae, new species
(Fig. 26)

TYPES. — Holotype male [EMEC] from MEXICO, Oaxaca, 11.1 km NW Diaz Ordaz, 2400 m., July 4, 1989 (E. Barchet). Allotype [HAHC] from Oaxaca, El Cerezal, 36 km NE Oaxaca, 2300 m., June 12, 1979 (H. & A. Howden).

DESCRIPTION. — *Male*: Length 6 mm. Integument dark brown, parts of pronotum, basal 1/3 of elytra, underside from head to metasternum, and parts of legs somewhat paler orange-brown, elytra with a single pair of eburneous fasciae. Head with eyes moderately small, lobes divided; antennae reaching past middle of elytra, fourth segment about 2/3 as long as third, segments unarmed apically. Pronotum about 1 1/4

FIGURE 26. *Euderces elvirae*, new species, Holotype male.

times as long as broad, sides moderately rounded, base narrowed and impressed, apex somewhat narrowed; discal surface moderately shining, finely, longitudinally striate at middle, base and apex finely scabrous and subasperate, pale pubescence moderately sparse at apex and extending forward from middle of base; entire surface sparsely clothed with long, erect, pale hairs; prosternum with posterior 2/3 bearing coarse punctures and indistinct pale pubescence; hind-lateral margins of mesepimera and metasternum indistinctly pale pubescent. Scutellum with apex broadly rounded, surface sparsely clothed with pale pubescence. Elytra about 2 1/2 times as long as width across humeri; sides subparallel, slightly wider behind middle; apices rounded; each side near base moderately broadly gibbose; a narrow, transverse, raised, somewhat arcuate eburneous fascia present from margin to near suture on each side at about basal 1/3; surface of basal 1/4 somewhat shining, moderately sparsely, shallowly punctate, with pale, subrecumbent pubescence bordering basal gibbosities, apical 2/3 shining, coarsely, moderately sparsely, shallowly punctate, punctures reduced to absent near apices; a moderately distinct, oblique fascia of pale pubescence present across apical 1/3; entire disk sparsely clothed with long, erect hairs. Abdomen shining, first sternite with indistinct lateral patches of recumbent, pale pubescence, remaining sternites sparsely pubescent; terminal sternite nearly as long as fourth, apex broadly rounded. Legs with femora moderately abruptly clavate, surface smooth, shining, sparsely clothed with pale recumbent pubescence and long, erect, pale hairs.

Female: Similar to male. Length 6 mm. Antennae slightly shorter, reaching to about middle of elytra. Prosternum lacking coarse punctures. Abdomen with terminal sternite slightly longer than fourth, apex rounded.

REMARKS. — This species may be recognized by its small size, shining brown integument, and by the lack of mid-elytral densely cribrate-punctate areas. It is a pleasure to name this species for Elvira Barchet Beierl in recognition of her collecting efforts.

Euderces grossistriatus, new species (Fig. 27)

TYPES. — Holotype male [EMEC] allotype and 1 female paratype from MEXICO, Veracruz, 10 km N Fortin, July 21–29, 1976 (E. Giesbert). Three additional paratypes from MEXICO, Veracruz as follows: 1 female, Orizaba, June 15, 1920 (Psota); 1 male, 1 female, 7 mi. SE Orizaba, June 19–20, 1983 (B. K. Dozier). Paratypes are deposited with EMEC, EFGC.

DESCRIPTION. — *Male*: Length 7 mm. Integument blackish, front of head, antennae, meso- and metasterna, legs, and small area of elytra surrounding lateral ends of the single pair of eburneous fasciae light brown. Head with eyes moderately small, lobes divided; antennae slightly exceeding middle of elytra, third segment nearly three times as long as fourth, apically armed with a long spine which is distinctly longer than the fourth segment, apex of fourth segment with a strong, sharp spine; fifth segment with a small spicule. Pronotum with sides widely rounded, basal 1/5 impressed and narrowed, apical 1/5 moderately narrowed; disk somewhat flattened, surface distinctly, strongly, longitudinally striate except at base and apex; base with fine, pale, appressed pubescence; entire surface sparsely clothed with long, erect, pale hairs; prosternum with posterior 1/2 bearing coarse punctures and moderately dense, subdepressed, white pubescence on both sides of glabrous middle; hind-lateral margins of mesepimera and sides of hind margin of metasternum clothed with dense, silvery-white pubescence. Scutellum with apex broadly rounded, surface moderately sparsely pale pubescent. Elytra nearly 2 1/2 times as long as width across humeri, sides slightly impressed at basal 1/2, subparallel, apices rounded; each side near base with a distinct, arcuate gibbosity near suture, surface somewhat depressed behind gibbosities; a narrow, transverse, raised, eburneous fascia present from margin to near suture on each side at basal 1/3; surface shining, indistinctly punctate anterior to eburneous fasciae, pale golden, recumbent pubescence present on and between basal gibbosities, middle 1/5 of elytra behind eburneous fasciae with a moderately wide, transverse, densely cribrate-punctate band, remainder of elytra shining, moderately sparsely, indistinctly punctate, an angulate fascia of moderately sparse

FIGURE 27. *Euderces grossistriatus*, new species, female.

golden pubescence present across apical 1/4; entire disk sparsely clothed with long, erect hairs. Abdomen shining; sternites sparsely pale pubescent; terminal sternite nearly as long as fourth, apex broadly rounded. Legs with femora moderately abruptly clavate; surface smooth, shining, with longitudinal vittae of fine, pale golden pubescence.

Female: Similar to male. Length 6–7 mm. Antennae slightly shorter, not reaching middle of elytra. Prosternum shining, nearly glabrous. Abdomen with terminal sternite slightly longer than fourth, apex rounded.

REMARKS. — This species may be distinguished by the distinct, coarse striations on the central portion of the pronotal disk, and by the shining blackish integument with appendages and parts of the underside light brown. The species name refers to the sculpture of the pronotal disk: *grossus* = coarse (L.) + *stria* = furrow (L.).

Euderces guatemalenus, new species
(Fig. 28)

TYPES. — Holotype male [EMEC], allotype and 7 paratypes (2 males, 5 females)from GUATEMALA, Baja Verapaz, 19–24 km N Salam, October 23–24, 1990 (E. Giesbert). Seven additional paratypes as follows: from GUATEMALA: 1 female, Baja Verapaz, 17.5 km N Salamá(on #5), 1650 m., "oak forest," June 29, 1993 (R. Anderson); 1 female, Escuintla, 4 km N Palin, 4500 ft., June 21, 1966 (J. M. Campbell); 1 female, San Jorge Muxbal, October 31, 1990 (Giesbert); 1 female, Guatemala, Guatemala (City), July, 1984 (R. Perez); from HONDURAS: 2 females, Ocotepeque, 10.5 km E Ocotepeque, 1400 m, on *Phoradendron* sp., June 16, 1994 (Anderson); 1 male, Intibuca, 1–5 km W La Esperanza, Sept 26, 1995, on flowers (F. T. Hovore); 1 female, Olancho, P. N. La Muralla, June 1, 1995 (R. Turnbow). Paratypes are deposited with CNMN, FTHC, EFGC, JEWC.

DESCRIPTION. — *Male*: Length 5–7 mm, form moderately slender. Integument black, mouthparts, front of head, scape and basal segments of antennae, base of prothorax, mesosternum, coxae, apex of metasternum, scutellum, basal 1/2 of elytral disk except sides and tops of gibbosities, wide band across middle of elytra behind single pair of eburneous fasciae, bases of femora, apices of tibiae, and tarsi reddish orange. Head with eyes moderately small, lobes divided; antennae reaching to about middle of elytra, third segment slightly more than 1 1/2 times as long as fourth, apically armed with a long, feebly sinuate, blunted spine which is about 3/4 as long as fourth segment, apex of fourth segment dentate. Pronotum about 1 1/3 times as long as broad; sides moderately rounded, base widely impressed and narrowed, apex somewhat narrowed; disk with surface dull, finely, densely asperate, indistinctly, finely, moderately sparsely pale pubescent; entire surface sparsely clothed with long, erect, pale hairs; prosternum with posterior 1/2 bearing coarse punctures and moderately dense, subdepressed, white pubescence; hind-lateral margins of mesepimera and

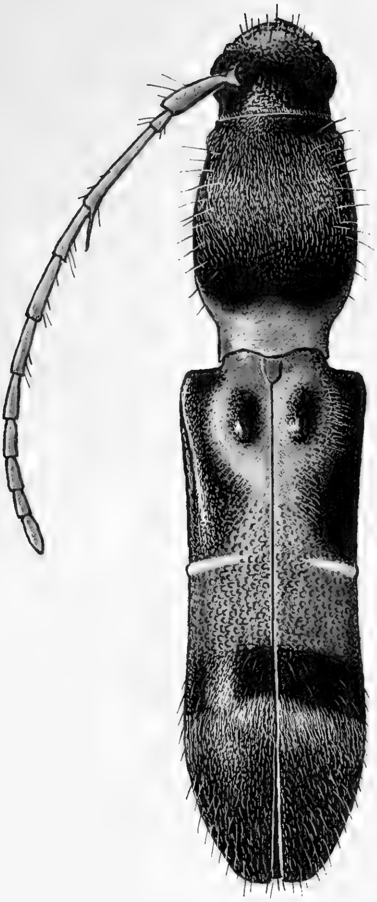

FIGURE 28. *Euderces guatemalenus*, new species, male.

metasternum clothed with silvery-white pubescence. Scutellum with apex broadly rounded, surface glabrous. Elytra about three times as long as width across humeri; sides slightly impressed at basal 1/2, rounded and widest behind middle; apices subtruncate to rounded; each side near base with an elevated, slightly elongated gibbosity near suture; a narrow, transverse or slightly oblique, raised, eburneous fascia present from margin to middle of disk on each side at about basal 1/3; surface moderately shining, indistinctly punctate anterior to eburneous fasciae, with fine, pale golden, recumbent pubescence surrounding basal gibbosities, middle 1/5 of elytra behind eburneous fasciae with a moderately wide, transverse, densely cribrate-punctate and finely pubescent area, apical 2/5 impunctate, a fascia of whitish pubescence present across apical 1/3, anterior to which the surface is finely, moderately sparsely, golden pubescent; entire disk sparsely clothed with long, erect hairs. Abdomen shining; first sternite with hind lateral margin clothed with a patch of white hairs, remaining sternites with sparse, erect, pale pubescence; terminal sternite nearly as long as fourth, apex broadly rounded. Legs with femora moderately abruptly clavate; surface smooth, shining, sparsely clothed with fine, pale golden pubescence.

Female: Similar to male. Length 5.5–7.5 mm. Antennae slightly shorter, not reaching middle of elytra. Prosternum lacking coarse punctures. Abdomen with terminal sternite slightly longer than fourth, apex rounded.

REMARKS. — This species is similar to the sympatric *E. bellus* in general form and color, but may be easily separated by the antennal spines, the finely, densely asperate pronotum, and the well-developed elytral gibbosities. The single specimen from Olancho, Honduras appears to be a melanic individual, without distinct reddish orange dorsal integument, giving an entirely black appearance to the body. The legs and underside, however maintain the typical integumental color. The species is named for the country of origin.

Euderces guerinii (Chevrolat), new combination

Apilocera Guerinii Chevrolat, 1862:535. (TYPE LOCALITY: Nouvelle-Grenade (Colombia).)
Apelocera Guerini Aurivillius, 1912:420.
Eplophorus guerini Blackwelder, 1946:583.

ORIGINAL DESCRIPTION (TRANSLATION). — "Slender, punctate, black; head, apical third of prothorax, and elytra toward apices widely gray, with narrow eburneous fasciae in middle; metathorax and sternum toward base with lateral transverse white lines; third antennal segment with long spine. Length 7 mm; width 1.5 mm."

REMARKS. — We have been unable to locate and examine the type of this species. Comparison of the types may prove *E. posticus* or *E. paraposticus* to be synonyms of *E. guerinii*.

Euderces hoegei (Bates)
(Figs. 4, 29)

Apilocera Högei Bates, 1885:305. (TYPE LOCALITY: Cerro de Plumas, Veracruz, Mexico.)
Apelocera Högei Aurivillius, 1912:420.
Eplophorus högei Blackwelder, 1946:583.
Eplophorus hoegei Chemsak, 1969:309.
Euderces hoegei Chemsak & Linsley, 1975:87.

REDESCRIPTION. — *Male*: Length 4.25–6 mm. Integument black, marked with dull orange as follows: apex of head and genae, antennal scape, wide fascia across elytra slightly before middle encompassing the eburneous fasciae and narrowest at suture, bases of femora, coxae, tibial apices, and tarsi; elytra with a single pair of eburneous fasciae. Head with eyes moderately small, lobes divided; antennae short, not quite reaching middle of elytra, third segment more than twice as long as fourth, armed at apex with a long, feebly sinuate, blunt spine which is about as long as fourth segment, apex of fourth segment with a very short spine. Pronotum with sides rounded; basal 1/6 impressed and narrowed; disk with surface dull, longitudinally rugulose; base and apex with fine, pale, recumbent pubescence; entire surface sparsely clothed with long, erect, pale hairs; prosternum with posterior 1/2 bearing coarse punctures and moderately dense, white pubescence; hind margins of mesepimera and metasternum distinctly marked with dense, silvery-white pubescence. Scutellum parallel-sided, apex broadly rounded, pubescence sparse. Elytra more than twice as long as width across humeri; sides slightly impressed at basal 1/2; apices broadly rounded; disk with well-developed subvertical gibbosities on each side near base, apices of gibbosities punctate; a narrow, transverse, raised, eburneous fascia present on each side slightly before middle, fasciae narrowed and subacuminate toward suture; surface shining, with a dense, cribrate punctured area across middle 1/3, mostly behind eburneous fasciae, basal 1/3 somewhat more sparsely punctate, apical 1/3 impunctate, alutaceous; recumbent pale pubescence present on area surrounding basal gibbosities, and behind a black band as a well-defined patch covering apical 1/4; entire disk sparsely clothed with erect, pale hairs. Abdomen shining, first sternite nearly glabrous, remaining sternites moderately pale pubescent; terminal sternite about as long as fourth, apex very broadly rounded. Legs with femora moderately abruptly clavate; surface smooth, shining, with longitudinal bands of short, pale pubescence.

Female: Similar to male. Length 4.5–6 mm. Antennae slightly shorter. Prosternum lacking coarse punctures. Abdomen with terminal sternite slightly longer than fourth, apex somewhat more narrowly rounded.

REMARKS. — This species is very close to *E. spinicornis*, differing only in minor details such as the form of the scutellum, the slightly smaller average size, and the predominantly black integument with paler areas differently placed. No intergradations between these two phenotypes were seen. The flight period is from July to October. The range appears to be confined to

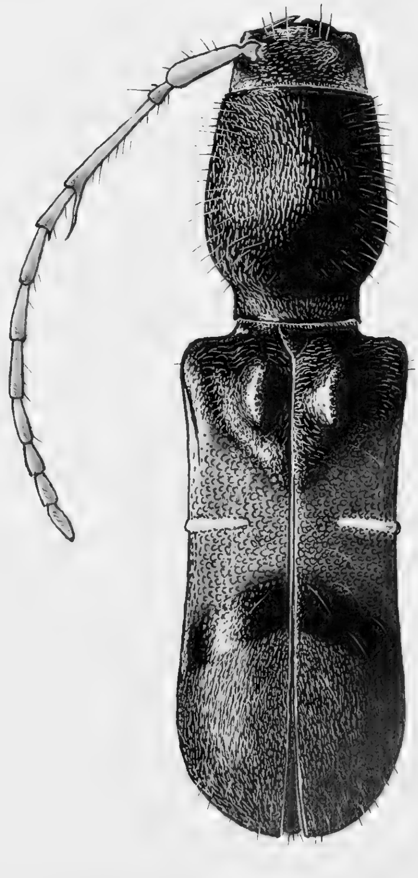

FIGURE 29. *Euderces hoegei* (Bates), male.

southern Mexico. All specimens examined were from the State of Chiapas. (Bates records a Veracruz type locality that is at present impossible to locate accurately.)

Euderces howdeni Chemsak
(Fig. 30)

Euderces howdeni Chemsak, 1969:314; Chemsak & Linsley, 1975:87. (TYPE LOCALITY: 24 miles W. La Ciudad, Durango, Mexico.)

REDESCRIPTION. — *Male*: Length 7 mm, form subcylindrical. Integument dark reddish brown; elytra with a single pair of eburneous fasciae. Head with erect and subdepressed, coarse white pubescence; eyes moderately small, lobes divided; antennae reaching to about elytral apex, third segment minutely dentate at apex, nearly 1 1/2 times as long as scape, which is subequal to fourth, remaining segments unarmed apically. Pronotum slightly longer than broad, sides moderately rounded, base impressed, each side shallowly impressed before somewhat narrowed apex; discal surface shining, moderately coarsely asperate-punctate across middle, with subdepressed, curved, moderately coarse, white pubescence and long, coarse, whitish erect hairs intermixed; sides of prothorax coarsely punctate; prosternum with posterior 3/5 bearing coarse punctures and moderately dense, subdepressed, white pubescence; underside bearing coarse white, depressed pubescence, which is denser at hind and lateral margins of mesepimera and metasternum. Scutellum moderately large, with apex broadly rounded, surface clothed with dense white pubescence. Elytra about 2 1/2 times as long as width across humeri, sides parallel; apices rounded; a narrow, transverse, raised, eburneous fascia present from near margin to about middle of disk on each side near basal 1/3; surface somewhat shining, moderately densely punctate, with moderately sparse, subdepressed, curved, coarse, white pubescence somewhat denser at suture, with a broad, oblique fascia of the same pubescence at apical 1/3; entire disk moderately sparsely clothed with very long, erect white hairs. Abdomen moderately densely clothed with white pubescence; terminal sternite nearly as long as fourth, apex broadly rounded. Legs sparsely clothed with long, erect, white hairs; femora moderately abruptly clavate, surface smooth, shining, bases with coarse, white depressed pubescence.

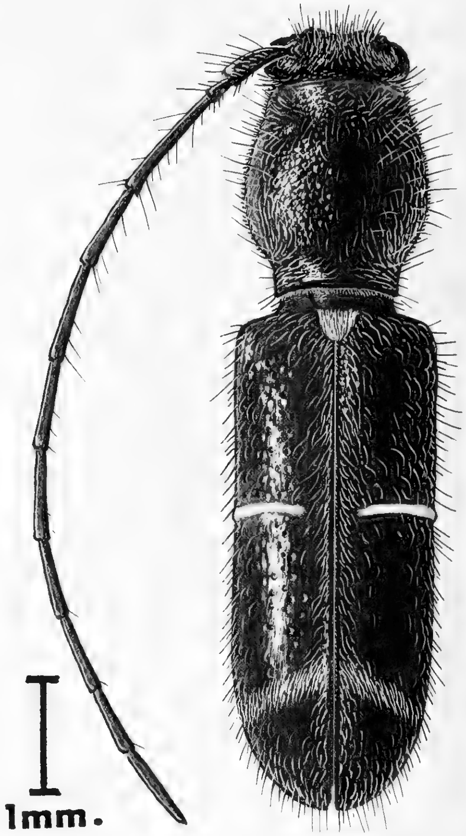

FIGURE 30. *Euderces howdeni* Chemsak, Holotype male.

Female: Not seen.

REMARKS. — This species differs by its coarse, white, curved, and subdepressed pubescence, and from all but *E. turnbowi*, *E. succinus* and *E. elvirae* by the lack of cribrate-punctate areas on the elytra. The type was collected in June.

Euderces laevicauda Bates
(Fig. 31)

Euderces laevicauda Bates, 1885:304; Aurivillius, 1912:419; Chemsak, 1969:317; Chemsak & Linsley, 1975:87. (TYPE LOCALITY: San Gerónimo, Guatemala.)

Euderces cribratus Bates, 1885:304; Aurivillius, 1912:419; Chemsak, 1969:314; Chemsak & Linsley, 1975:87. (TYPE LOCALITY: San Joaquin, Guatemala.) **NEW SYNONYMY.**

FIGURE 31. *Euderces laevicauda* Bates, male.

MATERIAL EXAMINED. — From GUATEMALA: 1 female, San Gerónimo (Champion); 1 male, Vera Paz, San Joaquin (Champion); 1 male, 4 females, Baja Verapaz, 19–24 km N Salamá, October 23–24, 1990 (E. Giesbert); 1 female, Baja Verapaz, 8 km S San Jeronimo, October 23–25, 1990 (E. Giesbert); from MEXICO: 13 males, 22 females, Chiapas, 2–6 km S La Trinitaria, October 19–20, 1988 (E. Giesbert, R. Turnbow, J. Wappes); 7 males, 5 females, same locality "on Compositae," October 22, 1990 (F. Hovore); 2 males, Chiapas, 11 km S Bochil "ex. Acacia," September 29–30, 1989 (Hovore).

REDESCRIPTION. — *Male*: Length 4–5 mm, form moderately slender. Integument blackish to dark brown, appendages usually slightly lighter brown, tarsi paler; elytra often with an ill-defined, pale, longitudinal area at middle of suture, with two pair of eburneous markings. Head with eyes moderately prominent, lobes divided, upper lobe small; antennae reaching to about middle of elytra, third segment slightly longer than scape, about twice as long as fourth, segments unarmed and slightly swollen apically. Pronotum slightly longer than broad, sides rounded, basal 1/6 narrowed and deeply impressed, apex somewhat narrowed; discal surface somewhat shining, moderately finely striolate or asperate-striolate, very sparsely clothed with long, erect, pale hairs; prosternum with posterior 2/3 bearing coarse punctures and moderately sparse whitish pubescence; lateral margins of mesepimera and metasternum indistinctly pale pubescent. Scutellum with apex subtruncate, surface indistinctly pale pubescent. Elytra slightly more than 2 1/2 times as long as width across humeri; sides subparallel, slightly wider behind middle; apices rounded; each side near base feebly tumid; a narrow, transverse, raised, somewhat arcuate eburneous fascia present from margin to middle of disk on each side at about basal 2/5, an additional small, raised, transverse eburneous lineole present on each side near suture at basal 1/5; surface of basal 1/5 somewhat shining, moderately densely punctate, median area densely cribrate-punctate from anterior eburneous markings to apical 2/5, remainder of elytra impunctate, alutaceous, with an indistinct, slightly oblique fascia of short, fine, appressed, pale pubescence across apical 1/3; entire disk sparsely clothed with long, erect hairs. Abdomen shining; first sternite with an indistinct, oblique marking of fine, pale pubescence on each side, remaining sternites sparsely pubescent; terminal sternite nearly as long as fourth, apex broadly rounded. Legs with femora abruptly clavate; surface smooth, shining, very sparsely clothed with long, erect, pale hairs.

Female: Similar to male. Length 4.5–6 mm. Antennae slightly shorter, not reaching middle of elytra. Prosternum lacking coarse punctures. Abdomen with terminal sternite slightly longer than fourth, apex rounded.

REMARKS. — This species may be separated from *E. perplexus*, *E. propinquus* and *E. batesi* by the long, slender, uninterrupted striae of the pronotal disk. From *E. batesi* it may also be separated by its single pair of eburneous markings and lack of femoral apical carinae and from *E. perplexus* and *E. propinquus* by the oblique pubescent macula at each side of the first abdominal sternite. Examination of the type specimen reveals that *E. cribratus* Bates is a somewhat melanic form of *E. laevicauda* with the pale area of elytral integument restricted to the suture.

Flight occurs in September and October from southern Mexico (Chiapas) to Guatemala.

Euderces linsleyi, new species
(Fig. 32)

TYPES. — Holotype male [EMEC] from PANAMA, Chiriquí prov., 7 km SE Fortuna Dam, 1200 m., May 8, 1993 (A. Gillogly, H. Stockwell). Allotype from PANAMA, Chiriquí prov., vicinity of Fortuna Dam, February 17, 1987 (E. Giesbert). Four additional paratypes as follows: 1 female, COSTA RICA, Cartago prov., 18 km NE Turrialba, February 4–10, 1978 (Giesbert); 1 female, PANAMA, Bocas del Toro prov., 15 km S Punta Peña, May 29, 1987 (F. Hovore); 1 male, PANAMA, Bocas del Toro prov., 10 km NE Fortuna Dam, 3400 ft., May 23–26, 1984 (Giesbert); 1 female, PANAMA, Panam prov., Cerro Campana, 2700 ft., June 3–5, 1981 (Giesbert). Paratypes are deposited with EFGC, FTHC.

FIGURE 32. *Euderces linsleyi*, new species, female.

DESCRIPTION. — *Male*: Length 6–9 mm. Integument blackish, mouthparts, coxae, tarsi, and sometimes parts of underside orange-brown, legs and antennae usually brownish, sides of elytra at base rarely orange-brown, elytra with two pairs of eburneous markings. Head with eyes moderately small, lobes divided; antennae exceeding middle of elytra, third segment slightly less than 1 1/2 times as long as fourth, armed at apex with a long, blunted, feebly sinuate spine which is 2/3 as long as fourth segment, apex of fourth segment with a small spine or sharply dentate. Pronotum about 1 1/2 times as long as wide, sides moderately sinuate, basal 1/5 strongly narrowed and impressed, slightly narrowed just behind apex, and somewhat narrower at apex; disk with surface longitudinally striate except near base and apex, clothed with depressed golden pubescence, which is interrupted at middle by an indistinct, transverse, somewhat arcuate, glabrous fascia, the hind margin of which is sharply extended posteriorly at middle and sides; entire surface sparsely clothed with long, erect, golden hairs; prosternum with posterior 1/2 bearing coarse punctures and moderately dense, subdepressed, white pubescence; lateral margins of mesepimera and hind margin of metasternum with wide markings of dense, white pubescence. Scutellum small, parallel-sided, apex broadly rounded, clothed with fine, golden pubescence. Elytra about three times as long as width across humeri; sides slightly impressed at middle; apices truncate to emarginate-truncate, outer angles often dentate; each side near base with a well-developed, elevated, elongate gibbosity; a narrow, oblique, raised, eburneous fascia present on each side at about basal 1/3, with a small, oval, raised, eburneous dot on each side near suture just behind basal gibbosity; surface shining, basal 1/3 sparsely punctate, glabrous except for a large, distinct posthumeral patch of appressed golden pubescence covering basal gibbosities, median 1/4 with a densely cribrate-punctate and pubescent band across middle just behind eburneous fasciae, apical 1/2 impunctate, with an arcuate fascia of golden pubescence across apical 1/3, front margin of pubescent fascia well-defined, whitish, area behind fascia moderately clothed with, short, appressed golden hairs; entire disk with scattered, long, erect, golden hairs. Abdomen shining; first sternite clothed with white pubescence at sides, remaining sternites sparsely pubescent; terminal sternite nearly as long as fourth, apex broadly rounded. Legs with femora moderately abruptly clavate; surface smooth, shining, partially clothed with short, pale pubescence.

Female: Similar to male. Length 7–9 mm. Antennae slightly shorter, not reaching middle of elytra. Prosternum lacking coarse punctures. Abdomen with terminal sternite slightly longer than fourth, apex rounded.

REMARKS. — This species shares with *E. laevicauda*, *E. perplexus*, and *E. longicollis* the distinct, small, oval, raised eburneous spot lying close to the suture in front of the transverse fascia on each elytron. From *E. laevicauda* and *E. perplexus* it may be separated by the larger size and spined antennae; from *E. longicollis* by the shining elytral surface, somewhat oblique orientation of the main eburneous fasciae, and by the presence of elevated basal gibbosities. It is a pleasure to dedicate this species to our friend, Dr. E. Gorton Linsley, a pioneer in modern cerambycid taxonomy in North America.

Euderces longicollis (Linsley)
(Figs. 4, 33)

Eplophorus longicollis Linsley, 1935:88; Chemsak, 1969:308. (TYPE LOCALITY: Bejucos, México, Mexico.)
Euderces longicollis Chemsak & Linsley, 1975:88.

REDESCRIPTION. — *Male*: Length 6–8.5 mm. Integument blackish, usually variably marked with reddish orange on parts of head and antennae, base of prothorax, mesosternum, elytral humeri, and femora; reddish markings sometimes increased to include metasternum and basal 1/2 of elytra, rarely altogether absent; elytra with two pairs of eburneous fasciae. Head with eyes rather small, lobes divided; antennae slightly exceeding apex of elytra, third and fourth segments longitudinally grooved, third segment about twice as long as fourth, armed at apex with a stout, sharp spine which is about 1/2 as long as fourth segment, apices of fourth and fifth segments with smaller spines. Pronotum 1 1/2 times as long as wide; sides feebly rounded to subparallel on apical 2/3, base somewhat impressed; disk with surface longitudinally carinulate-striate, basally subasperate, with a white pubescent fascia across base; entire surface clothed with long, erect, pale hairs; prosternum with posterior 3/5 bearing coarse punctures and moderately sparse, erect, white pubescence; hind margins of mesepimera, meso- and metasternum clothed with dense, white pubescence. Scutellum rounded, moderately sparsely clothed with appressed white pubescence. Elytra slightly less than three times as long as width across humeri; sides slightly impressed at middle; apices sinuate-truncate and bidentate; each side of disk near base feebly gibbose; a small, short, eburneous mark present near the suture at basal 2/5 on each side, immediately followed by a longer, narrow, transverse, feebly arcuate, raised, eburneous fascia extending from lateral margin nearly to suture; discal surface with basal 2/3 densely

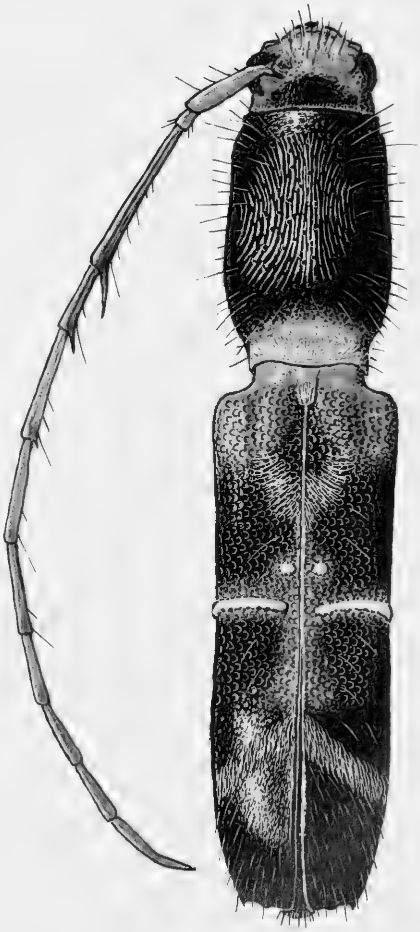

FIGURE 33. *Euderces longicollis* (Linsley), male.

cribrate-punctate with a patch of subrecumbent whitish hairs behind basal gibbosities, apical 1/3 sparsely punctate, alutaceous, with an inverted chevron of fine, appressed whitish pubescence at apical 1/4; entire disk sparsely clothed with long, pale, erect hairs. Abdomen with first sternite laterally marked with dense, white pubescence, remaining sternites very sparsely, finely pale pubescent; terminal sternite about as long as fourth, apex broadly rounded. Legs with femora moderately gradually clavate; surface smooth, shining.

Female: Similar to male. Length 5.5–8 mm. Antennae much shorter, reaching basal 1/3 of elytra; third segment feebly grooved. Prosternum lacking coarse punctures, pubescence less dense, subdepressed. Abdomen with terminal sternite slightly longer than fourth, apex rounded to subtruncate.

REMARKS. — The grooves of the third and fourth antennal segments are deeper in larger males. Specimens with entirely black integument (with eburneous markings) occur in coastal Jalisco. Flight occurs from May to July in southwestern Mexico (see Fig. 4).

Euderces magnus (Bates)
(Fig. 34)

Apilocera magna Bates, 1885:305. (TYPE LOCALITY: Purula (Purulhá), Verapaz, Guatemala.)
Apelocera magna Aurivillius, 1912:420.
Eplophorus magnus Blackwelder, 1946:583.
Euderces magnus Chemsak & Linsley, 1975:88.

FIGURE 34. *Euderces magnus* (Bates), Holotype male. Scale = 1 mm.

REDESCRIPTION. — *Male*: Length 12 mm. Integument blackish, legs and antennae dark brown, elytra with a single pair of eburneous fasciae. Head with eyes moderately small, lobes divided; antennae reaching about middle of elytra, third segment about twice as long as fourth, armed at apex with a long, feebly curved spine nearly as long as fourth segment, apex of fourth segment with a small, sharp spine, fifth segment with minute spicule, segments from fourth somewhat flattened and subserrate. Pronotum slightly more than 1 1/2 times as long as wide, sides moderately rounded, basal 1/6 impressed, apical 1/6 slightly impressed, apex slightly narrowed, with slight swellings on each side of disk at basal 1/3 and apical 1/3 ; disk with surface smooth, except for a very finely, densely punctate area across middle, which is interrupted by a median short, longitudinal, impunctate callus, clothed with fine, depressed, pale golden pubescence except on median callus and posterior swellings; entire surface sparsely clothed with long, erect hairs; prosternum with posterior 1/2 bearing moderately coarse punctures and pale golden pubescence; mesepimera and metasternum clothed with moderately dense, pale golden, subrecumbent pubescence. Scutellum with apex broadly rounded, moderately sparsely pale golden pubescent. Elytra about 2 1/2 times as long as width across humeri; sides slightly impressed before middle; apices broadly subtruncate; each side near base strongly, vertically gibbose near suture; an oblique, raised, eburneous fascia present on each side at basal 2/5, surface depressed behind gibbosities, obliquely impressed at outside of basal gibbosities, and near suture under pubescent markings; surface shining, basal 2/5 sparsely punctate, with appressed golden pubescence surrounding basal gibbosities, median 1/5 densely cribrate-punctate obliquely across middle behind eburneous fasciae, apical 2/5 impunctate, with a well-defined, broad fascia of golden pubescence across apical 1/3, front margin of pubescent fascia whitish, areas behind cribrate-punctate median band and behind pubescent fascia bearing scattered, short, erect, golden hairs; entire disk sparsely clothed with long, erect, golden hairs. Abdomen shining, first sternite clothed with pale golden pubescence at sides, remaining sternites sparsely pubescent laterally; terminal sternite nearly as long as fourth, apex broadly rounded. Legs with femora moderately abruptly clavate; surface smooth, shining, partially clothed with short, pale golden pubescence.

Female: Unknown.

REMARKS. — This large species is superficially similar to *E. boucardi* and *E. proximus*, but may be distinguished from both by the larger size, lack of distinct surface sculpturing on the pronotal disk, more flattened and subserrate antennal segments, more prominent elytral gibbosities, and additionally from *E. proximus* by the longer antennal spines. Only the holotype [BMNH] was seen in this study.

Euderces nelsoni Chemsak
(Figs. 6, 35)

Euderces nelsoni Chemsak, 1969:315; Chemsak & Linsley, 1975:87. (TYPE LOCALITY: 5 miles N. Mazatlan, Sinaloa, Mexico.)

REDESCRIPTION. — *Male*: Length 5–6 mm. Integument reddish, posterior portion of elytra, abdomen, meso- and metatibiae often darker brown to blackish, elytra with a single pair of eburneous fasciae. Head with eyes divided, upper lobes very small; antennae reaching to about apical 1/3 of elytra, third segment about 1 1/2 times as long as scape, nearly twice as long as fourth, armed at apex with a sharp spine which is shorter than second segment, apex of fourth segment spinose, fifth segment dentate. Pronotum about 1 1/3 times as long as broad; sides rounded, somewhat impressed at base, less strongly narrowed at apex; discal surface longitudinally reticulate-striolate, moderately sparsely asperate in middle, sparsely clothed with short, appressed pale pubescence; entire surface with sparse, long, erect, pale hairs; prosternum with posterior 3/5 bearing coarse punctures and sparse pale pubescence; lateral margins of mesepimera and sides of hind margin of metasternum pale pubescent. Scutellum small, rounded, surface sparsely pubescent. Elytra slightly more than twice as long as width across humeri; sides feebly impressed before middle, slightly wider before apex; apices broadly subtruncate to shallowly emarginate; each side near base with a fairly distinct, low gibbosity; a moderately wide, transverse, raised, eburneous fascia present on each side at about basal 1/3 from lateral margin to past middle of

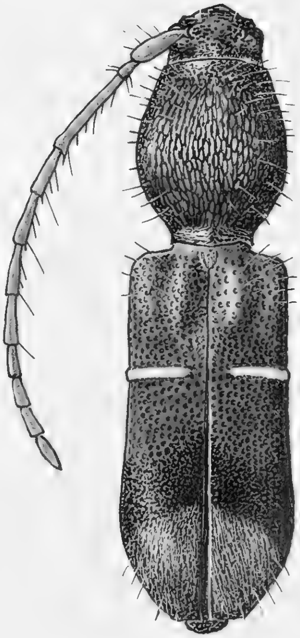

FIGURE 35. *Euderces nelsoni* Chemsak, male.

disk; discal surface with basal 1/4 densely punctate, slightly shining, becoming opaque and densely cribrate-punctate to apical 1/3, where surface becomes impunctate and moderately coarsely alutaceous to apex, apical 1/4 moderately densely clothed with fine, appressed, pale pubescence; entire disk clothed with long, erect, pale hairs. Abdomen shining, sparsely pubescent; terminal sternite about as long as fourth, apex broadly rounded. Legs with femora moderately abruptly clavate; surface smooth, shining, sometimes with longitudinal bands of short, pale pubescence.

Female: Similar to male. Length 5–6 mm. Antennae slightly shorter, barely reaching middle of elytra. Prosternum lacking coarse punctures. Abdomen with terminal sternite slightly longer than fourth, apex rounded.

REMARKS. — *Euderces nelsoni* resembles *E. rubellus*, but differs by the presence of low basal elytral gibbosities, more coarsely sculptured and less pubescent pronotal surface, and somewhat larger size. Also, the elytral eburneous fasciae are moderately wide, distinctly raised, and rounded at their inner apices, unlike the narrower, apically acuminate fasciae of *E. rubellus*. Although many individuals from the area of the type locality are nearly all reddish, specimens from southern populations usually have the apical half of the elytra black. The species flies in July and August in western Mexico (see Fig. 6).

Euderces noguerai, new species
(Fig. 36)

TYPES. — Holotype male [UNAM], allotype and 4 paratypes (2 males, 2 females) from MEXICO, Quintana Roo, 10 km N Puerto Morelos, June 15–16, 1983 (E. Giesbert). Additional 37 paratypes from MEXICO as follows: 3 males, 2 females,Quintana Roo, X-Can Nuevo, June 2–17, 1977 (E. Welling); 1 male, Yucatan, Pisté, March 14, 1980 (Welling); 1 female, Yucatan, 2 km E Chichén Itz , "dry trop. seas. for.," July 19–20, 1983 (R. Anderson, W. Maddison); 2 males, 5 females, same locality, on blossoms of woody plant, May 25, 1984 (R. Turnbow, J. Wappes); 1 male, 7 females, same locality, May 28–29, 1992 (R. L. Penrose); 2 males, 3 females, Quintana Roo, 20 km N Carillo Puerto, June 12–14, 1983 (Wappes, Giesbert); 3 males, Quintana Roo, 17 km NW Felipe Carillo Puerto, June 18, 1990 (Turnbow, M. C. Thomas, J. Huether); 1 male, 1 female, Quintana Roo, 16 km N Felipe Carillo Puerto, June 2, 1992 (Penrose); 3 males, 1 female, Quintana Roo, 11 km N Felipe Carillo Puerto, June 2, 1992 (Penrose); 1 female, Quintana Roo, 13 km NW Tulum, June 15, 1993 (Wappes). One additional male paratype from BELIZE, New Orleans, under bark of *Lignum vitae*, March 20, 1969 (A. D. Hanson, C. Whelchel). Paratypes are deposited with CNMN, EMEC, TAMU, EFGC, JEWC, RHTC RLPC.

DESCRIPTION. — *Male*: Length 7.5–13.5 mm. Integument dark brown to blackish, with two pairs of elytral eburneous markings, elytra often with a faint metallic green tint and sometimes with margins pale at basal 1/2. Head with eyes moderately small, lobes divided; antennal

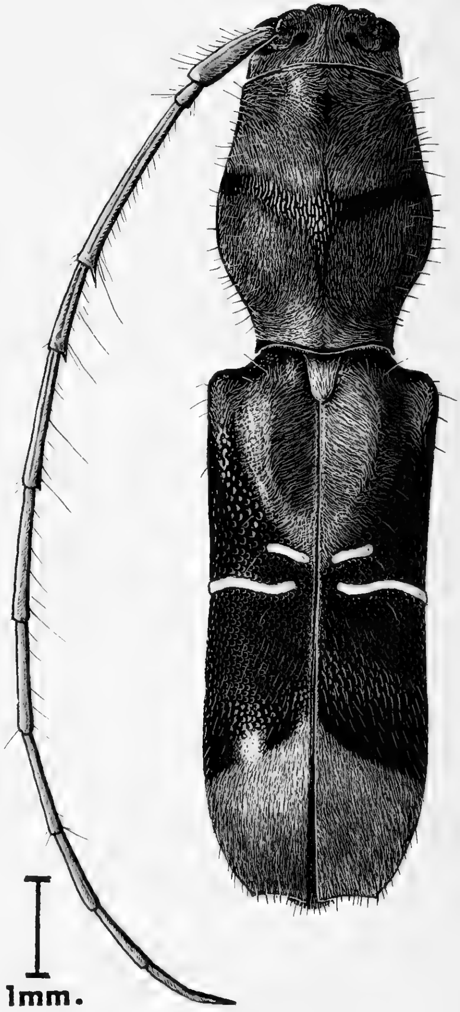

FIGURE 36. *Euderces noguerai*, new species, male.

tubercles small, acute; antennae exceeding apex of elytra by about two segments, third to fifth segments longitudinally grooved, third segment moderately stout, nearly twice as long as fourth, armed at apex with a short, sharp spine, apices of fourth and usually fifth segments with very small spines. Pronotum about 1 1/4 times as long as wide; sides rounded, widest slightly behind middle, narrowed toward base and apex; basal 1/6 somewhat impressed; disk with surface longitudinally rugose and striolate, moderately densely clothed with appressed golden pubescence except for a median, transverse, sinuate, glabrous fascia which branches back to base at middle; entire prothorax clothed with erect, pale hairs; prosternum with posterior 2/3 bearing coarse punctures and moderately dense, erect and subdepressed, white pubescence; hind portion of prosternum, lateral 1/2 of mesepimera, hind margin of mesosternum, and most of metasternum and metepisterna clothed with dense, pale pubescence. Scutellum moderately large, apex narrowly rounded, surface densely clothed with appressed, pale golden pubescence. Elytra slightly less than 2 1/2 times as long as width across humeri, sides slightly impressed at middle; apices truncate and bidentate; disk feebly gibbose on each side near base, with two pairs of narrow, slightly sinuate, raised, eburneous fasciae present, the anterior pair just behind the gibbosities short, oblique, extending from middle of disk to near suture, posterior pair premedian, extending from lateral margin past middle of disk; surface with basal 1/3 shining, moderately densely punctate, with a patch of subrecumbent pale golden hairs around basal gibbosities, median 1/3 dull, densely cribrate-punctate, moderately sparsely clothed with fine, subdepressed golden pubescence, apical 1/3 shining, with an inverted chevron of fine, appressed pale golden pubescence, the front margin of which is distinct, the hind margin indistinct; entire disk sparsely clothed with erect hairs. Abdomen moderately densely clothed with fine, pale pubescence, which is somewhat more dense and pale at sides of first sternite; terminal sternite about as long as fourth, apex broadly rounded. Legs with femora gradually clavate, apically carinate on each face; surface shining, very sparsely punctate and with longitudinal bands of short, pale pubescence.

Female: Similar to male. Length 8–12 mm. Antennae shorter, slightly exceeding middle of elytra. Prosternum lacking coarse punctures. Abdomen with terminal sternite slightly longer than fourth, apex rounded.

REMARKS. — *Euderces noguerai* appears to be related to *E. pulcher*, *E. longicollis*, and *E. bicinctus*. It is a pleasure to dedicate this species to Felipe A. Noguera M. of the UNAM Estación de Biología at Chamela, Jalisco, Mexico, for his interest in the Cerambycidae.

Euderces obliquefasciatus, new species (Fig. 37)

TYPE. — Holotype female[CNMN] from MEXICO, Guerrero, 5 mi. SW Filo de Caballo, 8000 ft., July 7, 1984 (J. B. Woolley).

FIGURE 37. *Euderces obliquefasciatus*, new species, Holotype female.

DESCRIPTION. — *Female*: Length 6 mm, form slender. Integument dark brown, head, pronotum, and elytral apices somewhat darker; elytra with two pair of eburneous markings. Head with eyes moderately prominent, lobes divided, upper lobe small; antennae slightly surpassing middle of elytra, third segment nearly 1 1/2 times as long as scape, nearly twice as long as fourth segment, segments unarmed and feebly expanded apically. Pronotum somewhat longer than broad; sides rounded, base narrowed and deeply impressed, apex moderately narrowed; discal surface shining, moderately, longitudinally rugose-striolate, very sparsely clothed with long, erect, pale hairs; prosternum with posterior 1/2 moderately clothed with appressed, pale hairs; lateral margins of mesepimera and metasternum indistinctly pale pubescent. Scutellum with apex subtruncate, clothed with whitish pubescence. Elytra about 2 2/3 times as long as width across humeri, sides subparallel, slightly wider behind middle; apices rounded; each side near base very feebly tumid; a strongly oblique, raised, eburneous fascia present on each side from before basal 1/3 at margin to behind basal 1/3 between middle of disk and suture, and an additional short, transverse, raised, eburneous lineole present close to suture slightly before basal 1/4; surface of basal 1/4 somewhat shining, moderately densely punctate, median area densely cribrate-punctate from anterior eburneous markings to apical 2/5, remainder of elytra impunctate, alutaceous, with a distinct, slightly oblique fascia of short, fine, appressed, whitish pubescence before apical 1/4; entire disk sparsely clothed with long, erect hairs. Abdomen shining, sparsely clothed with long, erect hairs; first sternite moderately densely clothed with appressed, pale pubescence on each side of middle; terminal sternite as long as fourth, apex moderately rounded. Legs with femora moderately abruptly clavate; surface smooth, shining, very sparsely clothed with long, erect, pale hairs and fine, indistinct, appressed shorter hairs.

Male: Unknown.

REMARKS. — This species differs from the similar *E. perplexa* by the strongly oblique posterior eburneous fasciae, and the pubescent patches of the first abdominal sternite. The species name refers to the oblique fasciae: *obliquus* = slanting (L.) + *fascia* = transverse band (L.).

Euderces parallelus LeConte
(Figs. 3, 38)

Euderces parallelus LeConte, 1873:202; Leng, 1887:24, 44; Horn, 1894:339; Aurivillius, 1912:419; Linsley, 1942:57; Chemsak & Linsley, 1975:87; Hovore, 1988:15 (ref.). (TYPE LOCALITY: Lower California.)

REDESCRIPTION. — *Male*: Length 3–5 mm. Integument blackish to dark brown, mouthparts, antennae, middle of elytra narrowly surrounding the eburneous markings, femoral apices, tibial apices, and tarsi orange-brown; elytra with two pairs of eburneous markings. Head with eyes divided, upper lobe small; antennae reaching nearly to middle of elytra, scape slender, not much wider than remaining segments, third segment about 1 1/2 times as long as scape, nearly twice as long as fourth segment, segments unarmed and slightly swollen apically. Pronotum about as long as wide; sides broadly rounded, basal 1/6 narrowed and deeply impressed, apex somewhat narrowed; discal surface moderately shining, longitudinally striate, base asperate at middle, with sparse, appressed, pale pubescence across base, entire surface with scattered, long, erect, pale hairs; prosternum with posterior 2/3 coarsely punctured and pale pubescent; lateral margins of mesepimera and hind margin of metasternum densely whitish pubescent. Scutellum with apex narrowly rounded, surface indistinctly pale pubescent. Elytra slightly more than twice as long as width across humeri; sides slightly narrowed behind humeri, widest behind middle; apices rounded; a narrow, transverse, raised, eburneous fascia present from margin nearly to suture on each side at about basal 1/3, an additional shorter, more narrow, transverse, eburneous fascia present near suture on each side at basal 1/4 (often reduced and sometimes absent); discal surface with basal 3/5 densely cribrate-punctate except for moderately shining, alutaceous, nearly impunctate humeri, apical 2/5 impunctate, alutaceous, sometimes with an indistinct fascia of sparse, pale pubescence across apical 1/3; entire disk moderately sparsely clothed with long, erect hairs. Abdomen shining, sparsely pubescent; terminal sternite nearly as long as fourth, apex broadly rounded. Legs with femora abruptly clavate; surface smooth, shining, very sparsely pubescent.

FIGURE 38. *Euderces parallelus* LeConte, male.

Female: Similar to male. Length 3–5 mm. Antennae slightly shorter, reaching about to basal 1/4 of elytra. Prosternum lacking coarse punctures. Abdomen with terminal sternite slightly longer than fourth, apex rounded.

REMARKS. — Flight typically occurs through most of lowland Baja California del Sur, Mexico from July to December (see Fig. 3). The length of the anterior eburneous fasciae appears to be quite variable and is lacking entirely on a few specimens. These individuals, more abundant in the northern part of the range, are very similar in appearance to typical *E. cribripennis*. They may be distinguished from that species by the remaining eburneous fasciae closely approaching the suture, and by the more slender antennal scape, as well as the peninsular distribution.

Euderces paraposticus, new species
(Figs. 2, 39)

TYPE. — Holotype male [FMNH] from COLOMBIA, Magdalena, Sierra de Perija, Socorpa Mission, 1350 m., August 7–9, 1968 (B. Malkin).

DESCRIPTION. — *Male*: Length 6.5 mm. Integument blackish, with mouthparts, genae, hind margin of prosternum, mesosternum, coxae and appendages orange-brown; elytra with a single pair of eburneous fasciae. Head with eyes rather small, lobes divided; antennae reaching about apical 1/3 of elytra, third segment nearly twice as long as fourth, armed at apex with a long, feebly curved spine about 2/3 as long as fourth segment, apex of fourth segment with a distinct, short spine. Pronotum slightly less than 1 1/2 times as long as wide; sides moderately rounded, basal 1/6 narrowed and impressed; disk with surface longitudinally rugose-striate and asperate, clothed with fine, short, golden pubescence at base and behind apex, entire surface moderately sparsely clothed with long, erect, pale hairs; prosternum with posterior 1/2 coarsely punctate and pale pubescent; lateral and hind margins of epimera, meso- and metasterna clothed with denser, pale pubescence. Scutellum rounded, moderately sparsely clothed with pale pubescence. Elytra about 2 1/4 times as long as width across humeri; sides slightly impressed before middle; apices narrowly truncate, outer angles dentate; each side near base moderately strongly gibbose, apices of gibbosities asperate; a narrow, transverse, raised, eburneous fascia present on each side at basal 2/5 from lateral margin to about middle of disk; discal surface with extreme base shining, moderately sparsely punctate, area of basal gibbosities more densely punctate, with fine, appressed pale pubescence around and behind gibbosities, median 1/5 densely cribrate-punctate, apical 2/5 shining, impunctate, apical 1/4 bearing a wide fascia of appressed pale pubescence; entire disk sparsely clothed with long, erect hairs. Abdomen shining, very sparsely punctate, sparsely pubescent; terminal sternite nearly as long as fourth, apex broadly rounded. Legs with femora moderately abruptly clavate, surface smooth, shining, with longitudinal bands of short, pale pubescence.

Female: Unknown.

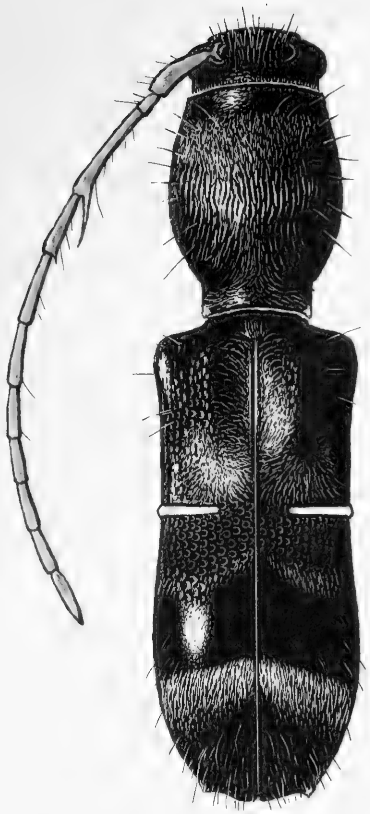

FIGURE 39. *Euderces paraposticus*, new species, Holotype male.

REMARKS. — This species, described from a unique specimen, is close to *E. posticus* geographically and in structure, but may be separated from that species by the somewhat shorter spine of the third antennal segment, the wider, shining, impunctate fascia between the median cribrate-punctate area and the preapical pubescent fascia, and by the contrasting color of the appendages. The specific name refers to the similarity to *E. posticus* (Pascoe): *par* = like (L.).

Euderces perplexus, new species
(Fig. 40)

TYPES. — Holotype male [EMEC], allotype and 2 paratypes (1 male,1 female) from MEXICO, Oaxaca, 38 km SW Oaxaca, Sierra de Zempoaltepetl, 2 km S Diaz Ordaz, 2075 m, July 4, 1989 (Barchet). Additional 16 paratypes from MEXICO as follows: 1 male, Guerrero, 23 km S Iguala, July 19, 1984 (J. Cope); 1 female, 3 km W Chilpancingo, July 20–27, 1987 (Cope); 1 male, Guerrero, 5.4 mi. SW La Laguna, July 14, 1985 (Jones, Schaffner); 1 male, 2 females, 15 mi. W Chichihualco, 5000 ft., July 15, 1984 (J. B. Woolley & Carroll, Schaffner, Friedlander); 1 female, 20.7 km SW Xochipala, 2000 m, "oak pastureland," July 17, 1992 (R. S. Anderson); 1 male, 1 female, Oaxaca, Hwy #131 70 km S Oaxaca, Rio de la Y, 20 km W of jct., 2150 m, June 17, 1979 (H. & A. Howden); 1 female, Oaxaca, 10 mi. SE Huajuapan de León, June 27, 1965 (Burke, Meyer, Schaffner); 1 female, Oaxaca, Rt. #131 15 mi. S Sola de Vega, 6000 ft., May 30, 1971 (H. F. Howden); 1 female, Oaxaca, 7 km NNW Diaz Ordaz, 2200 m, July 11, 1992 (C. L. Bellamy); 1 female, same locality, July 17, 1992 (G. H. Nelson & D. S. Verity); 1 female, Oaxaca, 3.5 mi. N Diaz Ordaz, 6400 ft., July 9–10, 1994 (E. Giesbert); 1 female, Oaxaca, 6 mi. NE Mitla, July 20, 1985 (Jones, Schaffner); 1 female, Morelos, 9 mi. S Juchiltepec, June 29, 1982 (M. A. Ivie). Paratypes are deposited with EMEC, CNMN, TAMU, MAIC, EFGC, JSCC, HAHC, JEBC, JEWC.

DESCRIPTION. — *Male*: Length 4–5 mm, form moderately slender. Integument blackish to dark brown, appendages usually slightly lighter brown; elytra with two pair of eburneous markings. Head with eyes moderately prominent, lobes divided, upper lobe small; antennae reaching to about middle of elytra, third segment slightly longer than scape, about twice as long as fourth segment, segments unarmed and slightly swollen apically. Pronotum slightly longer than broad; sides rounded, basal 1/6 narrowed and deeply impressed, apex somewhat narrowed; discal surface somewhat shining, with moderately short, irregular striations, feebly asperate-striolate in middle, very sparsely clothed with long, erect, pale hairs; prosternum with posterior 2/3 bearing coarse punctures and moderately sparse whitish pubescence; lateral margins of mesepimera and metasternum indistinctly pale pubescent. Scutellum with apex subtruncate, surface indistinctly pale pubescent. Elytra slightly more than 2 1/2 times as long as width across humeri; sides subparallel, slightly wider behind middle; apices rounded; each side near base feebly tumid; a narrow, transverse, raised, eburneous fascia present from margin to middle of disk on each side at about basal 2/5, an additional small, transverse, raised, eburneous lineole or oval spot present on each side near suture at basal 1/5; surface of basal 1/5 somewhat shining, moderately densely punctate, median area densely

FIGURE 40. *Euderces perplexus*, new species, male.

cribrate-punctate from anterior eburneous markings to apical 2/5, remainder of elytra impunctate, alutaceous, with an indistinct, transverse fascia of short, fine, appressed, pale pubescence across apical 1/3; entire disk sparsely clothed with long, erect hairs. Abdomen shining, sparsely clothed with long, erect hairs; terminal sternite nearly as long as fourth, apex broadly rounded. Legs with femora abruptly clavate; surface smooth, shining, very sparsely clothed with long, erect, pale hairs.

Female: Similar to male. Length 4.5–6 mm. Antennae slightly shorter, not reaching middle of elytra. Prosternum lacking coarse punctures. Abdomen with terminal sternite slightly longer than fourth, apex rounded.

REMARKS. — This species, historically treated in the literature as *E. cribratus* Bates, may be separated from the closely related *E. laevicauda* by the usually blackish integument (a few specimens were seen with basally reddish elytra, but in no case was the suture paler as in *laevicauda*), as well as by the shorter striations and feeble asperations of the pronotal disk, and the lack of pubescent markings on the first abdominal sternite. The species name refers to the previously unclear identity of this taxon: *perplexus* = puzzling (L.).

Euderces picipes (Fabricius)
(Figs. 1, 5)

Callidium picipes Fabricius, 1787:157; 1792:338; Olivier, 1790:269; 1795:57. (TYPE LOCALITY: not given.)

Clytus picipes Fabricius, 1801:353; Laporte & Gory, 1835:107; Haldeman, 1847:41.

Euderces picipes LeConte, 1850:30; White, 1855:289; Provancher, 1877:604; Popenoe, 1877:33; Leng, 1887:24; Packard, 1890:354 (habits); Chittenden, 1894:98 (habits); Beutenmüller, 1896:77 (habits); Wickham, 1897:152; Felt, 1907:445; Poulton, 1908:225 (habits); Morris, 1909:412; Aurivillius, 1912:419; Nicolay, 1917:94; Craighead, 1923:64 (larva); Knull, 1946:226; Hoffmann, 1940:59; 1942:11; Fattig, 1947:27 (habits); Linsley, 1964:184; Chemsak & Linsley, 1975:87; MacRae, 1993:235 (habits); Turnbow & Hovore, 1979:223; Turnbow & Franklin, 1980:343.

Euderces picipes picipes Linsley, 1957:38; 1964:184; Turnbow & Franklin, 1980:343 (record); Gosling, 1984:71 (habits); Waters & Hyche, 1984:287.

Euderces picipes occidentalis Linsley, 1957:38; 1964:185; Chemsak & Linsley, 1975:87; MacRae, 1993:235 (habits); Lingafelter & Horner, 1993:176. (TYPE LOCALITY: Fedor, Texas) **NEW SYNONYMY.**

REDESCRIPTION. — *Male*: Length 5–9 mm. Integument blackish to dark red-brown, legs and antennae usually medium-brown, elytra with a single pair of eburneous fasciae (basal 1/2 to 2/3 of elytra sometimes red). Head with eyes rather small, lobes divided; antennae nearly reaching apices of elytra, third segment slightly less than twice as long as fourth, apex dentate, fourth segment with apex minutely dentate. Pronotum somewhat longer than broad; sides rounded, narrowed and impressed at base, less so at apex; discal surface shining, longitudinally striate and minutely asperate nearly to apex, entire surface moderately sparsely clothed with long, erect, pale hairs; prosternum with coarse punctures indistinct, limited to lateral surfaces, basal 1/2 moderately densely, finely, white pubescent; lateral and hind areas of mesepimera and metasternum white pubescent. Scutellum rounded, indistinctly clothed with very fine, short, pale pubescence. Elytra slightly less than 2 1/2 times as long as width across humeri; sides slightly impressed before middle; apices rounded, sutural angle sometimes broadly, obtusely dentate; each side near base moderately strongly gibbose near suture; a narrow, somewhat oblique, raised, eburneous fascia present on each side at basal 2/5 from lateral margin to past middle of disk; discal surface with basal 2/3 dull, coarsely, densely cribrate-punctate, humeri shining, indistinctly punctate; apical 1/3 impunctate, alutaceous, often with an indistinct fascia of fine, pale pubescence across apical 1/4; entire disk clothed with long, erect, golden hairs. Abdomen shining; first sternite moderately densely pale pubescent, remaining sternites sparsely punctate and pubescent; terminal sternite nearly as long as fourth, apex broadly rounded. Legs with femora moderately abruptly clavate; surface smooth, shining, sparsely clothed with long, pale hairs.

Female: Similar to male. Length 6–9 mm. Antennae slightly shorter, reaching apical 1/3 of elytra. Abdomen with terminal sternite slightly longer than fourth, apex narrowly rounded.

REMARKS. — Flight typically occurs in June and July in the eastern half of North America (see Fig. 5), but may take place as early as late April in the southern part of the range. Populations from Texas, Oklahoma, and Minnesota tend to have a more reddish integument, as observed by Linsley (1957), but red specimens have been seen from Florida, New Jersey and Mississippi as well. We do not believe subspecific status is warranted for this apparently widespread color variety.

Euderces picipes is one of the few species of *Euderces* having the sexual punctation of the male prosternum indistinct.

The known host plants are *Acer rubrum, Carya glabra, Castanea sativa, C. vesca, Celtis, Cercis canadensis, Cornus florida, Nyssa, Pyrus, Quercus stellata, Q. velutina, Robinia, Ulmus.*

Euderces pini (Olivier)
(Figs. 5, 41)

Callidium pini Olivier, 1795:71. (TYPE LOCALITY: New York)

Euderces pini Fitch, 1857:417; LeConte, 1873:202; Hamilton, 1884:36; Leng, 1887:24, 44; Packard, 1890:700; Wickham, 1897:152; Aurivillius, 1912:419; Knull, 1946:226; Fattig, 1947:27 (records); Duffy, 1953:238; Linsley, 1964:182; Chemsak & Linsley, 1975:87; Turnbow & Hovore, 1979:223; Turnbow & Franklin, 1980:343 (record); Rice, 1981:461; Waters & Hyche, 1984:286; Rice, Turnbow & Hovore, 1985:20; Palmer, 1987:190; Wheeler & Longino, 1988:26; MacRae, 1993:236 (habits); Lingafelter & Horner, 1993:177.

Clytus piniadeus Fabricius, 1801:353; Laporte & Gory, 1835:109; Haldeman, 1847:41. (TYPE LOCALITY: Carolina)

Tillomorpha piniadea White, 1855:289; Lacordaire, 1869:91.

Clytus piniadeus var. *testaceipes* Haldeman, 1847:41. (TYPE LOCALITY: Carolina)

REDESCRIPTION. — *Male*: Length 6–9 mm. Integument pale reddish brown, apical 2/5 to 1/2

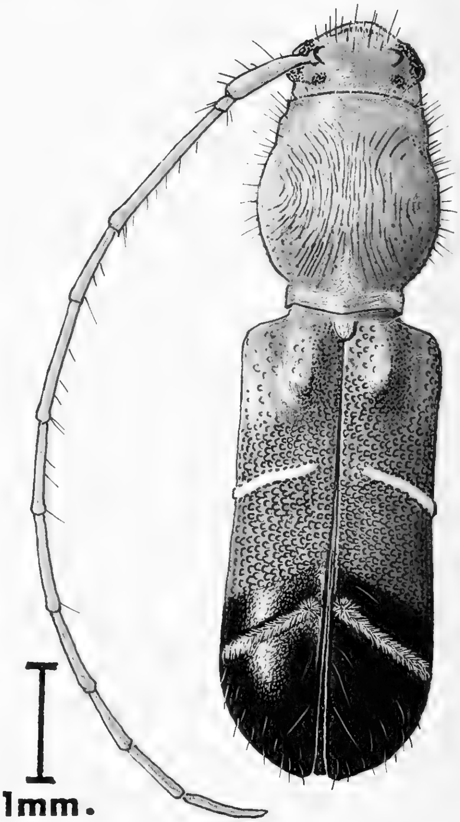

FIGURE 41. *Euderces pini* (Olivier), male.

of elytra and abdomen black (rarely all blackish with pale reddish brown antennae), elytra with a single pair of eburneous fasciae. Head with eyes rather small, lobes divided; antennae exceeding apices of elytra by two or three segments, third segment nearly twice as long as fourth, apex minutely dentate. Pronotum somewhat longer than broad, sides rounded, narrowed at base, less so at apex; disk deeply impressed across base, shallowly, widely impressed across apex, surface shining, finely, longitudinally striate and minutely asperate to apical impression, clothed with appressed whitish pubescence across base and on basal 1/3 in middle; entire surface moderately sparsely clothed with long, erect, pale hairs; prosternum with posterior 2/3 bearing coarse punctures and sparse, indistinct pubescence; lateral and hind areas of mesepimera and metasternum white pubescent. Scutellum rounded, moderately densely clothed with fine, pale pubescence. Elytra slightly slightly less than 2 1/2 times as long as width across humeri, slightly wider behind middle; apices rounded or feebly subtruncate; each side near base moderately strongly, distinctly gibbose; a narrow, somewhat oblique, raised, eburneous fascia present on each side at basal 2/5 from lateral margin to past middle of disk; discal surface with basal 1/4 somewhat shining, coarsely, densely punctate, outer surface of gibbosities shining, impunctate; median 3/8 dull, densely cribrate-punctate, apical 3/8 shining, impunctate, with a narrow, distinct fascia of fine, pale pubescence across apical 1/3, surface beneath fascia slightly impressed; entire disk clothed with long, erect, golden hairs. Abdomen shining, sparsely punctate and pubescent; terminal sternite nearly as long as fourth, apex broadly rounded. Legs with femora moderately abruptly clavate; surface smooth, shining, with longitudinal bands of pale pubescence, sparsely clothed with long, erect, pale hairs.

Female: Similar to male. Length 6–9 mm. Antennae shorter, reaching apical 1/3 of elytra. Abdomen with terminal sternite slightly longer than fourth, apex narrowly rounded.

REMARKS. — Occasional melanistic individuals have been seen, with pale reddish antennae. There does not appear to be any geographical pattern for this color form. Flight period is from March to May in the southeastern U. S. A. westward to Texas and Kansas (see Fig. 5).

The known host plants are *Carya illinoensis, Cornus florida, Maclura pomifera, Sapindus drummondi, Sophora secundifolia, Ulmus alata.*

Euderces posticus (Pascoe), new combination (Figs. 2, 42)

Apilocera postica Pascoe, 1866:295. (TYPE LOCALITY: Santa Marta, Colombia.)
Apelocera postica Aurivillius, 1912:420.
Eplophorus posticus Blackwelder, 1946:583.

REDESCRIPTION. — *Male*: Length 5–6.5 mm. Integument usually blackish to dark red-brown, sometimes with head and pronotum reddish; elytra with a single pair of eburneous fasciae. Head with eyes rather small, lobes divided; antennae exceeding middle of elytra, third segment about twice as long as fourth, armed at apex with a long, feebly sinuate, blunt spine which is about as long as fourth segment, apex of fourth segment

FIGURE 42. *Euderces posticus* (Pascoe), male.

with a distinct, short spine. Pronotum 1 1/4 times as long as wide, sides rounded, basal 1/6 strongly narrowed and impressed; disk with surface longitudinally striate and rugulose, apical 2/5 and base clothed with short, golden pubescence, entire surface moderately sparsely clothed with long, erect, pale hairs; prosternum with posterior 3/5 bearing coarse punctures and moderately dense, subdepressed, white pubescence; lateral and hind margins of epimera, meso- and metasternum clothed with dense, white pubescence. Scutellum rounded, moderately sparsely clothed with appressed golden pubescence. Elytra slightly more than twice as long as width across humeri; sides slightly impressed before middle; apices narrowly truncate, marginal angles dentate; each side near base moderately strongly, arcuately gibbose, apices of gibbosities asperate; a narrow, transverse, raised, eburneous fascia present on each side at basal 2/5 from lateral margin to past middle of disk; discal surface with basal 1/3 coarsely, densely punctate, with moderately sparse, golden pubescence in area of basal gibbosities, median 1/3 densely cribrate-punctate, with indistinct golden pubescence, apical 1/3 somewhat alutaceous, impunctate, with apical 1/4 clothed with appressed pale golden pubescence; entire disk sparsely clothed with long, erect, golden hairs. Abdomen shining, very sparsely punctate, sparsely pubescent; terminal sternite nearly as long as fourth, apex broadly rounded. Legs with femora moderately abruptly clavate; surface smooth, shining, with longitudinal bands of short, pale pubescence.

Female: Similar to male. Length 5–6 mm. Antennae slightly shorter, barely reaching middle of elytra. Prosternum lacking coarse punctures. Abdomen with terminal sternite slightly longer than fourth, apex rounded.

REMARKS. — In Pascoe's type specimen and accompanying description the integumental color is given as brownish red, with the tibiae, tarsi, and terminal antennal segments darker. The basically brownish color, however, appears to be variable, and specimens have been seen which range from all dark brown, to dark brown with a reddish head and pronotum. Flight occurs from January to May from central and eastern Panama to northern Colombia (see Fig. 2).

Euderces postipallidus, new species
(Fig. 43)

TYPES. — Holotype male [HAHC] and allotype from MEXICO, Oaxaca, 15 mi. S Sola de Vega, 6000 ft., May 30, 1971 (H. F. Howden). Additional 38 paratypes from Oaxaca, MEXICO as follows: 2 females, Hwy. #131, 70 km S Oaxaca, Rio de la Y, km 20 W of jct., 2150 m., June 17, 1979 (H. & A. Howden); 1 male, 12.5 km SW Gueletao, 1900 m., oak scrub, July 27, 1992 (R. S. Anderson); 1 female, 12 km S Benito Juarez, 2100 m., July 1, 1989 (Barchet); 1 female, 8 mi. NE El Punto, July 18, 1985 (Jones, Schaffner); 2 males, Hwy. #175, 6.7 km N El Punto, 2100 m., June 29, 1989 (Barchet); 2 males, 1 female, 13–14 km E Mitla, 2100 m., August 5–8, 1986 (Howdens); 1 male, 6 mi. NE Mitla, July 20, 1985 (Jones, Schaffner); 4 males, 3 females, 7–8 mi. NE Mitla, 6200 ft., July 3–9, 1994 (E. Giesbert); 3 males, 1 female, 8 km NW Diaz Ordaz, 2400 m., June 15, 1979 (Howdens); 1 female, N of Hwy #190, 7 km N Diaz Ordaz, July 17, 1992 (G. H. Nelson, D. S. Verity); 1 male, 4 females, 3.5 mi. N Diaz Ordaz, 6400 ft., July 9–10, 1994 (Giesbert); 1 male, 1 female, El Cerezal, 36 km NE Oaxaca, 2300 m., June 12, 1979 (Howdens); 1 male, 3 females, 10.8 km N Jct. #175/#195, 1859m., "oak-Acacia woodland," June 19, 1987 (R. Anderson); 1 male, Sierra de Ixtlán, El Studiante, 1800 m., June 29, 1989 (Barchet); 1 male, 3 km NW Sola de Vega on Rio Miahuatlan, 1400 m., July 7, 1989 (Barchet); 1 male, Zempoaltepetl, 2 km S Diaz Ordaz, 2075m., July 4, 1989 (Barchet); 1 female, 5.7 mi. NW Tetixtlahuaca, July 22, 1987 (P. W. Kovarik). Paratypes are deposited with EMEC, MAIC, CNMN, TAMU, HAHC, EFGC, JEBC, JEWC.

DESCRIPTION. — *Male*: Length 6–6.5 mm. Integument blackish, apical half of elytra gradually paler dull yellowish, elytra with a single pair of eburneous elytral fasciae. Head with eyes moderately prominent, lobes divided; antennae reaching nearly to elytral apices, third segment about twice as long as fourth, segments unarmed apically. Pronotum about 1 1/3 times as long as broad; sides moderately rounded, base impressed, apex somewhat narrowed; discal surface moderately finely, longitudinally reticulate, finely asperate, base and apex indistinctly, sparsely, pale golden pubescent; entire surface moderately sparsely clothed with long, erect, pale hairs; prosternum with posterior 2/3 bearing coarse punctures and moderately dense, subdepressed, pale pubescence; hind-lateral margins of mesepimera and hind margin of metasternum whitish pubescent. Scutellum with apex broadly

FIGURE 43. *Euderces postipallidus*, new species, male.

rounded, surface densely golden pubescent. Elytra about 2 1/2 times as long as width across humeri; sides subparallel, slightly wider behind middle; apices rounded; each side near base somewhat gibbose; a narrow, transverse, raised, often strongly arcuate eburneous fascia present from margin to middle of disk on each side at about basal 1/3; surface with basal 1/4 somewhat shining, moderately densely punctate, cribrate-punctate on gibbosities, with pale, subrecumbent pubescence surrounding basal gibbosities, premedian 1/3 of elytra densely cribrate-punctate around and mostly behind eburneous fasciae, remainder of elytra impunctate, finely alutaceous, with a fascia of fine, pale golden, appressed pubescence across apical 1/3, pubescence finer, sparser behind fascia; entire disk sparsely clothed with long, erect hairs. Abdomen shining; first sternite with a small, oblique, pale pubescent marking on each side, remaining sternites sparsely pubescent; terminal sternite nearly as long as fourth, apex broadly rounded. Legs with femora smooth, moderately abruptly clavate, shining, with longitudinal bands of pale pubescence, sparsely clothed with long, erect, pale hairs.

Female: Similar to male. Length 5.5–7.5 mm. Antennae slightly shorter, slightly exceeding middle of elytra. Prosternum lacking coarse punctures. Abdomen with terminal sternite slightly longer than fourth, apex rounded.

REMARKS. — *Euderces postipallidus* shares the apically paler integumental coloration with the often sympatric *E. auricaudus*, but differs by the lack of antennal spines and the much lower elytral gibbosities. This species is very similar to *E. basimaculatus*, differing primarily by color. In *E.basimaculatus* the blackish integument of the body is marked with orange-brown on the elytral base and the pubescence at the pronotal base is coarser, more extensive, and whitish. In addition, this species usually has arcuate or sinuate eburneous fasciae, while these markings on *E. basimaculatus* tend to be more or less straight. The specific name refers to the elytral color pattern: *post* = behind (L.) + *pallidus* = pale (L.).

Euderces propinquus, new species
(Fig. 44)

TYPES. — Holotype male [EMEC], allotype and 9 paratypes (5 males, 4 females) from MEXICO, Oaxaca, 7–8 mi. E Mitla, 6200 ft., July 3–9, 1994 (E. Giesbert). Four additional paratypes, all from Oaxaca, MEXICO, as follows: 1 female, 14 km NW Diaz Ordaz, 2600 m, June 15, 1979 (H. & A. Howden); 1 male, 1 female, 11.1 km NW Diaz Ordaz, 2400 m, July 4, 1989 (Barchet); 1 female, N of Hwy #190, 7 km N Diaz Ordaz, July 17, 1992 (G. H. Nelson, D. S. Verity). Paratypes are deposited with EMEC, CNMN, JEBC, HAHC, EFGC.

DESCRIPTION. — *Male*: Length 4.5–5 mm, form moderately slender. Integument dull orange-brown, front and vertex, prothorax except basal impression, apical 1/3 and along each side of disk to basal 1/3 of elytra, abdomen, and parts of legs infuscated with dark brown; elytra with a pair of slightly oblique eburneous markings preceded by (usually) a pair of small evanescent eburneous spots. Head with eyes moderate-sized,

FIGURE 44. *Euderces propinquus*, new species, male.

lobes divided; antennae surpassing middle of elytra, third segment 1 1/2 times as long as scape, slightly longer than fourth segment, segments unarmed and feebly swollen apically. Pronotum about 1 1/4 times as long as broad; sides rounded, base narrowed and deeply impressed, apex somewhat narrowed, and slightly impressed; discal surface moderately finely striolate, asperate in median area; entire surface with sparse, long, erect, pale hairs; prosternum with posterior 2/3 bearing coarse punctures; lateral margins of mesepimera and hind margin of metasternum indistinctly pale pubescent. Scutellum with apex subtruncate, surface pale pubescent. Elytra slightly more than 2 1/2 times as long as width across humeri; sides somewhat impressed slightly before middle, widest at apical 1/3; apices narrowly rounded; each side near base feebly gibbose; a narrow, slightly raised, eburneous fascia present on each side from margin obliquely back to slightly beyond middle of disk at about basal 2/5, a small, evanescent (sometimes absent) eburneous spot present on each side of suture slightly anterior to fascia; surface with basal 3/5 densely cribrate-punctate, apical 2/5 alutaceous, with an indistinct, oblique fascia of short, fine, appressed, pale pubescence across apical 1/3; entire disk sparsely clothed with long, pale, erect hairs. Abdomen shining, with very sparse, erect, pale hairs; terminal sternite nearly as long as fourth, apex broadly rounded. Legs with femora abruptly clavate; surface smooth, shining, very sparsely clothed with long, erect, pale hairs.

Female: Similar to male. Length 4.5–5.5 mm. Antennae slightly shorter, reaching about to middle of elytra. Prosternum lacking coarse punctures. Abdomen with terminal sternite slightly longer than fourth, apex rounded.

REMARKS. — This species appears to be closely related to *E. laevicauda*, *E. perplexus*, and *E. batesi*. *E. propinquus* may be separated from the similarly colored *E. batesi* by the presence of a second pair of small eburneous spots (although these are often evanescent, and sometimes absent), the broader elytral humeri, longer antennae, lack of apical carinae on the femora, and absence of pubescence on the first abdominal sternite. From *E. laevicauda*, *E. propinquus* may be distinguished by the shorter striations of the pronotal disk, lack of pubescent markings on the first sternite, and size and position of the smaller pair of eburneous spots. It may be separated from *E. perplexus* by the bicolored integument, broader elytral humeri, and reduction of the anterior eburneous spots. The species name refers to the taxonomic position of the species relative to *E. batesi*, *E. perplexus*, and *E. laevicauda*: *propinquus* = near (L.).

Euderces proximus, new species
(Fig. 45)

TYPES. — Holotype female [EMEC] and 1 female paratype from GUATEMALA, Baja Verapaz, 19–24 km N Salamá, 4500 ft., May 25–31, 1989 (E. Giesbert) [EFGC].

DESCRIPTION. — *Female*: Length 8.5–10.5 mm. Integument blackish, antennae, bases and tips of femora, apices of tibiae, and tarsi dark orange-brown; elytra with a single pair of eburneous fasciae. Head with eyes moderately small, lobes divided; antennae slightly exceeding middle of elytra, third segment about twice as

FIGURE 45. *Euderces proximus*, new species, female.

long as fourth, armed at apex with a slender spine less than 1/2 as long as fourth segment, apices of fourth and fifth segments with smaller, slender, sharp spines. Pronotum slightly more than 1 1/3 times as long as wide; sides moderately rounded and widest at middle; base and apex moderately, gradually impressed, feebly widened just before apex; disk with surface dull, longitudinally striate except at base and apex, with fine appressed golden pubescence forming wide, indistinct fasciae before middle and across base; entire surface sparsely clothed with long, erect, golden hairs; prosternum with posterior 1/2 clothed with very fine, short, moderately dense, whitish pubescence; lateral margins of mesepimera and hind margin of metasternum with wide bands of dense, white pubescence. Scutellum small, parallel-sided, apex broadly rounded, very finely golden pubescent. Elytra nearly three times as long as width across humeri; sides very slightly impressed at middle; apices truncate, hind angles not rounded; each side at base with a distinct, elongate, slightly oblique, coarsely punctate gibbosity near suture; a narrow, transverse, raised, slightly oblique, eburneous fascia present on each side at basal 1/3 from margin to past middle of disk; surface shining, with basal 1/3 very sparsely punctate except on gibbosities, golden pubescence surrounding basal gibbosities; median 1/5 densely cribrate-punctate and pubescent across middle behind eburneous fasciae, with dense punctures extending up suture to gibbosities, remainder of surface nearly impunctate, with a well-defined, broad, arcuate fascia of golden pubescence across apical 1/3, front margin of pubescent fascia slightly paler, area behind fascia bearing scattered, short, erect, golden hairs; entire disk sparsely clothed with long, erect, golden hairs. Abdomen shining; first sternite clothed with white pubescence on hind lateral angles, remaining sternites more sparsely pubescent; terminal sternite about as long as fourth, apex rounded. Legs with femora moderately abruptly clavate, indistinctly carinate at apices; surface smooth, shining, with longitudinal bands of short, pale pubescence.

Male: Unknown.

REMARKS. — This species is very similar to *E. boucardi*, differing only by the shorter spine of the third antennal segment and spined fifth segment, the somewhat more developed, punctate and less pubescent basal elytral gibbosities and the basad extension of the cribrate-punctate elytral area. The specific name refers to the similarity to *E. boucardi*: *proximus* = nearest (L.).

Euderces pulcher (Bates), new combination
(Figs. 4, 12c, 46)

Cleozona pulchra Bates, 1874:223; 1880:60; Aurivillius, 1912:420; Chemsak, 1967:75; 1969:304. (TYPE LOCALITY: Chontales, Nicaragua.)

Cleozona pulchra var. *rufipes* Bates, 1885:307; Aurivillius, 1912:420; Chemsak, 1967:75; Chem-

FIGURE 46. *Euderces pulcher* (Bates), male.

sak, Linsley & Mankins, 1980:32. (TYPE LOCALITY: Tehuantepec, Mexico.)
Cleozona rufipes; Linsley, 1935:89.

REDESCRIPTION. — *Male*: Length 8–15 mm. Integument black, usually marked with a wide, mid-elytral band of orange which encompasses four oblique, narrow eburneous fasciae; legs often entirely orange. Head with eyes moderately small, lobes divided; antennal tubercles small, acute; antennae exceeding apex of elytra by about three segments, third to fifth segments longitudinally grooved, third segment nearly twice as long as fourth, armed at apex with a short, sharp spine which is about 1/2 as long as second segment, apices of fourth and fifth segments with smaller spines. Pronotum about 1 1/3 times as long as wide; sides rounded, widest at middle, base and apex narrowed, somewhat transversely impressed before base; disk with surface almost asperate-punctate, with an indistinct fascia of white appressed pubescence behind apex, entire surface moderately densely clothed with long and short, erect, pale hairs, with a broad oval of dense, erect, darker hairs at middle of disk; prosternum with posterior 2/3 bearing coarse punctures and moderately dense, erect, white pubescence; hind margins of prothorax, mesepimera, meso- and metasternum and metepisterna clothed with dense, white pubescence. Scutellum moderately large, apex narrowly rounded, surface densely clothed with appressed white pubescence. Elytra about 2 1/2 times as long as width across humeri; sides subparallel; apices sinuate-truncate, sometimes bidentate; disk on each side near base feebly gibbose, each side with a pair of narrow, oblique, raised, yellowish, eburneous fasciae extending from lateral margin nearly to suture, apices of fasciae separated across suture by about length of fourth antennal segment; surface with basal 3/4 densely cribrate-punctate, with a patch of subrecumbent whitish hairs around basal gibbosities, which continues narrowly on suture to connect with the apex of a narrow, inverted chevron of fine, appressed whitish pubescence, apical 1/4 coarsely alutaceous, with punctation indistinct; disk sparsely clothed with pale, erect hairs. Abdomen with first sternite clothed laterally and on both sides of apex with dense, white pubescence, remaining sternites finely pale pubescent; terminal sternite about as long as fourth, apex broadly rounded. Legs with femora gradually clavate; surface shining, very sparsely punctate and pubescent.

Female: Similar to male. Length 8.5–14 mm. Antennae shorter, slightly exceeding middle of elytra. Prosternum lacking coarse punctures. Abdomen with terminal sternite slightly longer than fourth, apex rounded to subtruncate.

REMARKS. — The characters given by Bates (1874) to separate *Cleozona*, such as grooved antennal segments, gradually clavate metafemora, and tibial carinae, all appear among the many species of *Euderces* described subsequently. A few specimens have been seen in which there are irregular, incomplete, eburneous lineoles between the paired fasciae. As in the related *E. longicollis*, specimens from coastal Jalisco are usually all black, but do not differ structurally from other populations with bicolored elytra. The flight period is June to August from western Mexico to Nicaragua (see Fig. 4).

Euderces pusillus, new species
(Fig. 47)

TYPES. — Holotype male [NMNH], allotype and 8 paratypes (1 male, 7 females) from COSTA RICA, El Congo, January 20–February 5, 1934 (H. Paez). Three additional paratypes as follows: 1 female, GUATEMALA, Zacapa, 3 km N La Union, 3500 ft., April 14–20, 1990 (E. Giesbert); 1 female, GUATEMALA, Quetzaltenango, 5 mi. E Coatepeque, July 4, 1965 (Slobodchikoff & Raske); 1 male, MEXICO, Chiapas, 4 mi. SW Simojovel, March 18, 1953 (R. C. Bechtel & E. I. Schlinger). Paratypes are deposited with NMNH, EMEC, EFGC.

DESCRIPTION. — *Male*: Length 3.5–5 mm. Integument blackish to dark brown, antennae, coxae, femoral bases, and tarsi brown; elytra with a single pair of eburneous fasciae. Head with eyes divided, upper lobes very small; antennae slightly exceeding middle of elytra, third segment twice as long as fourth, armed at apex with a sharp spine which is about 2/3 as long as fourth segment, apex of fourth segment with a short spine, fifth segment dentate. Pronotum with sides broadly rounded to apex, strongly narrowed and impressed across basal 1/6; disk with surface finely alutaceous, moderately sparsely asperate, sparsely, indistinctly clothed with short, appressed, pale pubescence near base and apex; entire surface moderately clothed with long, erect, pale hairs; prosternum with posterior 1/2 bearing scattered, coarse punctures and fine, subdepressed, pale pubescence at sides, middle glabrous; lateral margins of mesepimera and hind margins of meso- and metasternum clothed with pale pubescence. Scutellum small, rounded, surface clothed with fine, pale pubescence. Elytra slightly more than twice as long as width across humeri; sides somewhat impressed at basal 1/2; apices broadly rounded; each side slightly gibbose near base, with an indistinct, oblique impression between humerus and gibbosity; a narrow, transverse, raised, eburneous fascia present on each side at basal 1/3 from lateral margin to just past middle of disk; discal surface with basal 1/4 shining, base and humeri impunctate, moderately densely punctate behind base, premedian 1/4 dull, densely cribrate-punctate before and behind eburneous fasciae, remainder of surface somewhat shining, alutaceous, sparsely punctate, with a usually indistinct chevron of appressed pale pubescence across apical 1/3; entire surface very sparsely clothed with long, erect, pale hairs. Abdomen shining, sparsely pubescent; terminal sternite nearly as long as fourth, apex broadly rounded. Legs with femora moderately abruptly clavate, apically carinate; surface smooth, shining, with indistinct, longitudinal lineoles of short, pale pubescence.

Female: Similar to male. Length 4.25–5.25 mm. Antennae slightly shorter, barely reaching middle of elytra. Prosternum lacking coarse punctures. Abdomen with terminal sternite slightly longer than fourth, apex rounded.

REMARKS. — This species may be distinguished by its small size, dark integument, long antennal spines, asperate pronotum, and poorly developed elytral gibbosities. The specific name refers to the small size: *pusillus* = little (L.).

FIGURE 47. *Euderces pusillus*, new species, male.

Euderces reichei LeConte
(Figs. 6, 48)

Euderces reichei LeConte, 1873:202; Leng, 1887:24, 44; Aurivillius, 1912:419; Knull, 1946:226; Fattig, 1947:27 (record); Linsley,1964:182; Hoffmann, 1971:109; Chemsak & Linsley, 1975:87; MacRae, 1993:236 (habits). (TYPE LOCALITY: Texas.)

Euderces reichei reichei Linsley, 1964:182; Turnbow & Franklin, 1980:343 (record); Lingafelter & Horner, 1993:176.

Euderces exilis Casey, 1893:591; Leng & Hamilton, 1896:173; Linsley & Martin, 1933:191 (habits); Vogt, 1949:144 (habits); Manley & French, 1976:49; WARD et al, 1977:13 (hosts). (TYPE LOCALITY: Texas.) **NEW SYNONYMY.**

Apelocera exilis Aurivillius, 1912:420.

Euderces reichei exilis Linsley, 1964:182; Chemsak & Linsley, 1975:87; Hovore, Penrose & Neck, 1987: 307 (habits).

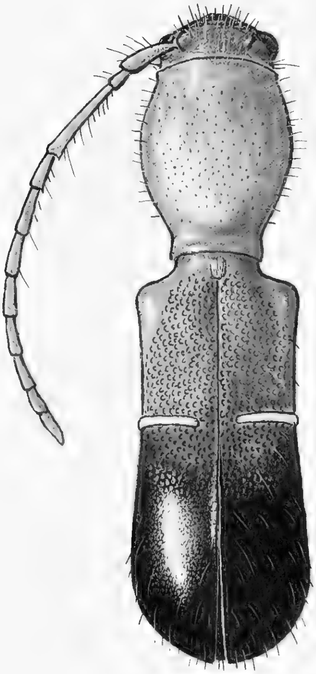

FIGURE 48. *Euderces reichei* LeConte, male.

REDESCRIPTION. — *Male*: Length 3.5–5 mm. Integument orange to light red-brown, with abdomen and about apical 1/2 of elytra blackish (in southern populations integument often entirely blackish except red-brown mouthparts, antennae, tarsi, and parts of legs). Head with eyes rather small, lobes divided; antennae exceeding middle of elytra, third segment about 2 1/3 times as long as fourth, apex dentate or with a fine, short spine, fourth segment with apex minutely dentate or spiculate. Pronotum about 1 1/3 times as long as broad; sides rounded, strongly impressed at base, slightly narrowed at apex; discal surface shining near apex, moderately sparsely covered with distinct, small asperites except near base and apex, entire surface clothed with long, erect, pale hairs; prosternum with basal 1/2 moderately distinctly punctate, indistinctly, finely, pale pubescent; lateral and hind areas of mesepimera and metasternum clothed with white pubescence. Scutellum small, slightly elongate, clothed with pale pubescence. Elytra slightly more than twice as long as width across humeri; sides slightly impressed before middle, widest before apex; apices jointly rounded; a narrow, transverse, raised, eburneous fascia present on each side at basal 1/3 from lateral margin nearly to suture; disk feebly gibbose near base on each side of suture; surface with extreme base, humeri, and apical 1/2 smooth, shining, or somewhat alutaceous, discal area surrounding eburneous fasciae from just behind base to middle opaque, coarsely, densely cribrate-punctate; entire disk clothed with long, erect, pale hairs. Abdomen shining, sparsely pubescent; terminal sternite nearly as long as fourth, apex broadly rounded. Legs with femora moderately abruptly clavate, with short, indistinct apical carinae; surface smooth, shining, sparsely clothed with long, pale hairs.

Female: Similar to male. Length 3.5–5 mm. Antennae slightly shorter, reaching basal 1/3 of elytra. Abdomen with terminal sternite slightly longer than fourth, apex narrowly rounded.

REMARKS. — This species may be distinguished by the small size, finely asperate pronotum, lack of elytral gibbosities and preapical pubescent fascia, and feebly armed antennal segments. This latter character, as well as the integumental color, is somewhat variable. The flight period is from March to July.

Euderces reichei, with an unusually wide range from Ohio, Indiana, and southern Illinois, southeast to Florida and west to Texas, through San Luis Potosí to Veracruz, Mexico (see Fig. 6), has several character states which appear to intergrade clinally. Northern and eastern U. S. populations differ slightly by the dentate apices of the third and fourth antennal segments, and by the smooth, shining integument of the body. In Texas and south into Mexico, the antennae have fine, short spines and somewhat more alutaceous integument. Individuals seen from San Luis Potosí and Veracruz, Mexico differ by an increase in melanism: the integument in this part of the range is often all black and only feebly alutaceous.

Euderces exilis Casey, which has been regarded as a subspecies by Linsley (1964), differs from *E. reichei* only by the tendency toward the somewhat more developed antennal spines. The two are sympatric in Texas (Bexar Co.).

Recorded host plants are *Acacia farnesiana, A. tortuosa, Celtis, Citrus, Condalia obovata, Cornus florida, Diospyrus texana, Prosopis glandulosa, Salix, Sapindus drummondi, Zanthoxylum fagara.*

FIGURE 49. *Euderces reticulatus* (Bates), male.

Euderces reticulatus (Bates)
(Fig. 49)

Apilocera reticulata Bates, 1885:306. (TYPE LOCALITY: San Joaquin, Guatemala.)
Apelocera reticulata Aurivillius, 1912:420.
Eplophorus reticulatus Blackwelder, 1946:583.
Euderces reticulatus Chemsak & Linsley, 1975:88.

MATERIAL EXAMINED. — MEXICO: Chiapas, 21 km N Ocozocoautla, August 24, 1982 (Clark & Cave) [EMEC]; 1 female, Chiapas, 2 mi. S Simojovel, June 9, 1969 (J. M. Campbell); 1 male, Chiapas, 11 km S Bochil, September 29–30, 1989 (F. Hovore) [FTHC]; 1 female, Veracruz, UNAM Est. Biol. Las Tuxtlas, April 21–27, 1990 (Hovore) [FTHC].

REDESCRIPTION. — *Male*: Length 5.5 mm. Integument blackish or reddish brown, abdomen and apical 1/3 of elytra usually somewhat infuscated; elytra with a single pair of eburneous fasciae. Head with eyes moderately small, lobes divided, upper lobes very small; antennae reaching nearly to middle of elytra, third segment nearly three times as long as fourth, armed at apex with a long, blunt spine which is subequal in length to the fourth segment, apex of fourth segment unarmed. Pronotum about 1 1/4 times as long as wide; sides rounded, basal 1/4 strongly impressed; disk with surface moderately finely, longitudinally rugulose and asperate, finely, indistinctly pubescent at base and apex; entire surface clothed with long, erect, pale hairs; prosternum with posterior 1/2 bearing punctures and moderately dense, subdepressed, white pubescence; lateral and hind margins of prosternum and epimera, mesocoxae and posterior 1/2 of metasternum clothed with dense, white pubescence. Scutellum apically subtruncate, impunctate, glabrous. Elytra slightly less than 2 1/2 times as long as width across humeri; sides feebly impressed before middle; apices rounded; each side near base with a strong, highly elevated gibbosity which is moderately coarsely scabrous-punctate at its apex; a narrow, transverse, raised, eburneous fascia present on each side at basal 2/5 from near lateral margin to past middle of disk; discal surface with basal 1/3 somewhat shining, obsoletely punctate, alutaceous, moderately sparsely, indistinctly clothed with subdepressed, pale pubescence, median 1/4 densely cribrate-punctate before and behind eburneous fasciae, remainder of surface to apex impunctate, somewhat alutaceous, apical 1/3 moderately clothed with fine, pale pubescence which is slightly denser anteriorly; entire disk clothed with long, erect, pale hairs. Abdomen shining, very sparsely punctate, nearly glabrous; terminal sternite slightly shorter than fourth, apex broadly rounded. Legs with femora moderately abruptly clavate, surface smooth, shining, with short longitudinal bands of pale pubescence.

Female: Similar to male. Length 5–6 mm. Antennae slightly shorter, reaching basal 1/3 of elytra. Prosternum lacking distinct punctures. Abdomen with terminal sternite slightly longer than fourth, apex rounded.

REMARKS. — Bates (1885) described this species as having the pronotal surface reticulate. Examination of the type and a number of more recently collected specimens has shown this to be misleading. The pronotal disk is asperate and moderately finely, longitudinally rugulose, and the reticulation is unclear. This species may be separated from the similar *E. sculpticollis* by its smaller size, longer, blunt spine of the third antennal segment, and slightly more widely separated inner ends of the eburneous fasciae. The body color is sometimes reddish as in the type, but large series with piceous integument have also been seen. The appendages are usually reddish brown in both color forms. Flight occurs from April to October from southern Mexico (southern Veracruz to Chiapas) to Guatemala and Belize.

Euderces rubellus (Bates)
(Fig. 50)

Apilocera rubella Bates, 1885:307. (TYPE LOCALITY: Volcan de Atitlan, Guatemala.)
Apelocera rubella Aurivillius, 1912:420.
Eplophorus rubellus Blackwelder, 1946:583.
Euderces rubellus Chemsak & Linsley, 1975:88.

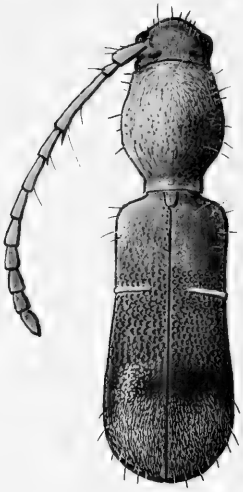

FIGURE 50. *Euderces rubellus* (Bates), Holotype male.

REDESCRIPTION. — *Male*: Length 4 mm. Integument reddish, posterior portion of elytra, abdomen, and legs brown, elytra with a single pair of eburneous fasciae. Head with eyes divided, upper lobes very small; antennae reaching to about apical 1/3 of elytra, third segment slightly more than 1 1/2 times as long as scape, slightly more than twice as long as fourth, armed at apex with a sharp spine which is subequal to second segment, apex of fourth segment minutely spinose. Pronotum about 1 1/3 times as long as broad; sides rounded, somewhat impressed at base, less strongly narrowed at apex; discal surface moderately finely, indistinctly asperate and rugulose, clothed on apical 1/4 and at base with fine, short, appressed pale pubescence; entire surface with sparse long, erect, pale hairs; prosternum with posterior 3/5 bearing coarse punctures and sparse pale pubescence; lateral margins of mesepimera and sides of hind margin of metasternum pale pubescent. Scutellum small, rounded, clothed with pale pubescence. Elytra slightly more than twice as long as width across humeri; sides slightly impressed before middle, somewhat wider before apex; apices broadly rounded; each side near base with gibbosity only very feebly indicated; a narrow, transverse, raised, acuminate, eburneous fascia present on each side at about basal 1/3 from lateral margin to about middle of disk; discal surface with basal 3/5 densely punctate, slightly shining near base, becoming opaque and cribrate-punctate in middle, apical 2/5 indistinctly punctate and alutaceous, apical 1/3 moderately clothed with fine, appressed, pale golden pubescence; entire disk clothed with long, erect, pale hairs. Abdomen shining, sparsely pubescent; terminal sternite about as long as fourth, apex broadly rounded.

Legs with femora moderately abruptly clavate; surface smooth, shining, with longitudinal bands of short, pale pubescence.

Female: Not seen.

REMARKS. — Only the holotype [BMNH] was examined in this study. *Euderces nelsoni* is very similar in form and color, differing by the presence of low gibbosities on the elytral humeri, more strongly developed eburneous fasciae, differences in sculpture and pubescence of the pronotum, and apparently somewhat larger size.

Euderces sculpticollis (Bates)
(Fig. 51)

Apilocera sculpticollis Bates, 1885:306; Chemsak, 1967:74 (lectotype). (TYPE LOCALITY: Cerro Zunil, Guatemala.)
Apelocera sculpticollis Aurivillius, 1912:420.
Eplophorus sculpticollis Blackwelder, 1946:583; Chemsak, 1967:74.
Euderces sculpticollis Chemsak & Linsley, 1975:88.

MATERIAL EXAMINED. — One male, one female (type specimens), GUATEMALA, El Zumbador, 2500 ft. (Champion) [BMNH] (This is a location in San Marcos province, 19 km NW of Coatepeque).

REDESCRIPTION. — *Male*: Length 4.5 mm. Integument blackish to dark reddish brown; elytra with a single pair of eburneous fasciae. Head with eyes moderately small, lobes divided; antennae reaching about middle of elytra, third segment slightly less than 2 1/2 times as long as fourth, armed at apex with a moderately long, acute spine which is slightly more than 1/2 as long as fourth segment, apex of fourth segment with a distinct, short spine. Pronotum about 1 2/5 as long as wide; sides rounded, basal 1/4 widely impressed; disk with surface longitudinally striolate and rugulose, with an indistinct, wide fascia of moderately dense, appressed, golden pubescence across apical 1/5, sparse, appressed golden pubescence at middle and more densely golden pubescent near base; entire surface moderately sparsely clothed with long, erect, pale hairs; prosternum with posterior 3/5 bearing coarse punctures and moderately dense, subdepressed, pale pubescence; lateral and hind margins of epimera, mesocoxae and hind margin of metasternum clothed with dense, pale pubescence. Scutellum rounded, impunctate, finely pale pubescent. Elytra about 2 1/2 times as long as width across humeri; sides slightly impressed before middle; apices rounded; each side near base with a strong, moderately elevated gibbosity which is asperate-punctate at its apex; a narrow, transverse, raised, eburneous fascia present on each just behind basal 1/3 from lateral margin to very near suture; discal surface with basal 1/3 shining, with moderately dense punctures and moderately dense, fine, pale pubescence surrounding gibbosities, a moderately wide fascia of opaque cribrate-punctures present behind eburneous fasciae; apical 1/2 impunctate, somewhat alutaceous; apical 1/3 clothed with appressed pale golden pubescence which is denser anteriorly; entire disk sparsely clothed with long, erect, golden hairs. Abdomen shining, very sparsely punctate, first segment with a distinct, oblique marking of dense, pale pubescence, remaining segments sparsely pubescent laterally; terminal sternite slightly shorter than fourth, apex broadly rounded. Legs with femora moderately abruptly clavate; surface smooth, shining, with longitudinal bands of short, pale pubescence.

FIGURE 51. *Euderces sculpticollis* (Bates), Holotype male.

Female: Similar to male. Length 5.5 mm. Antennae slightly shorter, reaching middle of elytra. Prosternum lacking coarse punctures. Abdomen with terminal sternite slightly longer than fourth, apex rounded.

REMARKS. — Only the lectotype and one other specimen of this species were examined. In the female, the integumental color is reddish brown. The male is piceous.

Euderces spinicornis (Chevrolat)
(Figs. 4, 52)

Clytus spinicornis Chevrolat, 1835, fasc. 4, no. 7; Thomson, 1860:229. (TYPE LOCALITY: Mexico)
Eplophorus spinicollis Chevrolat, 1861:248 (error).
Apelocera spinicornis Chevrolat, 1862:62.
Apilocera spinicornis Chevrolat, 1862:535; Bates, 1880:60; 1885:305.
Eplophorus spinicornis Blackwelder, 1946:583; Chemsak, 1969:309.
Euderces spinicornis Chemsak & Linsley, 1975:88.
Clytus elegans Laporte & Gory, 1835, pl. 20, fig. 129. (TYPE LOCALITY: not given.)

FIGURE 52. *Euderces spinicornis* (Chevrolat), male.

REDESCRIPTION. — *Male*: Length 5–6 mm. Integument dull orange, prothorax except base and apex, a wide, strongly sinuous band (sometimes interrupted) across humeri behind scutellum across basal gibbosities and extending down suture to area of eburneous fasciae, apical 2/5 of elytra, base of metasternum, and abdomen black; hind femoral club infuscated with dark brown; elytra with a single pair of eburneous fasciae. Head with eyes moderately small, lobes divided; antennae short, reaching middle of elytra, third segment more than twice as long as fourth, armed at apex with a long, feebly sinuate, blunt spine which is slightly longer than fourth segment, apex of fourth segment with a short spine. Pronotum with sides rounded; basal 1/6 impressed and narrowed; disk with surface dull, longitudinally rugulose; base and apex with fine, pale, recumbent pubescence; entire surface sparsely clothed with long, erect, pale hairs; prosternum with posterior 1/2 bearing coarse punctures and moderately dense white pubescence; hind margins of mesepimera and metasternum with distinct fasciae of dense, silvery-white pubescence. Scutellum subtriangular, apex narrowly rounded, pubescence sparse. Elytra more than twice as long as width across humeri; sides slightly impressed at basal 1/2; apices broadly rounded; disk with a well-developed, subvertical gibbosity on each side near base, apices of gibbosities punctate; a narrow, transverse, raised, eburneous fascia present on each side slightly before middle, narrowed and subacuminate toward suture; surface shining, with a dense, cribrate-punctate area across middle 1/3, mostly behind the eburneous fasciae, basal 1/3 more sparsely punctate, apical 1/3 impunctate, alutaceous; recumbent pale pubescence present on area surrounding basal gibbosities and behind a narrow black band as a well-defined patch covering apical 1/4; entire disk sparsely clothed with long, erect, pale hairs. Abdomen shining, first sternite nearly glabrous, remaining sternites moderately pale pubescent; terminal sternite about as long as fourth, apex very broadly rounded. Legs with femora moderately abruptly clavate; surface smooth, shining, with longitudinal bands of short, pale pubescence.

Female: Similar to male, with antennae slightly shorter. Length 5–6 mm. Prosternum lacking coarse punctures. Abdomen with terminal sternite slightly longer than fourth, apex somewhat more narrowly rounded.

REMARKS. — This species is structurally similar to *E. hoegei*, but differs consistently by its more complex and contrasting reddish and blackish integumental pattern. Flight occurs from May to August in eastern Mexico, Guatemala and Honduras (see Fig. 4).

Euderces succinus, new species
(Fig. 53)

TYPE. — Holotype male [EMEC] from GUATEMALA, Baja Verapaz, 6–9 km E Purulhá, approx. 5000 ft., April 15–24, 1990 (E. Giesbert).

DESCRIPTION. — *Male*: Length 5 mm. Integument yellow-brown; head, pronotum and scutellum light orange-brown; an indistinct area immediately behind a single pair of elytral eburneous fasciae, tibiae and outer antennal segments brown. Head with eyes moderately small, lobes divided; antennae reaching apical 1/4 of elytra, third segment 2 1/2 times as long as fourth, armed at apex with a long, blunt spine which is slightly longer than fourth segment, apex of fourth segment acutely dentate. Pronotum slightly longer than wide; sides widely rounded at middle, impressed and narrowed at base, less so at apex; disk somewhat flattened, lateral margins abrupt, surface moderately coarsely, longitudinally rugulose-striate between basal and apical impressions; entire surface sparsely clothed with long, erect, pale brown hairs; prosternum with posterior 1/2 bearing indistinct punctures and pale pubescence; hind lateral areas of mesepimera and metasternum with indistinct, large spots of dense, pale pubescence. Scutellum shining, subtriangular, apex narrowly rounded. Elytra slightly less than 2 1/2 times as long as width across humeri; sides feebly impressed before middle; apices broadly rounded; disk with a long, low, arcuate gibbosity on each side near scutellum; a raised, eburneous fascia present on each side slightly before middle from near margin forward to near suture; surface shining, basal 1/2 sparsely punctate, punctures slightly denser immediately behind eburneous fasciae, apical 1/2 impunctate, with a narrow, distinct fascia of white hairs across apical 1/4; entire disk sparsely clothed with long, erect, pale brown hairs. Abdomen shining, nearly glabrous, with very sparse, pale, erect, short hairs; terminal sternite about as long as fourth, apex very broadly rounded. Legs with femora moderately abruptly clavate; surface smooth, shining.

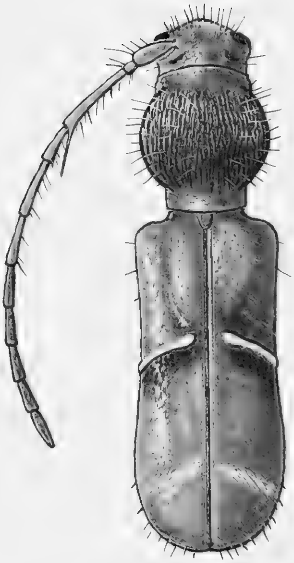

FIGURE 53. *Euderces succinus*, new species, Holotype male.

Female: Unknown.

REMARKS. — This species, known only from the type, may be easily separated by the yellow-brown and orange-brown integument, the long spine of the third antennal segment, and by the lack of cribrate-punctate areas of the elytra. The specific name describes the integumental color: *succinum* = amber (L.).

Euderces tibialis, new species
(Figs. 12d, 54)

TYPES. — Holotype male [EMEC], allotype and 3 paratypes (2 males, 1 female) from MEXICO, Veracruz, E slope of Volcán San Martin Tuxtla, 2200 ft., running on recently dead "Bejuco" trunk and branches, July 5, 1994 (E. Giesbert). Five additional paratypes from MEXICO as follows: 1 male, Veracruz, UNAM Los Tuxtlas Biological Station, April 21–27, 1990 (F. T. Hovore); 2 males, 2 females, Chiapas, 4 mi. S Palenque, 200 ft., "tropical lowland forest," July 25–30, 1983 (R. Anderson). One female paratype from GUATEMALA, Petén, Tikal (at light

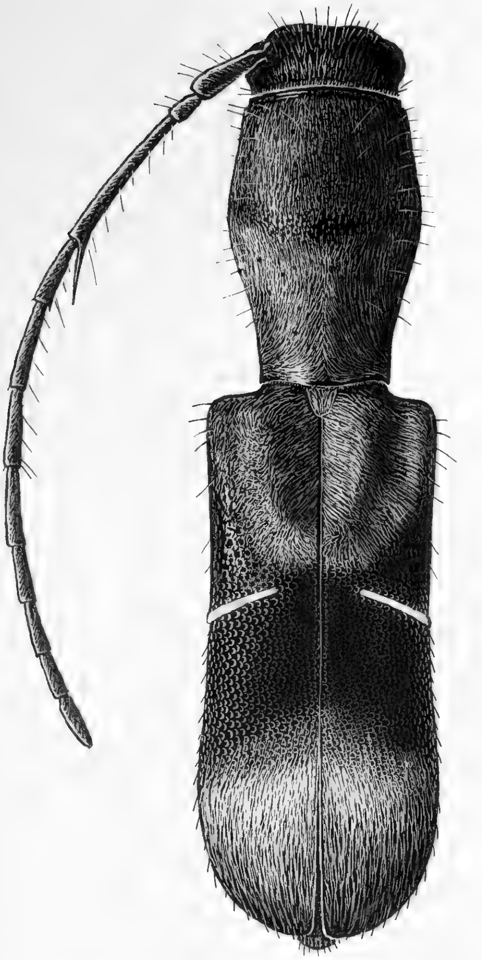

FIGURE 54. *Euderces tibialis*, new species, male.

at camp), March 14, 1956 (I. J. Cantrall). Paratypes are deposited with CNMN, TAMU, EFGC, FTHC.

DESCRIPTION. — *Male*: Length 7.5–9.25 mm. Integument blackish; elytra with a single pair of eburneous fasciae. Head with eyes moderately small, lobes divided; antennae slightly exceeding middle of elytra, third segment more than twice as long as fourth, armed at apex with a long, sharp spine which is nearly as long as fourth segment, apex of fourth segment with a minute tooth or spine. Pronotum somewhat elongate, more than 1 1/2 times as long as broad; sides slightly rounded, gradually narrowed to base; disk with surface longitudinally rugulose and asperate, moderately densely clothed with short, appressed, golden pubescence with sparsely scattered minute asperations visible as small dark spots, interrupted by a narrow, arcuate, subglabrous fascia slightly before middle; entire surface moderately sparsely clothed with long, erect, pale hairs; prosternum with posterior 1/2 bearing coarse punctures and moderately dense, subdepressed, white pubescence; lateral and hind margins of epimera, meso- and metasternum, and pro- and mesocoxae clothed with dense, white pubescence. Scutellum subtriangular, apex rounded, moderately sparsely clothed with appressed golden pubescence. Elytra about 2 1/3 times as long as width across humeri; sides slightly impressed before middle; apices broadly rounded; each side near base moderately gibbose; a narrow, slightly oblique, raised, eburneous fascia present on each side at about basal 1/3 from lateral margin to past middle of disk; discal surface with basal 1/3 coarsely, densely punctate, with moderately dense, golden pubescence in area of basal gibbosities, remaining 2/3 densely cribrate-punctate and finely pubescent where surface is visible, apical 1/3 obscured by dense, appressed, golden yellow pubescence; entire disk clothed with long, erect, golden hairs. Abdomen moderately densely golden yellow pubescent; terminal sternite nearly as long as fourth, apex broadly rounded. Legs with femora moderately abruptly clavate, apices indistinctly carinate; surface smooth, shining, with longitudinal bands of short, pale pubescence; meso- and metatibiae somewhat curved, carinate, compressed, strongly flattened, nearly as broad as widest part of femoral club (see Fig. 12d).

Female: Similar to male. Length 7.25–8 mm. Antennae shorter, slightly exceeding middle of elytra. Prosternum lacking coarse punctures. Abdomen somewhat less densely pubescent, with terminal sternite slightly longer than fourth, apex rounded. Metatibiae slightly less modified, about as wide as femoral club.

DIAGNOSIS. — This species, along with *E. velutinus*, may be recognized by the lack of glabrous and impunctate areas on the elytra, the wide, compressed meso- and metatibiae, and the golden yellow pubescent elytral apex and abdomen. It may be separated from *E. velutinus* by the more elongate pronotum, less prominent elytral gibbosities which do not diverge posteriorly, the unarmed fifth antennal segment, and the generally less robust form. The specific name refers to the unusual form of the tibiae.

Euderces turnbowi, new species
(Fig. 55)

TYPES. — Holotype male [EMEC], allotype female, and 2 paratypes (1 male, 1 female) from MEXICO, Chiapas, 17 km W Tuxtla Gutierrez, June 21–25, 1987 (E. Giesbert, J. Wappes). Eleven additional paratypes as follows from Chiapas, MEXICO: 1 female, Pq. Nac. Sumidero, 1000 m., June 6, 1990 (H. & A. Howden); 2 males, same locality and date (B. D. Gill); 2 males, Pq. Nac. Sumidero, Coyota Mirador, 1700 m., June 17, 1989 (H. Howden); 1 male, 1 female, Pq. Nac. Sumidero, km. 11 on road, 1500 m., June 19, 1989 (Howden); 1 male, El Sumidero, June 23, 1990 (R. Turnbow); 2 males, Chicoasen, 400 m., June 8, 1990 (Gill); 1 female, 2 km S Chicoasen, Rd. to Mirador, June 18, 1989 (Howden). Six additional paratypes from GUATEMALA: 3 males, 2 females, Baja Verapaz, 19–24 km N Salamá, 4500 ft., May 25–31, 1989 (Giesbert, Wappes); 1 female, Zacapa, 16 km S San Lorenzo, 210 m, June 9, 1993 (H. & A. Howden). Paratypes are deposited with CNMN, EFGC, JEWC, RHTC, HAHC.

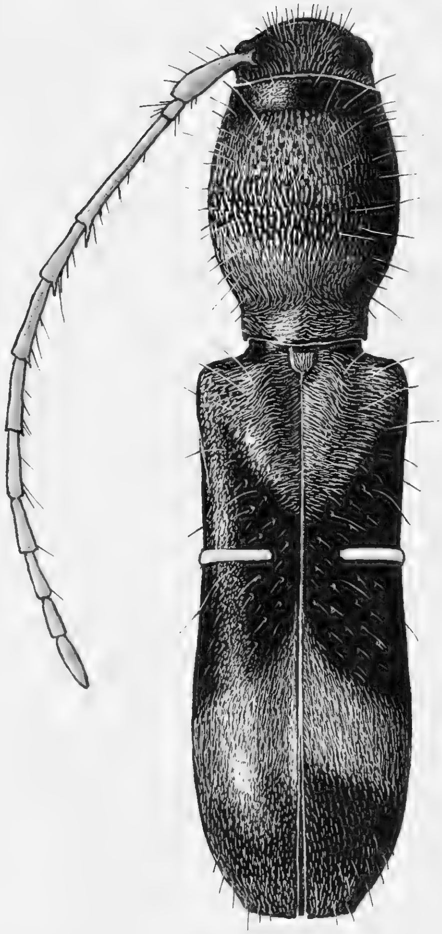

FIGURE 55. *Euderces turnbowi*, new species, female.

DESCRIPTION. — *Male*: Length 6–8 mm. Integument blackish, mouthparts, antennae, femoral bases, tibial apices, and tarsi orange-brown; elytra with a single pair of eburneous fasciae. Head with eyes moderately small, lobes divided; antennae exceeding apices of elytra, third segment slightly more than twice as long as fourth, armed at apex with a short, sharp spine, apex of fourth segment with a smaller spine. Pronotum about 1 1/3 times as long as wide; sides moderately rounded, somewhat narrowed and impressed across base; disk with surface longitudinally striate and rugulose, clothed with depressed golden pubescence, which is interrupted at middle by an indistinct, transverse, subglabrous fascia, and across apex by a distinct, impunctate and glabrous band; entire surface sparsely clothed with long, erect, golden hairs; prosternum with posterior 3/5 bearing coarse punctures and moderately dense, subdepressed, white pubescence; lateral and hind margins of prothorax, mesepimera and metasternum with wide bands of dense, white pubescence. Scutellum small, parallel-sided, apex broadly rounded, surface moderately golden pubescent. Elytra about 2 1/2 times as long as width across humeri; sides very slightly impressed before middle; apices truncate, or emarginate-truncate; each side near base feebly, broadly gibbose; a narrow, transverse, raised, eburneous fascia present on each side at basal 1/3 from margin to past middle of disk; surface shining, sparsely punctate, basal 1/3 glabrous except for a distinct patch of golden pubescence covering basal gibbosities, apical 1/3 with a well-defined, broad fascia of golden pubescence which is most dense at its posterior margin, area behind fascia bearing moderately sparse, short, suberect golden hairs; entire disk sparsely clothed with long, erect, golden hairs. Abdomen shining; first sternite marked with white pubescence at sides, remaining sternites sparsely pubescent; terminal sternite nearly as long as fourth, apex broadly rounded. Legs with femora moderately abruptly clavate; surface smooth, shining, with longitudinal bands of short, pale pubescence.

Female: Similar to male. Length 6–8 mm. Antennae slightly shorter, barely reaching middle of elytra. Prosternum lacking coarse punctures. Abdomen with terminal sternite slightly longer than fourth, apex rounded.

REMARKS. — This species may be recognized by a combination of the absence of densely cribrate-punctate areas on the elytra and piceous integument. The apical pubescent chevron is quite variable, being clearly defined and margined on some specimens, much less so on others. It is a pleasure to name this species for Robert H. Turnbow, Jr., in recognition of his many years of productive work in the collection of Neotropical Cerambycidae.

Euderces velutinus (Fisher)
(Fig. 56)

Eplophorus velutinus Fisher, 1931:100. (TYPE LOCALITY: Prieta, Republic of Honduras.)
Euderces velutinus Chemsak & Linsley, 1975:88.

REDESCRIPTION. — *Male*: Length 8.25 mm, form somewhat robust. Integument blackish; elytra with a single pair of eburneous fasciae. Head with eyes moderately small, lobes divided; antennae slightly exceeding middle of elytra, third segment nearly three times as long as fourth, armed at apex with a long, sharp spine which is about 3/4 as long as fourth segment, fourth segment with a distinct apical spine, fifth segment distinctly dentate at apex. Pronotum slightly longer than broad; sides moderately widely rounded, narrower at base than at apex; disk with surface moderately finely, longitudinally rugulose, moderately clothed with short, appressed, golden pubescence, which is interrupted by a narrow, arcuate, dark fascia slightly before middle connected with a narrow, dark vitta at middle between fascia and base; entire surface moderately sparsely clothed with long, erect, coarse hairs, which are denser at each end of premedian fascia; prosternum with basal 2/3 finely granulate and pale pubescent; lateral and hind margins of epimera and metasternum clothed with dense, whitish pubescence. Scutellum subtriangular, apex narrowly rounded, clothed with appressed golden pubescence. Elytra slightly more than twice as long as width across humeri; sides somewhat impressed before middle, widest at apical 2/3; apices broadly rounded; each side near base moderately strongly gibbose, gibbosities moderately coarsely punctate, and slightly divergent posteriorly; a slightly oblique, raised, eburneous fascia present on each side at about basal 3/8 from lateral margin to about middle of disk; discal surface with basal 1/3 finely, densely punctate, moderately sparsely clothed with recumbent golden pubescence, area behind eburneous fasciae densely cribrate-punctate where surface is visible, apical 1/2 obscured by dense, appressed, shining, golden-yellow pubescence; entire disk clothed with long, coarse, erect, dark hairs. Abdomen moderately densely golden yellow pubescent; terminal sternite shorter than fourth, apex broadly rounded. Legs

FIGURE 56. *Euderces velutinus* (Fisher), Holotype male.

with femora moderately abruptly clavate, apices indistinctly carinate; surface smooth, shining, with longitudinal bands of short, pale pubescence; meso- and metatibiae somewhat curved, carinate, compressed, strongly flattened.

Female: Unknown.

REMARKS. — Only the type of *E. velutinus* [NMNH] was seen in this study. This specimen, though apparently a male, does not exhibit the prosternal sexual punctation usually found in males of the genus. The metatibiae are similar to those of *E. tibialis* (see Fig. 12d). The type specimen was captured in Honduras in April.

Euderces venezuelensis, new species
(Figs. 2, 57)

TYPES. — Holotype male [FMNH] and 1 female paratype from VENEZUELA, Caracas Valley, May 6, 1922 (F. Psota) [FMNH].

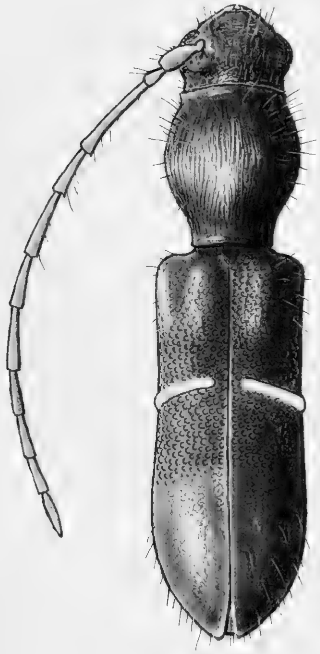

FIGURE 57. *Euderces venezuelensis*, new species, Holotype male.

DESCRIPTION. — *Male*: Length 4.5 mm. Integument orange-brown, head, prothorax and scutellum slightly darker brown. Head with eyes moderately small, lobes divided; antennae reaching about apical 1/4 of elytra, scape moderately short, third segment about twice as long as fourth, apex dentate, fourth and fifth segments with apices feebly dentate. Pronotum somewhat longer than broad; sides moderately rounded, impressed at base, slightly narrowed at apex; discal surface shining, moderately finely striate, basal 1/2 feebly tumid and asperate at middle; entire surface bearing long, erect, pale hairs; prosternum with basal 1/2 rugose, moderately finely scabrose-punctate, lacking distinct, large punctures, finely, pale pubescent; lateral and hind areas of mesepimera and metasternum moderately clothed with golden pubescence. Scutellum small, nearly glabrous. Elytra slightly more than 2 1/2 times as long as width across humeri; sides feebly impressed before middle; apices narrowly rounded; a slightly oblique, raised, eburneous fascia present on each side at basal 1/3 from lateral margin to near suture; disk moderately gibbose near base on each side of suture, surface with basal 2/3 coarsely, densely cribrate-punctate except at extreme base, apical 1/3 nearly impunctate, alutaceous; entire disk sparsely clothed with long, erect, pale hairs. Abdomen shining, sparsely punctate and pubescent; terminal sternite nearly as long as fourth, apex broadly rounded. Legs with femora moderately abruptly clavate; surface smooth, shining, sparsely clothed with long, pale hairs.

Female: Similar to male. (Antennae broken on only specimen, but probably slightly shorter than those of male.) Abdomen with terminal sternite slightly longer than fourth, apex narrowly rounded. Length 5 mm.

REMARKS. — This species represents the southeastern extreme of the presently known distribution of *Euderces* and is one of only 5 species presently recorded from South America. *Euderces venezuelensis* may be distinguished by the combination of brown integument, shining, striate pronotum, and dentate third antennal segment. The species is named for the country of origin.

Euderces waltli, Chevrolat, new combination

Apelocera Waltli Chevrolat, 1862:62 (TYPE LOCALITY: Brasil.)
Eplophorus waltli Blackwelder, 1946:583.

DIAGNOSIS (Drawn from original description). — Color black; head with eyes somewhat emarginate; antennae slender, filiform, third segment apically spinose; prothorax globose, widely convex, strongly impressed at base, with a median longitudinal elevation, surface subreticulately punctate; elytra each with a basal gibbosity; and with four indistinct transverse white pubescent lines, the first under the humeri, the second oblique, not reaching the margin or the suture, the third elongate, angulate at the suture, the fourth trasverse, located slightly behind middle, integument reddish between the posterior two, apical 1/4 cinereous, apices truncate; abdomen with first segment with an apical white band. Legs with femora moderately clavate. Length 7.5 mm, width 2 mm.

REMARKS. — We have been unable to locate the type specimen or material assignable to this species. As pointed out by Chemsak (1969), it is doubtfully congeneric with *Euderces* due to the lack of eburneous elytral fasciae and moderately emarginate eyes. In his description, Chevrolat (1862) suggested a similarity to *Microclytus compressicollis* (Laporte & Gory), in the tribe Anaglyptini.

Euderces wappesi, new species
(Fig. 58)

TYPES. — Holotype male [HAHC], allotype from GUATEMALA, Baja Verapaz, 14.5 km N Salamá on Pantín rd., 1620 m, May 23–June 1, 1991 (H. & A. Howden). Additional 14 paratypes, 11 from Baja Verapaz, GUATEMALA: 1 female, from type locality, May 29, 1994 (E. Giesbert); 1 female, 16 km N Salamá on Pantín rd., 1550 m., May 23, 1991 (Howdens); 1 female, 1 km S same locality, June 5, 1991 (J. Wappes); 2 males, 3 females, 19–24 km N Salamá, 4500 ft., May 25–31, 1989 (Wappes, Giesbert); 1 male, 1 female, same locality, October 23–24, 1990 (Giesbert);1 male, 4 km W Cob n Hwy. on Pantín rd., May 25, 1991 (Howdens), and 5 from Chiapas, MEXICO: 1 female, Sumidero Canyon, September 28–October 4, 1986 (Wappes); 1 male, 1 female, same locality, October 2, 1986 (R. Turnbow); 1 female, 8 km N Bochil, July 17, 1962 (J. M. Campbell); 1 female, 8 mi. SE Teopisca, July 9, 1969 (Campbell & Bright). Paratypes deposited with EMEC, CNMN, EFGC, JEWC, HAHC, RHTC.

DESCRIPTION. — *Male*: Length 5.5–7 mm. Integument blackish, mouthparts and tarsi reddish brown, extreme apices of elytra usually somewhat pale; elytra with a single pair of eburneous fasciae. Head with eyes moderately small, lobes divided; antennae reaching about to apical 2/3 of elytra, third segment more than 2 1/2 times as long as fourth, armed at apex with a moderately long, acute spine which is slightly more than 1/2 as long as fourth segment, apex of fourth segment with a distinct, short spine. Pronotum about 1 2/5 as long as wide; sides

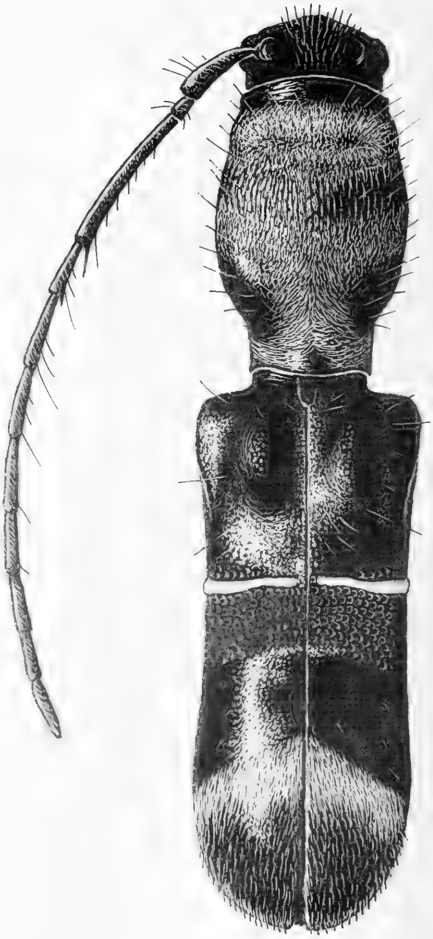

FIGURE 58. *Euderces wappesi*, new species, male.

rounded, basal 1/4 widely impressed; disk with surface longitudinally rugulose and asperate before middle, basal 1/4 smooth, nearly impunctate, an indistinct, wide fascia of moderately dense, appressed, golden pubescence across apical 1/5, formed in part by whorls on each side of middle, and less dense areas of appressed golden pubescence across middle and near base, middle of base and lateral rounded area on each side of basal 1/4 glabrous; entire surface moderately sparsely clothed with long, erect, pale hairs; prosternum with posterior 3/5 bearing coarse punctures and moderately dense, subdepressed, white pubescence; lateral and hind margins of epimera, mesocoxae and hind margin of metasternum clothed with dense, white pubescence. Scutellum rounded, impunctate, glabrous. Elytra about 2 1/2 times as long as width across humeri; sides slightly impressed before middle; apices rounded; each side near base with a strong, highly elevated gibbosity which is moderately coarsely, densely punctate at its apex; a narrow, transverse, raised, eburneous fascia present on each side slightly before basal 1/3 from lateral margin to very near suture; discal surface with basal 1/3 coarsely, obsoletely punctate, nearly glabrous, premedian 1/6 densely cribrate-punctate behind eburneous fasciae, apical 1/2 impunctate, somewhat alutaceous, apical 1/3 clothed with appressed pale golden pubescence which is denser anteriorly; entire disk clothed with long, erect, golden hairs. Abdomen shining, very sparsely punctate, sparsely pubescent laterally; terminal sternite slightly shorter than fourth, apex broadly rounded. Legs with femora moderately abruptly clavate, indistinctly carinate near apices; surface smooth, shining, with longitudinal bands of short, pale pubescence.

Female: Similar to male. Length 6–7 mm. Antennae slightly shorter, reaching middle of elytra. Prosternum lacking coarse punctures. Abdomen with terminal sternite slightly longer than fourth, apex rounded.

REMARKS. — This species is very close to *E. sculpticollis*, differing with the latter in having a slightly more basad orientation of the elytral eburneous fasciae, the shining basal half of the elytra with somewhat more abruptly raised basal gibbosities and the lack of distinct pubescence surrounding them, the more extensive striations of the pronotum, and the lack of an oblique densely pubescent mark on each side of the first abdominal segment. It is a pleasure to dedicate this species to James E. Wappes in recognition of his years of interest in the Neotropical Cerambycidae.

Euderces westcotti Hovore
(Fig. 59)

Euderces westcotti Hovore, 1988:13. (TYPE LOCALITY: Santa Victoria trail, W. La Laguna, Baja California Sur, Mexico.)

MATERIAL EXAMINED. — 1 female paratype from type locality, August 30–31, 1977 (R. L. Westcott) [FTHC].

REDESCRIPTION. — *Male*: Length 4–5 mm. Integument blackish to dark brown, scape, mouthparts, bases of femora, and tarsi dark reddish brown; elytra with two pairs of eburneous markings. Head with eyes moderately prominent, lobes divided, upper lobe small; antennae reaching to about middle of elytra, third segment slightly longer than scape, about 1 1/2 times as long as fourth segment, segments unarmed and

FIGURE 59. *Euderces westcotti* Hovore, female.

slightly swollen apically. Pronotum about as long as wide; sides broadly rounded, basal 1/8 narrowed and deeply impressed; apices somewhat narrowed; discal surface somewhat shining, irregularly striolate, asperate-striolate at base, with a triangular patch of subdepressed, pale pubescence in middle of base, entire surface with scattered, long, erect, pale hairs; prosternum with posterior 2/3 bearing coarse punctures and pale pubescence; lateral margins of mesepimera and hind margin of metasternum densely pale pubescent. Scutellum with apex narrowly rounded, surface densely pale pubescent. Elytra about twice as long as width across humeri; sides subparallel, slightly narrowed behind humeri, slightly wider behind middle; apices rounded; each side near base with a small, moderately distinct gibbosity; a narrow, transverse, raised, eburneous fascia present from margin to near suture on each side at about basal 1/3, an additional shorter, oblique, raised, eburneous macula present on each side near suture at basal 1/5 extending from base of humerus to posterior side of basal gibbosity; surface with basal 3/5 densely cribrate-punctate except for the shining, nearly impunctate humeri, apical 2/5 impunctate, alutaceous, with a slender, transverse, chevron-shaped fascia of short, fine, appressed, whitish pubescence across apical 1/3; entire disk sparsely clothed with long, erect hairs. Abdomen shining, sparsely pubescent; terminal sternite nearly as long as fourth, apex broadly rounded. Legs with femora abruptly clavate; surface smooth, shining, very sparsely pubescent.

Female: Similar to male. Length 5 mm. Antennae slightly shorter, not reaching middle of elytra. Prosternum rugose, lacking coarse punctures. Abdomen with terminal sternite slightly longer than fourth, apex rounded.

REMARKS. — This species differs from *E. parallelus* in several elytral characters: the more anteriorly placed and obliquely directed anterior eburneous marking, the more distinct basal gibbosities, and the slender, fairly distinct pubescent chevron at the apical 1/3. Flight appears to be during the brief wet season of southern Baja California in August and September.

Euderces yucatecus (Bates)
(Figs. 3, 60)

Apilocera yucateca Bates, 1892:165. (TYPE LOCALITY: Temax, N. Yucatan, Mexico.)
Apelocera yucateca Aurivillius, 1912:420.
Eplophorus yucateca Blackwelder, 1946:583.
Euderces yucateca Chemsak & Linsley, 1975:88.

REDESCRIPTION. — *Male*: Length 5.5–7 mm. Integument reddish brown, elytra usually infuscated at sides and toward apex; elytra with a single pair of eburneous fasciae. Head with eyes rather small, lobes divided, upper lobes small; antennae slightly exceeding elytral apices, third segment about twice as long as fourth, armed at apex with a long, feebly sinuate, sharp spine which is nearly as long as fourth segment, apex of fourth segment minutely dentate. Pronotum with sides broadly rounded, widest at middle, narrowed and impressed across base and apex;

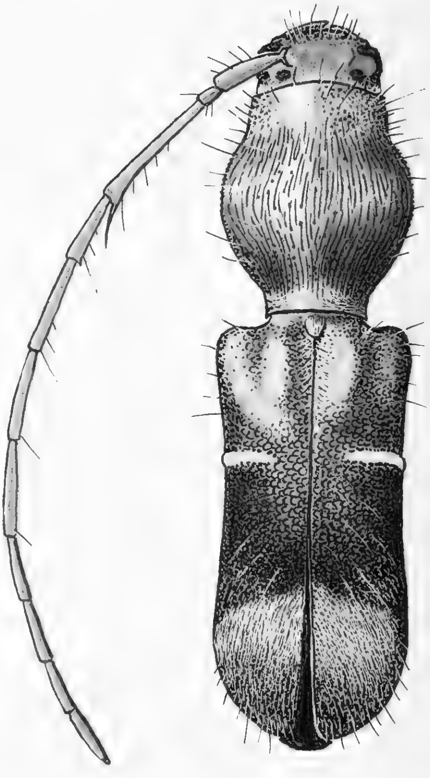

FIGURE 60. *Euderces yucatecus* (Bates), male.

disk slightly flattened, surface finely, longitudinally striate, rugulose, and asperate; base and apex clothed with short, appressed, pale pubescence, entire surface moderately sparsely clothed with long, erect, pale hairs; prosternum with posterior 2/3 coarsely punctate and moderately densely pale pubescent; lateral margins of mesepimera and hind margin of metasternum clothed with dense, white pubescence. Scutellum rounded at apex, densely clothed with appressed, pale golden pubescence. Elytra about 2 1/4 times as long as width across humeri; sides subparallel; apices subtruncate with angles minutely, feebly dentate; each side near base moderately gibbose; a narrow, transverse, raised, eburneous fascia on each side at basal 1/3 from lateral margin to about middle of disk; discal surface with basal 1/3 shining, coarsely, densely punctate, tops of gibbosities asperate-punctate, sparsely clothed with subdepressed pale pubescence, median 1/4 dull, densely cribrate-punctate behind eburneous fasciae, remainder of elytra impunctate, moderately alutaceous, with a fascia of appressed whitish pubescence across apical 1/4, area behind fascia very fine, pale golden pubescent; entire disk clothed with long, erect, golden hairs. Abdomen shining, sparsely pubescent; terminal sternite nearly as long as fourth, apex broadly rounded. Legs with femora moderately abruptly clavate; surface smooth, shining, with longitudinal bands of short, pale pubescence.

Female: Similar to male. Length 5–7 mm. Antennae shorter, slightly exceeding middle of elytra. Prosternum lacking coarse punctures. Abdomen with terminal sternite slightly longer than fourth, apex rounded.

REMARKS. — This species appears to be limited to the Yucatán Peninsula of Mexico (see Fig. 3) and may be recognized by the reddish brown integument and by the long antennae of the males. Flight occurs throughout the year.

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DESCRIPTION OF FOUR NEW SPECIES OF PHANEROBRANCH DORIDS (MOLLUSCA: NUDIBRANCHIA) FROM THE INDO-PACIFIC, WITH A REDESCRIPTION OF *GYMNODORIS AURITA* (GOULD, 1852)

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Four species of phanerobranch dorid nudibranchs are described. *Nembrotha mullineri* is known only from the Philippine Islands; *Nembrotha milleri* is known from the Philippines and Indonesia. *Nembrotha chamberlaini* has a somewhat wider distribution and is a member of the *Nembrotha lineolata* complex. *Notodoris serenae* occurs from Indonesia to Belau and north to Okinawa and differs externally and internally from its congeners, all of which have a yellow rather than gray body color. *Gymnodoris aurita* (Gould, 1852) is redescribed from specimens collected from the Philippines.

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The tropical Indo-Pacific is rich in its diversity of opisthobranch gastropods (Gosliner, 1993; Ghiselin, 1993; Gosliner and Draheim, 1996). The western Pacific is especially diverse in its opisthobranch fauna. Recent collections from several western Pacific localities, including Papua New Guinea, Indonesia, the Philippines and Okinawa have yielded specimens of several large, conspicuous phanerobranch nudibranchs. This paper redescribes one species, not recorded in the literature since its original description in 1852, and describes three species of *Nembrotha* and one of *Notodoris*.

SPECIES DESCRIPTONS

Family GYMNODORIDIDAE Odhner, 1941

Gymnodoris Simpson, 1855

Gymnodoris aurita (Gould, 1852)
(Figs. 1A, 2A-D, 3A-D)

Doris aurita Gould, 1852:299, pl. 23, figs. 394, 394a.
Gymnodoris sp. Gosliner, Behrens and Williams, 1996:172, fig. 607.

MATERIAL EXAMINED. — Neotype: CASIZ 096243, one specimen, 2 m depth, near Bonito Island Resort, Culebra Island, Batangas Province, off Luzon, Philippines, 18 March 1994, R. Jackson. CASIZ 103751, two specimens, one dissected, 7 m depth, Sabang, Mindoro, Philippines, 1 March 1995, T. M. Gosliner and G. C. Williams. CASIZ 105636, one specimen, 1 m depth, Cemetary Beach, Maricaban Island, Batangas Province, Luzon, Philippines, 19 February 1995, R. McPeak. CASIZ 106524, one specimen, 10 m depth, Layaglayag, Maricaban Island, Batangas Province, Luzon, Philippines, 19 April 1996, M. D. Miller.

DISTRIBUTION. — This species, described from Fiji (Gould, 1852), is also known from the Batangas Province, Philippines and from photos by Roger Steene from Rinca Island, Indonesia (present study).

NATURAL HISTORY. — This species has been observed feeding upon tritoniid nudibranchs of the genus *Marionia* (Mark Prein, pers. comm.). It inhabits shallow water reefs and is active nocturnally.

EXTERNAL MORPHOLOGY. — The body is firm and limaciform. The mantle is reduced and indistinct. The preserved specimens are up to 70 mm in length. The living animals (Fig. 1A, 2A), measure over 100 mm and are orange to deep red with large white to yellowish white tubercles dispersed uniformly over the body. The tubercles are situated on a series of longitudinal wrinkles and folds in the notal surface. The margin of the foot also has a yellowish white band as do the bases of the auriculate oral tentacles. The eight multipinnate gills are large, twice the animal's width, translucent white to red, with white to yellowish white ridges. The rhinophores are white to yellow, short and perfoliate, with 15 steeply set lamellae. They appear to attach to the body more at an angle rather than being strictly perpendicular to the axis of the rhinophore.

The body wall is thick and muscular. There is a network of numerous, densely set subcutaneous glandular tubes, presumably having a defensive function (Fig. 2B). They occur much more densely anteriorly to the gills than posteriorly. The genital aperture is located anteriorly, just posterior to and at the level of the rhinophores.

BUCCAL ARMATURE. — The buccal mass is thick and muscular. At its posterior end are massive salivary glands (Fig. 2C), measuring over one half the length of the body. The labial cuticle is reduced to a thin chitinous membrane. The radular formula in one specimen is 27 × 37.0.37. All the radular teeth lack denticles. The inner lateral tooth (Fig. 3A) is broad and thick, with a wide triangular cusp. The succeeding laterals (Fig. 3B-D) are markedly different from the inner lateral and have a thin, elongate cusp. They become increasingly elongate towards the outer margin.

REPRODUCTIVE SYSTEM. — As in other members of the genus, the gonad is separated from the digestive system. The reproductive system is triaulic (Fig. 2D). The preampullary duct is short and narrow. It expands into a wide saccate ampulla, which divides into the short oviduct and elongate vas deferens. The oviduct has a bulbous dilation that may function as a fertilization chamber. From this point the oviduct enters the massive female gland mass via a short duct and branches to an elongate uterine duct. It joins the saccate receptaculum seminis via a short, curved duct, and continues proximally until it widens slightly and enters the massive, thin-walled bursa copulatrix. The elongate, wide vagina also emerges from the base of the bursa and joins the vas deferens near the genital aperture. The vas deferens widens into a huge, curved prostatic portion which has a series of longitudinal glandular ridges along its surface. The vas deferens again narrows into an elongate, curved ejaculatory segment that is muscularized. Towards the distal end of this muscular portion are a series of rows of curved, chitinous spines (Fig. 2E).

DISCUSSION. — Most species of *Gymnodoris* are white or yellowish in general body color. Only a few species are orange or reddish, including *Gymnodoris inornata* (Bergh, 1880) (Gosliner, 1987, fig. 187) and *Gymnodoris* sp. (Wells and Bryce, 1993, fig. 99, as *G. aurita*). The only described, large reddish species with

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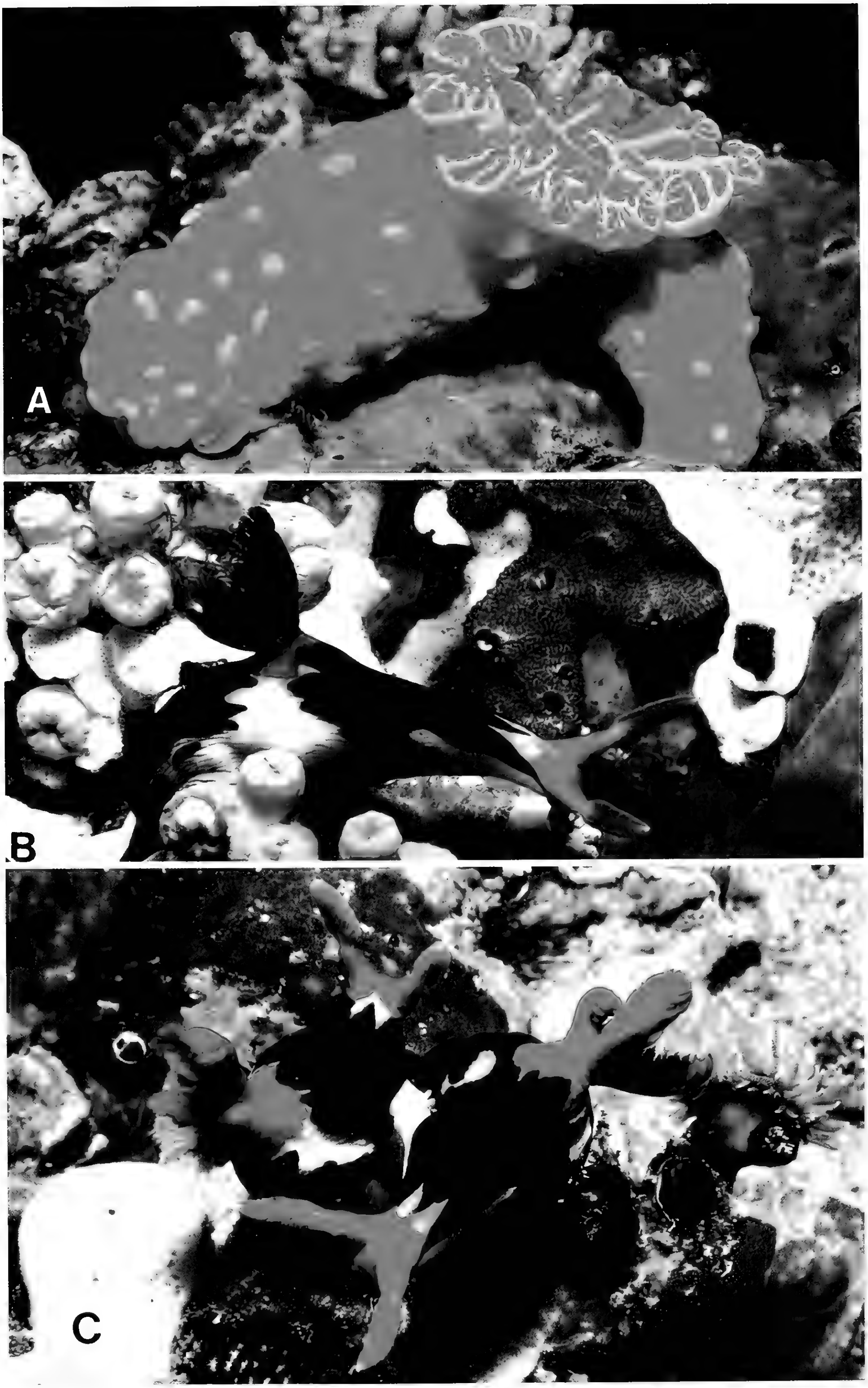
FIGURE 1. Living animals. A. *Gymnodoris aurita* (Gould, 1852), specimen from Rinca Island, Indonesia, photo by Roger Steene. B., C. *Nembrotha chamberlaini* sp. nov. specimens from Batangas, Luzon, Philippines, photos by Marc Chamberlain.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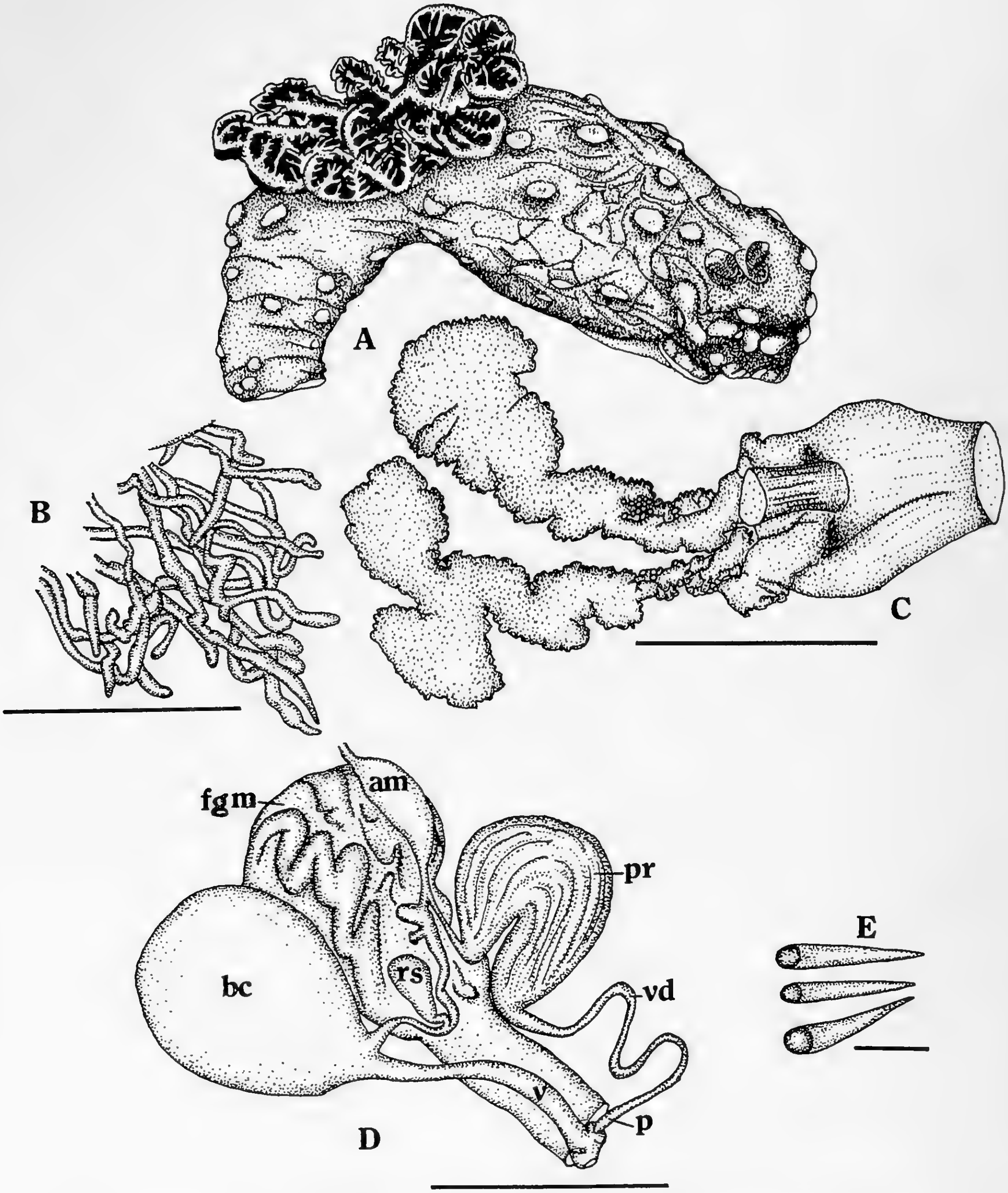

FIGURE 2. *Gymnodoris aurita* (Gould, 1852). A. Living animal. B. Subcutaneous glandular network, scale = 10 mm. C. Buccal bulb and salivary glands, scale = 10 mm. D. Reproductive system, am = ampulla, bc = bursa copulatrix, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina, vd = vas deferens, scale = 10 mm. E. Penial armature, scale = 0.05 mm.

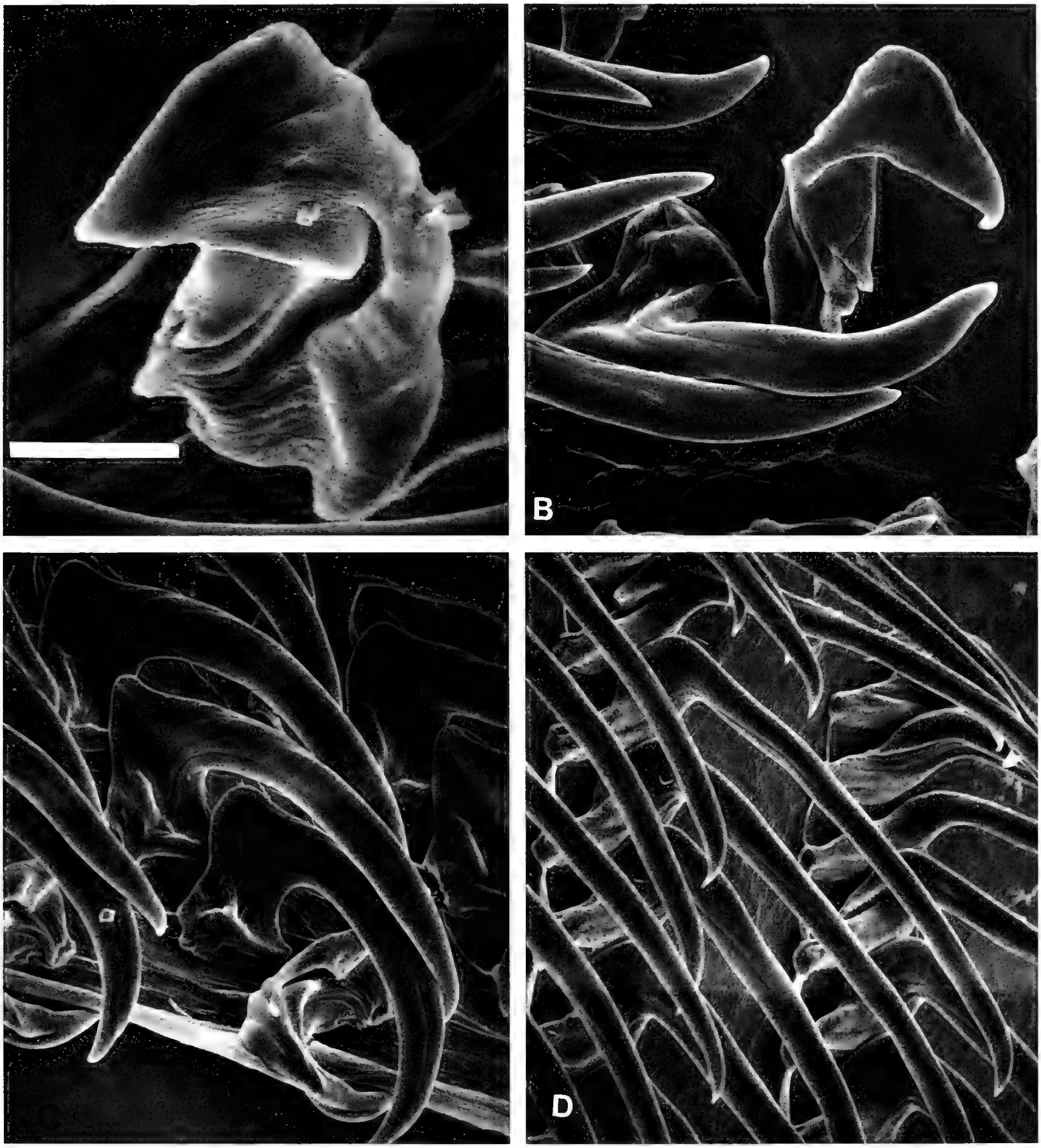

FIGURE 3. *Gymnodoris aurita* (Gould, 1852). Scanning electron micrographs of radula. A. Right inner lateral tooth, scale = 25 µm. B. Left inner lateral tooth, scale = 60 µm. C. Medial lateral teeth, scale = 75 µm. D. Outer lateral teeth, scale = 75 µm.

prominent tubercles is *Gymnodoris aurita* (Gould, 1852). The present material closely matches the original color plates depicted by Gould (1856), and there is little question that they represent the same species. No description of internal anatomy was presented in the original or subsequent descriptions. No type specimen is extant. All of the nudibranch types from the United States Exploring Expedition have been lost, if indeed they were ever preserved (Johnson, 1964:32). Owing to the absence of type material, a neotype of *Doris aurita* is here designated, as this represents the first revision of the taxon.

Another large tuberculate, reddish species was illustrated from Australia and identified by Wells and Bryce (1993, fig. 98) as *G. aurita*. This species is likely undescribed and differs in having dark maroon rhinophores and gills while those of *G. aurita* are the same whitish yellow color as the body tubercles. It also has larger, more densely distributed tubercles than does *G. aurita*. Also, *G. aurita* has a wide yellow margin to the foot that is absent in *Gymnodoris* sp. The internal anatomy of *Gymnodoris* sp. is unknown. Nevertheless, the two species are clearly distinct in their external anatomy and coloration.

Family POLYCERATIDAE Alder and Hancock, 1845

Nembrotha Bergh, 1877

Nembrotha chamberlaini sp. nov.
(Figs. 1B, C; 4A, B; 5; 6A-D)

Nembrotha sp. Okutani, 1994:222; Colin and Arneson, 1995:188, fig. 890; Gosliner, Behrens and Williams, 1996:170, fig. 602.

TYPE MATERIAL. — Holotype: CASIZ 107227, 10-25 m, Kirby's Rock, Maricaban Island, off Batangas, Luzon, Philippines, 18 February 1992, T. M. Gosliner. Paratypes: CASIZ 083689, two specimens, one dissected, same locality, date and collector as holotype.

ETYMOLOGY. — *Nembrotha chamberlaini* is named for Dr. Marc Chamberlain of San Diego, California, a friend, underwater photographer and opisthobranch enthusiast, who has contributed much to our understanding of Pacific biodiversity and has supported publication of these works.

DISTRIBUTION. — Thus far this species is known only from the Luzon and Mindoro Islands in the Philippines (present study) and Okinawa (Okutani, 1994).

NATURAL HISTORY. — *Nembrotha chamberlaini* is a predator upon the tunicates *Rhopalaea* sp., *Clavellina moluccensis* (Sluiter, 1904) and *Oxycorynia fascicularis* Drasche, 1882 (Gosliner, Behrens and Williams, 1996; present study).

EXTERNAL MORPHOLOGY. — The body is elongate and limacifiorm reaching, up to 62 mm in length, in preserved animals and 100 mm in living ones. The color is complex and variable. The living animals (Fig. 1B, C; 4A) are white with a dark brown to black saddle. The dorsal surface of the head and rhinophores is uniformly bright red, as are the gills, their bases and the posterodorsal portion of the foot. The entire body surface is textured with a pattern of longitudinal wrinkles. The wrinkles are more noticeable on lightly colored surfaces. The margin of the foot is delineated by a blue to purple band, within which a yellow band is present. The foot corners and cephalic ridge are also bluish purple. The anteriormost edge of the notum below the rhinophores is dark brown to black. Ventral to the limit of the red and dark brown pigment is a thin line of yellow, which traces the irregular edges of the red and brown patches. Ventral to the yellow line is an area of opaque white, which may be small or may occupy most of the lateral surface of the animal (Fig. 5). There are two, variably sized, translucent spots posterior to the rhinophores, through which the dermal eyes are visible. These patches may vary from tear drop-shaped to attached rhomboids. These patches are outlined in yellow. The genital apertures, when extended, form a trumpet-shaped structure that is blue to purple. The rhinophores are perfoliate bearing 41–46 lamellae. The five gills are tripinnate. The body wall is highly muscular. The genital aperture is located midway between the gills and rhinophores.

BUCCAL ARMATURE. — There is a large, well-developed blood gland, which is granular in texture and which inserts into the dorsal surface of the esophagus. The buccal mass is relatively elongate and tubular. The salivary glands are short and thick. The labial cuticle is well-developed and chitinous, but devoid of thickenings or denticles. The radular formula is 32 × 8.1.1.1.8 (Fig. 6A) in the single specimen examined. The broad rachidian teeth are asymmetrical with two elongate denticles on the left side and three on the right (Fig. 6B). The two inner denticles of the right half of the rachidian may represent a single bifurcate denticle that are united only at the base.The innermost lateral is a large, hamate hook, with a large basal triangular cusp and a similarly shaped primary cusp. No other denticles are present. The outer laterals are rectangular

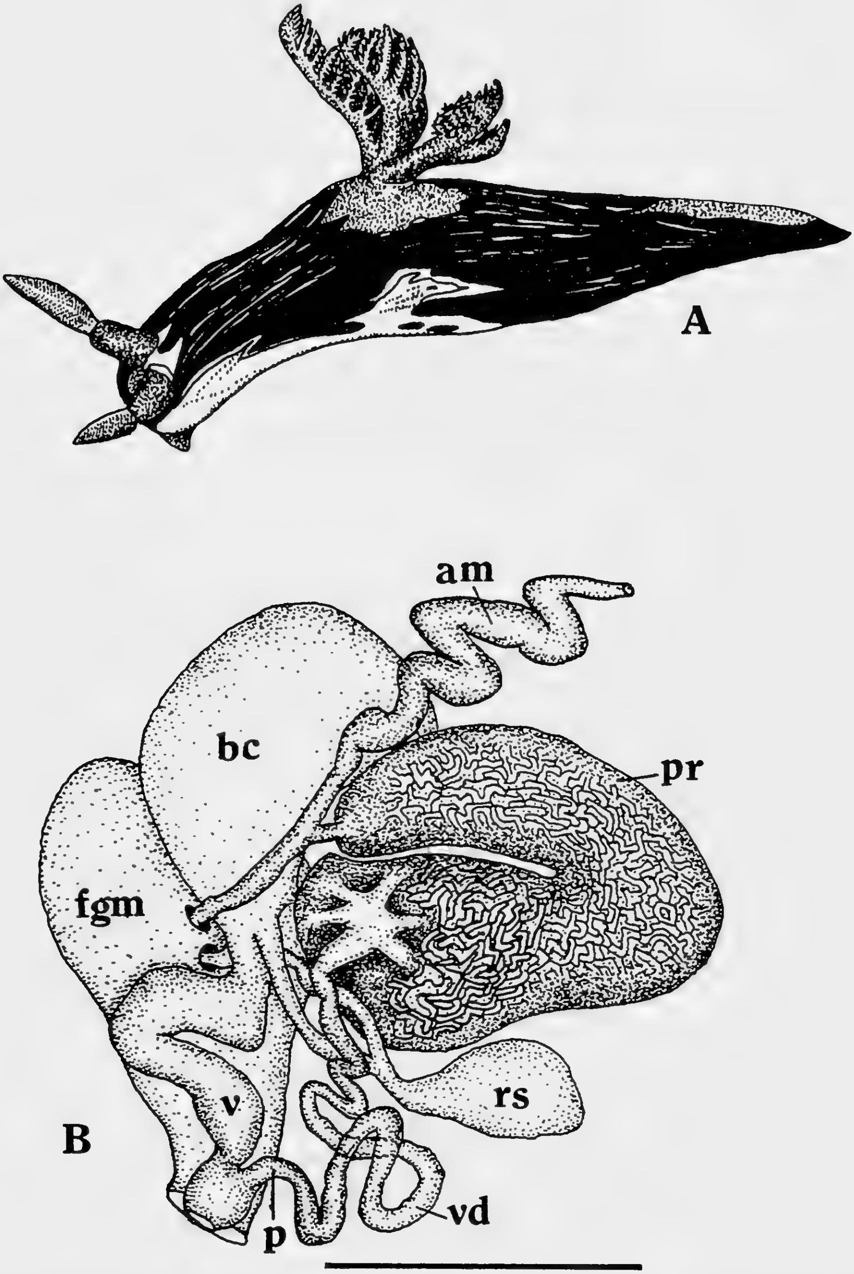

FIGURE 4. *Nembrotha chamberlaini* sp. nov. A. Living animal. B. Reproductive system, am = ampulla, bc = bursa copulatrix, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina, vd = vas deferens, scale = 10 mm.

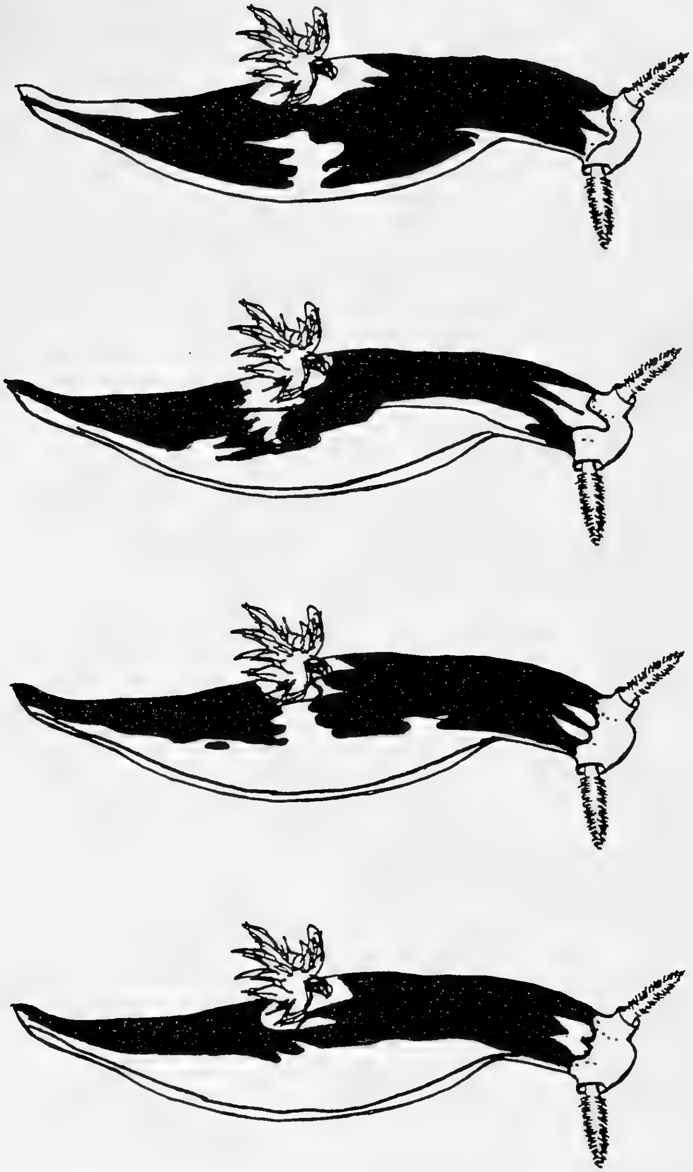

FIGURE 5. *Nembrotha chamberlaini* sp. nov. Variation in distribution of color pattern.

plates, which lack cusps or dentition and become smaller near the margin.

REPRODUCTIVE SYSTEM. — The reproductive system is triaulic (Fig. 4B). The preampullary duct is short and narrow. It expands into a narrow highly convoluted ampulla which divides into an elongate oviduct and the vas deferens. From this point the oviduct enters the massive female gland mass. The short branch of the vas deferens widens into a huge, curved prostatic portion which has a dense network of interconnecting tubules over its surface. The vas deferens again narrows into an elongate, highly convoluted ejaculatory segment that is muscularized. Within the distal end of this muscular portion are a series of 14 rows of curved, chitinous hooks which evert into

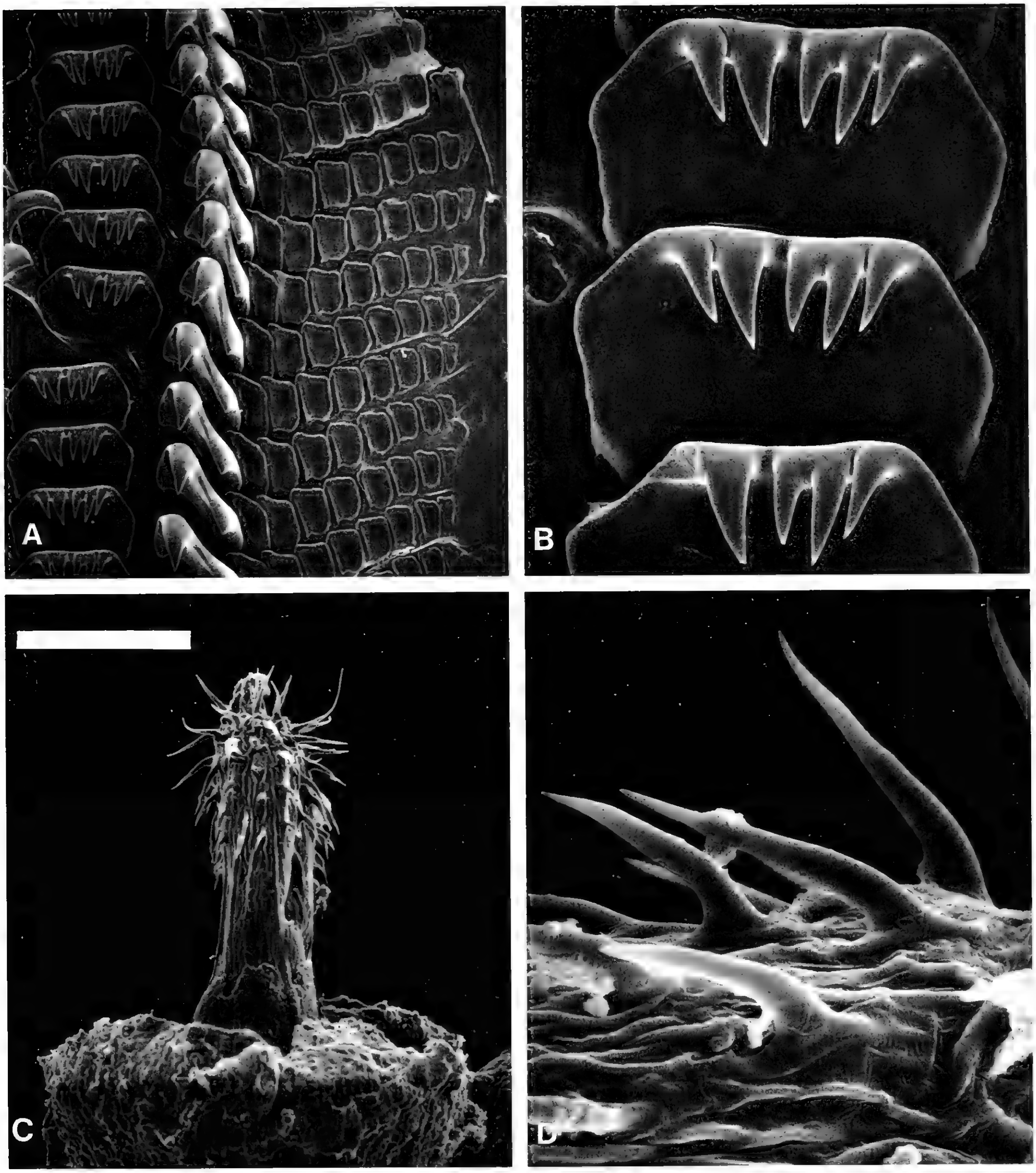

FIGURE 6. *Nembrotha chamberlaini* sp. nov. Scanning electron micrographs. A. Half-row of radular teeth, scale = 250 µm. B. Rachidian teeth, scale = 75 µm. C. Protruded penis, scale = 150 µm. D. Penial armature, scale = 25 µm.

a penial papilla (Fig. 6C, D). The elongate uterine duct emerges from the female gland mass and joins the saccate receptaculum seminis via a curved duct, and continues proximally until it widens slightly and enters the massive, thin-walled bursa copulatrix. In situ, the bursa is entirely surrounded by the prostate. In Fig. 4B, the prostate has been teased apart from the prostate and is shown positioned to the side. The elongate, wide vagina also emerges from the base of the bursa and joins the vas deferens near the genital aperture.

DISCUSSION. — This species with its broad, simply denticulate rachidian, is clearly placed in

Nembrotha, as characterized by Burn (1967) and Cervera, Gárcia-Gómez and Megina (1996). Cervera, Gárcia-Gómez and Megina compared the four described species of *Nembrotha* that have whitish bodies with darker markings on the dorsal and lateral surface: *N. lineolata* Bergh, 1905 (Coleman, 1989:10; Wells and Bryce, 1993, fig. 96; Colin and Arneson, 1995:189, fig. 888; Gosliner, Behrens and Williams, 1996:170, fig. 601), *N. purpureolineata* O'Donoghue, 1924 (Wells and Bryce, 1993, fig. 91), *N. rutilans* (Pruvot-Fol, 1931) (Kent, 1893, pl. 13, fig. 9; Coleman, 1989:10; Wells and Bryce, 1993, fig. 97) and *N. megalocera* Yonow, 1990. Three of these species have an asymmetrical arrangement of denticles on the rachidian teeth. The radula is unknown in *Nembrotha rutilans*. In addition to the species listed by Cervera et al., *Nembrotha tabescens* (Risbec, 1928) also appears to be closely related to these species and has a similar color pattern (Risbec, 1928, pl. 5. fig. 9, as *Polycera tabescens*; Coleman, 1989:11). Of these species, all but *N. megalocera* have reddish rhinophores. Those of *N. megalocera* are black. All five of these species have reddish gills, as in *N. chamberlaini*. However, *N. chamberlaini* is unique in having the rhinophores and gills with a uniform red pigment throughout. The remaining species have purplish, white and yellow pigment on the gill bases. Cervera et al. (1996) stated that specimens depicted by Baba (1976) and Gosliner (1987), as *N. purpureolineata*, probably represent one or more undescribed species. We concur with this view. These species will be treated in a subsequent paper.

The radula of all of the above species, where described, is similar in its formula, and shape and dentition of teeth. All of these species, with the exception of *N. tabescens*, have an asymmetrical rachidian tooth with a shallowly or deeply bifid cusp on the inner right side. In *N. tabescens*, the rectangular rachidian tooth was described as lacking denticles (Risbec, 1928). In *N. lineolata* and *N. megalocera* the rachidian tooth is broadest basally, while in *N. chamberlaini* and *N. purpureolineata* it is broadest near the middle of the tooth.

Of the above mentioned species, the reproductive system has been described only for *N. megalocera* (Cervera et al., 1996). There are no significant differences in reproductive anatomy between this species and *N. chamberlaini*, although the number of rows of penial spines was not indicated for *N. megalocera*.

The consistent differences in color of the living animal of *N. chamberlaini* clearly distinguish it from other species of *Nembrotha* with a similar color pattern.

Nembrotha milleri sp. nov.
(Figs. 7A; 8A, B; 9A-D)

TYPE MATERIAL. — Holotype: CASIZ 088086, 17 m depth, 200 m south of lighthouse, Dakak, Mindanao, Philippines, 1 April 1993, T. M. Gosliner. Paratypes: USNM 880178, one specimen, 13–19 m depth, s. side Pescador Island, off Cebu, Philippines, 7 May 1979, C. A. Child. CASIZ 096302, one specimen, 29 m depth, Black Forest, Balcasag Island, off Bohol, Philippines, 22 March 1994, G. C. Williams. CASIZ 085944, three specimens, one dissected, 12 m depth, Devil's Point, Maricaban Island, off Batangas, Luzon, Philippines, 23 March 1993, T. M. Gosliner. CASIZ 093968, one specimen, 7 m depth, Lehaga Island, off Manado, Sulawesi, Indonesia, 18 October 1993, Pauline Fiene-Severns. CASIZ 078579, one specimen, Bunaken Island, off Madando, Sulawesi, Indonesia, 19 May 1991, Pauline Fiene-Severns.

ETYMOLOGY. — *Nembrotha milleri* is named for Michael D. Miller, of San Diego, California. Mike is a good friend and webmaster extraordinaire, who first introduced us to the diversity of the Philippine opisthobranch fauna.

DISTRIBUTION. — Known from Luzon, Cebu and Mindanao, Philippines and Sulawesi, Indonesia.

NATURAL HISTORY. — *Nembrotha milleri* has not been found in association with specific prey. It has been observed crawling actively on reef and surfaces in 10–29 m depth.

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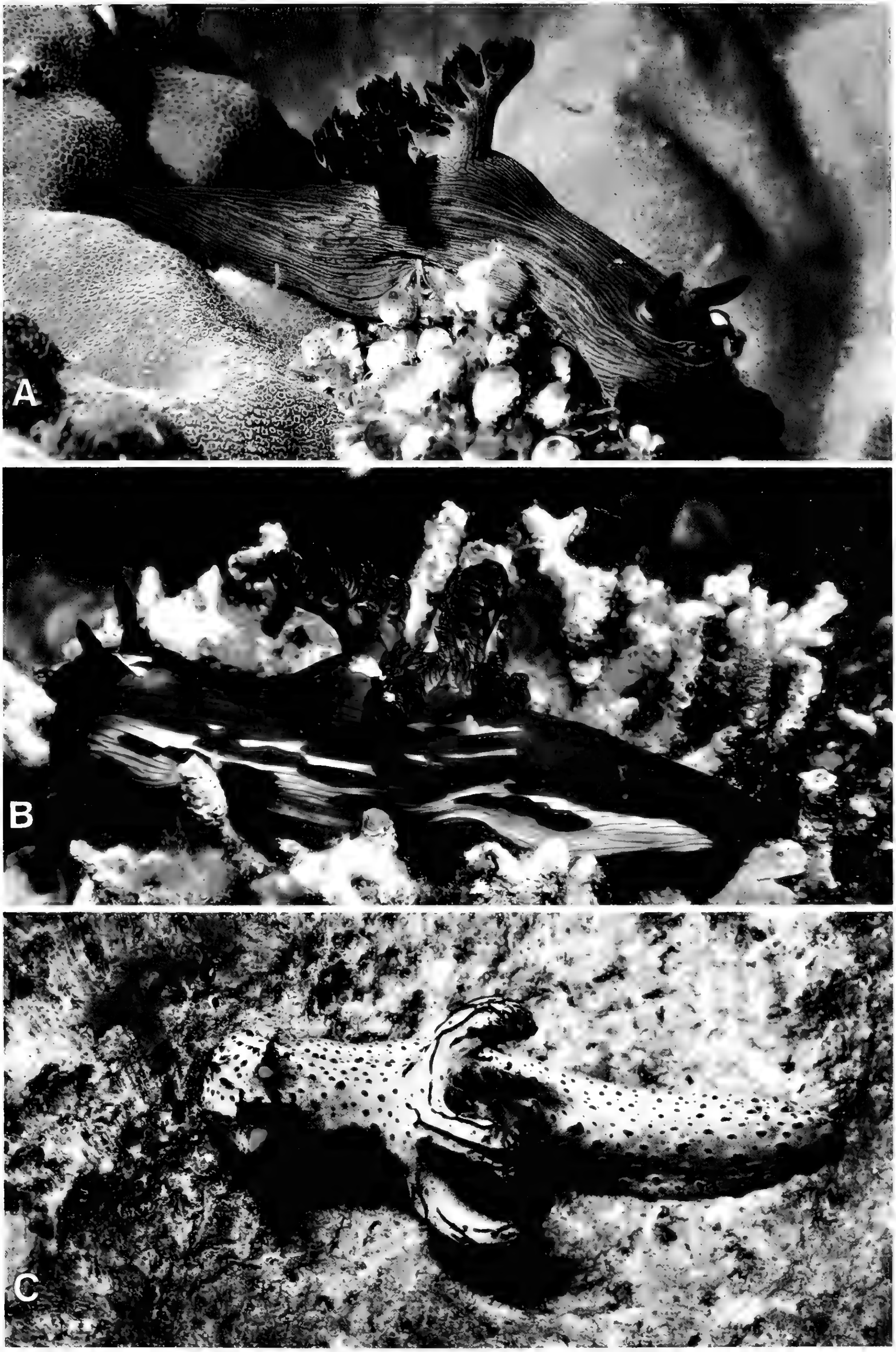
FIGURE 7. Living animals. A. *Nembrotha milleri* sp. nov. specimen from Batangas, Luzon, Philippines, photo by Mike Miller. B. *Nembrotha mullineri* sp. nov. specimen from Batangas, Luzon, Philippines, photo by Mike Miller. C. *Notodoris serenae* sp. nov. specimen from Papua New Guinea, photo by T. M. Gosliner.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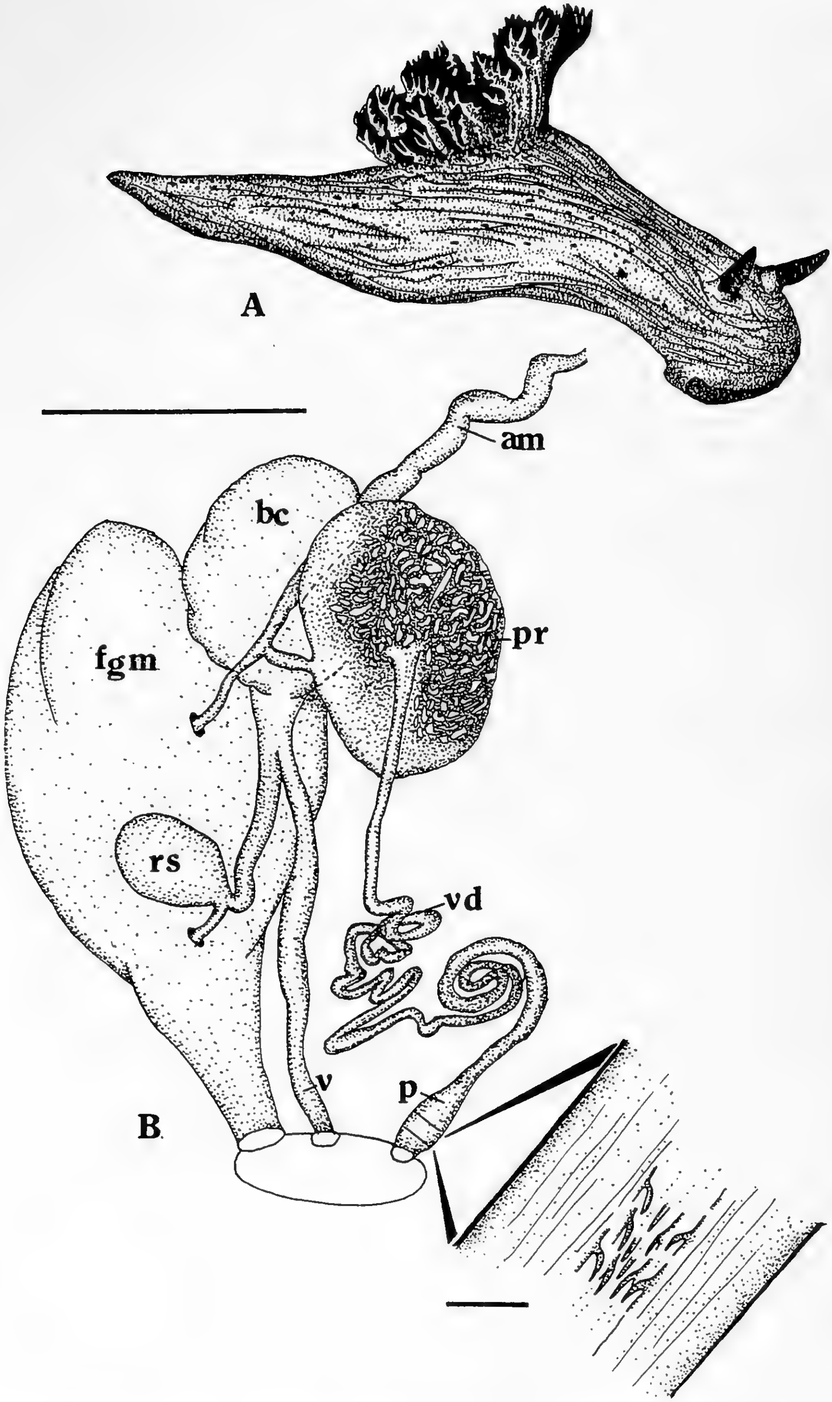

FIGURE 8. *Nembrotha milleri* sp. nov. A. Living animal. B. Reproductive system, am = ampulla, bc = bursa copulatrix, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina, vd = vas deferens, scale = 10 mm. Detail of penial armature, scale = 0.05 mm.

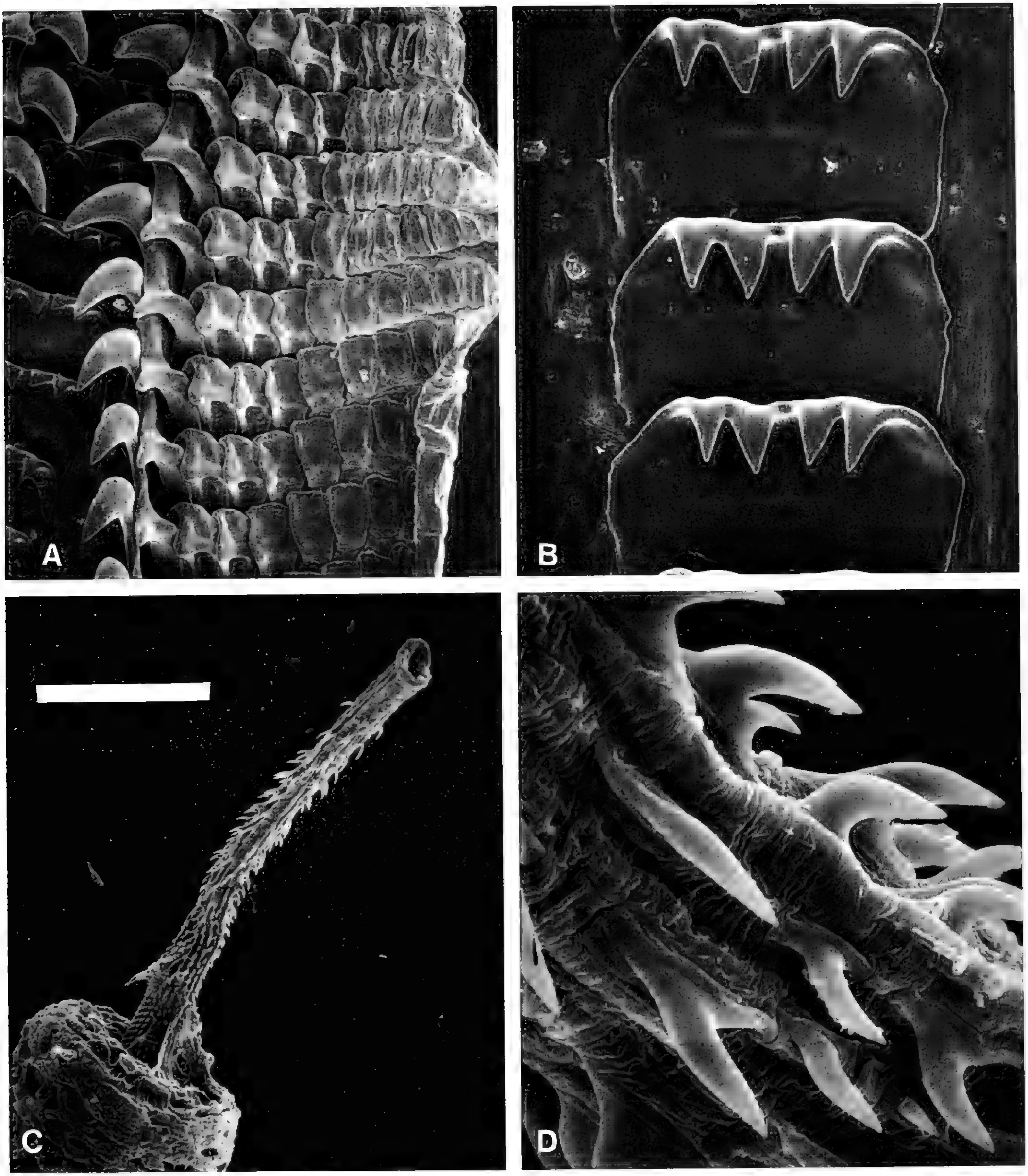

FIGURE 9. *Nembrotha milleri* sp. nov. Scanning electron micrographs. A. Half-row of radular teeth, scale = 430 µm. B. Rachidian teeth, scale = 200 µm. C. Protruded penis, scale = 200 µm. D. Penial armature, scale = 15 µm.

EXTERNAL MORPHOLOGY. — The body is elongate, limaciform and slightly undulate. The preserved animals are 30–60 mm in length. The living animals (Fig. 7A, 8A) are deep grey-green with longitudinal creases over the entire body surface. These creases extend up the gill stalks and are black in color. The tips of the five multipinnate gills, arising from three basal mounds, are black. The anus is a tall tube situated in the middle of the three gill bases. The rhinophores are perfoliate with 33 lamellae and arise from a smooth tapering sheath, similar in color to that of the body. The clavus is black. The genital aperture is situated midway between the rhinophores and the anterior portion of the gills. There are two circular-shaped oral tentacles with a depression at the center of each. The body wall is highly muscularized.

BUCCAL ARMATURE. — The buccal mass is a large glandular oral tube anteriorly. The labial cuticle forms a brown chitinous disk, without distinct armature or rodlets. The radular formula of one specimen is 30 × 8–10.1.1.1.8–10 (Fig. 9A, B). The rachidian teeth (Fig. 9B) are broad and quadrangular with four symmetrically arranged triangular denticles. The inner laterals are much larger than the outer ones and have an elongate, curved terminal cusp and a shorter more basal one. The second, third and fourth laterals bear large cusps of decreasing size, while the remaining laterals are quadrangular without cusps (Fig. 9A).

REPRODUCTIVE SYSTEM. — The reproductive system is triaulic (Figure 8B). The preampullary duct is short and narrow. It expands into an elongate, slightly convoluted ampulla which divides into an elongate oviduct and the vas deferens. From this point the oviduct enters the massive female gland mass. The short branch of the vas deferens widens into a huge, spherical prostatic portion, which has a dense network of interconnecting tubules over its surface. The vas deferens again narrows into an elongate, straight section followed by a highly convoluted ejaculatory segment that is muscularized. Within this muscular portion are a series of 14–24 crowded rows of curved, chitinous hooks (Fig. 9C, D). Basally there are up to 24 rows of spines which gradually diminish to 14 rows at the apex. The distal spines are slightly more elongate than the proximal ones. The short uterine duct emerges from the female gland mass and joins the saccate receptaculum seminis via a very short, curved duct, and continues proximally until it widens slightly, joining with the vagina. Together they enter the massive, thin-walled bursa copulatrix. In situ, the bursa is entirely surrounded by the prostate. In Fig. 8B, the prostate has been teased apart from the bursa and is shown positioned to the side. The elongate, wide vagina also emerges from the base of the bursa and shares a common base with the uterine duct. The vagina is separate from the vas deferens for its entire length.

DISCUSSION. — *Nembrotha milleri* and *N. mullineri* are both stockier, more robust species than other members of the genus. Three other described species of *Nembrotha* have greenish pigment on the body. However, the primary body color of *N. kubaryana* Begh, 1877 and *N. cristata* Bergh, 1877 is black rather than green. In both of these species, the green pigment is found on large rounded tubercles, which are absent in *N. milleri*. The radular teeth of *N. cristata* are rounded rather than quadrangular and with five denticles rather than four. The penial armature of *N. cristata* and *N. mullineri* differs markedly from that of *N. milleri*. In these species, the basal spines are much larger than the distal ones, while in *N. milleri* the distal spines are slightly larger than the basal ones. *Nembrotha milleri* has far more rows of penial spines (up to 24) than do *N. cristata* (10–12) or *N. mullineri* (16–18). It appears that the distribution and size of penial spines can be used to differentiate species of *Nembrotha*. However, at present this feature has not been described for the majority of members of the genus.

Nembrotha milleri can be distinguished by its shiny, satin, gray-green body color.

Nembrotha mullineri sp. nov.
(Figs. 7B; 10A, B; 11A-D)

TYPE MATERIAL. — Holotype: CASIZ 085941, 23 m depth, Layaglayag Point, Maricaban Island, Batangas, Luzon, Philippines, 22 March 1993, Kay Lieb. Paratypes: CASIZ 106507, one specimen, dissected, 8 m depth, Layaglayag Point, Maricaban Island, Batangas, Luzon, Philippines, 16 April, 1996, T. M. Gosliner. CASIZ 106508, two specimens, 12 m depth, Sepok Point, Maricaban Island, Batangas, Luzon, Philippines, 16 April 1996, M. Miller and J. Allen. CASIZ 103724, one specimen, 10 m depth, Hamilo, Batangas Province, Luzon, Philippines, 4 March 1995, T. M. Gosliner.

ETYMOLOGY. — *Nembrotha mullineri* is named for David K. Mulliner of San Diego, California, who first collected this species. Dave is an old friend and has contributed much to our knowledge of opisthobranch mollusks.

DISTRIBUTION. — Thus far, known only from Batangas Province, Luzon, Philippines.

NATURAL HISTORY. — *Nembrotha mullineri* is found crawling in the open on reef and rubble surfaces in 8–23 m depth. One specimen was observed on an unidentified arborescent bryozoan.

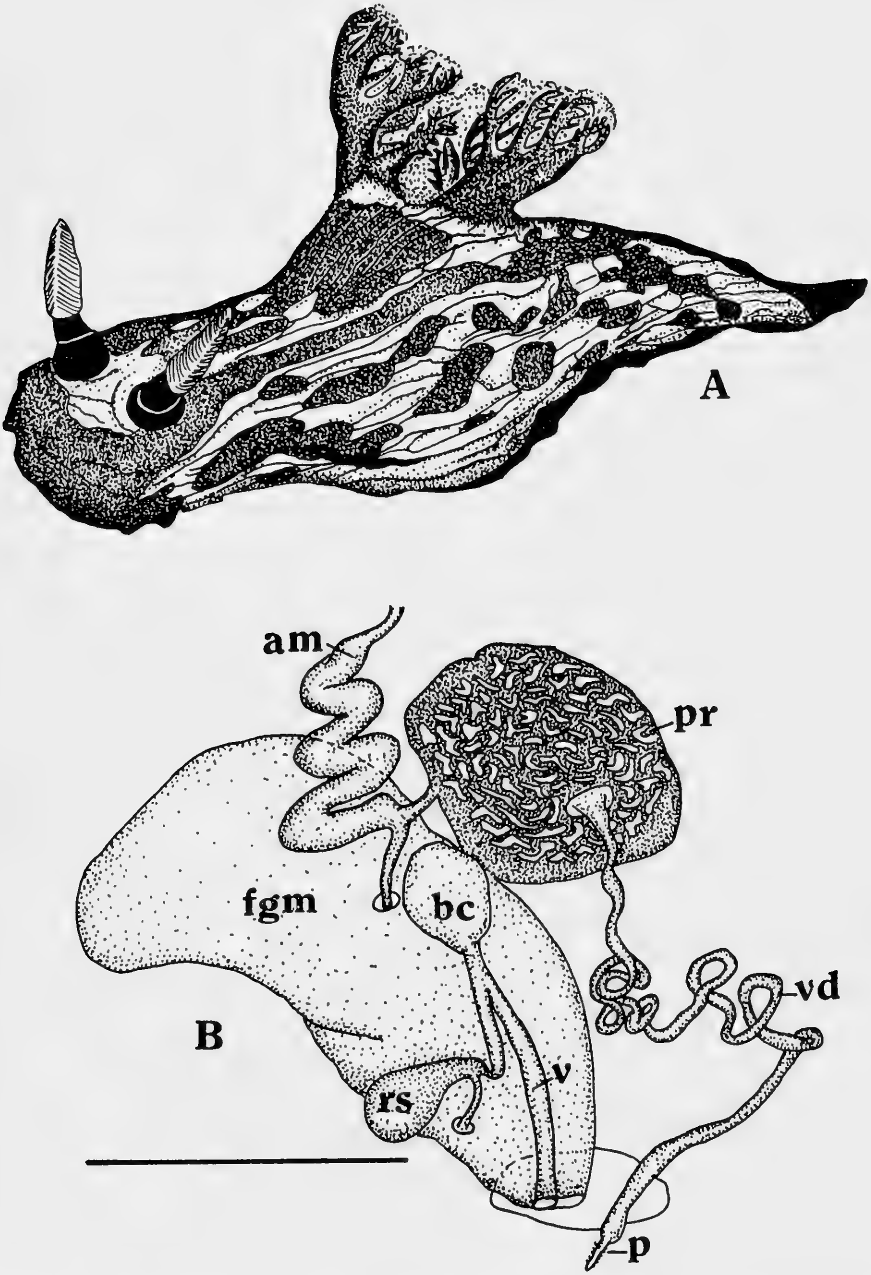

FIGURE 10. *Nembrotha mullineri* sp. nov. A. Living animal. B. Reproductive system, am = ampulla, bc = bursa copulatrix, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina, vd = vas deferens, scale = 10 mm.

EXTERNAL MORPHOLOGY. — The body is robust and limaciform. The preserved animals are 30–70 mm in length. The living animals (Fig. 7B, 10A) may exceed 100 mm in length. They are creamy white, covered with a series of longitudinally oriented creases or wrinkles. There are large blotches and areas of brown over the entire body. The amount of brown blotching varies

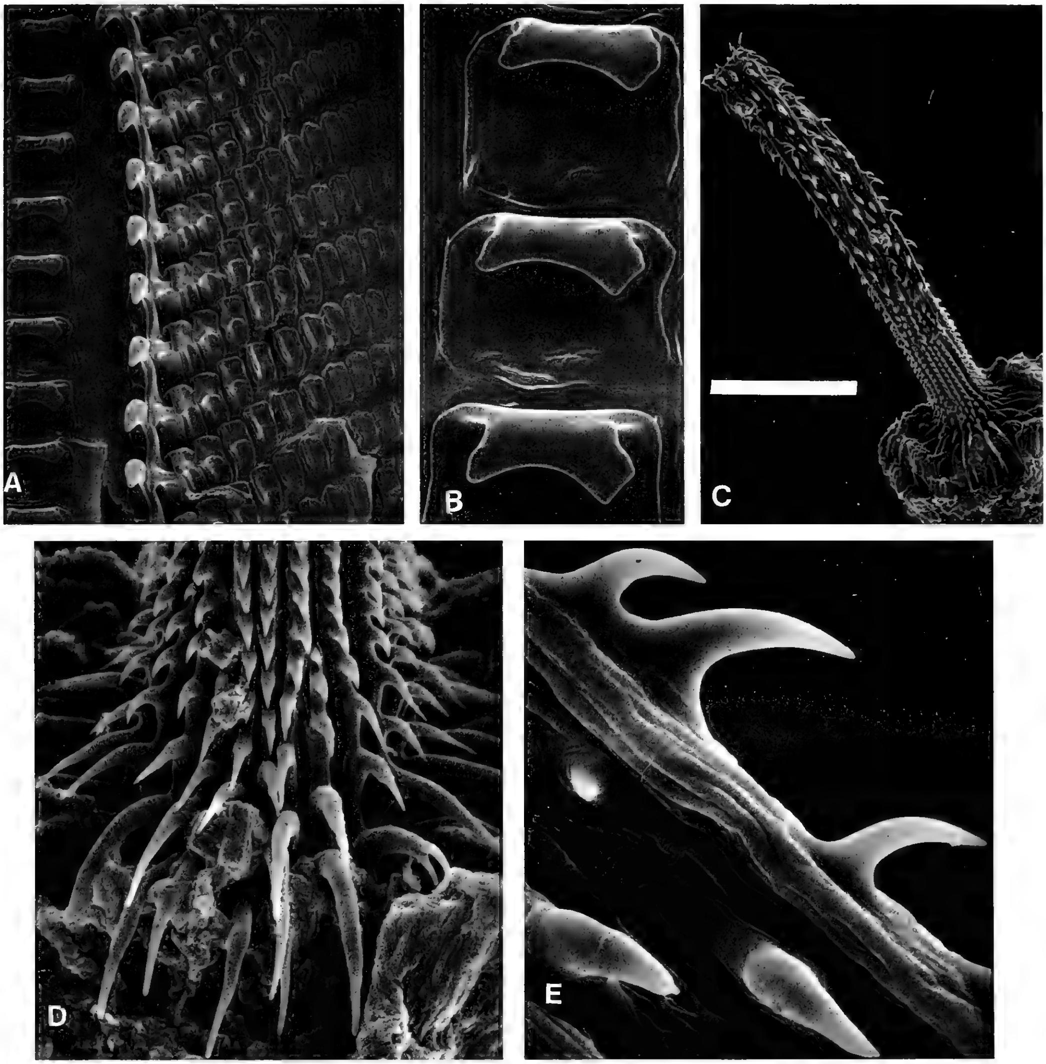

FIGURE 11. *Nembrotha mullineri* sp. nov. Scanning electron micrographs. A. Half-row of radular teeth, scale = 600 µm. B. Rachidian teeth, scale = 200 µm. C. Protruded penis, scale = 200 µm. D. Detail of basal penial spines, scale = 43 µm. E. Detail of distal penial spines, scale = 15 µm.

considerably in different individuals. It may be limited to a series of spots, elongate lines or form dense patches of brown. There are a few scattered, low, pointed tubercles situated between the creases in the brown areas. They are a greyish brown in color with dark brown tips. The head is rounded and dark brown in color. The rhinophores and outside of the five multipinnate gills are dark brown. The inner side of the gill base is cream and brown pigment is situated on the gill rachis and pinnae. The two posterior gills on each side have a common base. The anus is situated between the gills on an elongate papillae. The genital aperture is located on the right side of the body, midway between the rhinophores and the anterior end of the branchial plume. The oral tentacles are short, blunt folds.

BUCCAL ARMATURE. — The buccal mass is large and muscular. The labial cuticle is devoid of rodlets or other armature. The radular formula in one specimen is 26 × 11.1.1.1.11 (Fig. 11 A, B). The rachidian teeth (Fig. 11B) are broad and quadrangular. The masticatory margin has two triangular denticles that are joined by a curved marginal arch. The inner lateral teeth are elongate with a short, curved apical cusp and a short secondary cusp near the base of the tooth. The second, third and fourth laterals have a short cusp on their inner side, while the remaining teeth entirely lack a cusp and are quadrangular in shape decreasing in size towards the outer radular margin.

REPRODUCTIVE SYSTEM. — The reproductive system (Fig 10B) is triaulic. The preampullary duct is short and narrow. It expands into an elongate, highly convoluted ampulla which divides into an elongate oviduct and the vas deferens. From this point the oviduct enters the massive female gland mass. The short branch of the vas deferens widens into a huge, spherical prostatic portion which has a dense network of interconnecting tubules over its surface. The vas deferens again narrows into an elongate, highly convoluted ejaculatory segment that is muscularized. Within the distal end of this muscular portion are a series of 10–18 crowded rows of curved, chitinous hooks (Fig. 10C, D). Basally, there are up to 18 rows of spines which gradually diminish to 10 rows at the apex. The spines are of three different sizes and shapes (Fig. 11C). The basal spines (Fig. 11D) are elongate and curved, more than five times the length of the spines immediately distal to them. These short spines are short and curved. The distal two-thirds of the penis is armed with medium-sized spines that are about twice the length of the shortest ones (Fig. 11E), a few of which are bifid. The short uterine duct emerges from the female gland mass and joins the saccate receptaculum seminis via a short, curved duct, and continues proximally until it widens slightly and enters the spherical, thin-walled bursa copulatrix. In situ, the bursa is entirely surrounded by the prostate. In Fig. 11B, the prostate has been teased apart from the bursa and is shown positioned to the side. The elongate, wide vagina also emerges from the base of the bursa and shares a common base with the uterine duct. The vagina is separate from the vas deferens for its entire length.

DISCUSSION. — *Nembrotha mullineri* is most similar to *N. milleri* in its body form and shape. *Nembrotha mullineri* is the only member of the genus that is cream colored with brown spots or blotches. It has some scattered tubercles, but they are less prominent than in species such as *N. guttata* (Yonow, 1993, fig. 6e), *N. cristata*, *N. kubaryana* and *N. nigerrima*. These four other tuberculate species have a black body color with green or orange pigment on the tubercles.

The rachidian tooth of *N. mullineri* is unique among described members of the genus in having an arched masticatory margin without distinctly separated denticles. The reproductive system of *N. mullineri* is similar to that described for *N. milleri*, except that the portion of the ejaculatory duct near the prostate is more highly convolute. The penial morphology of *N. mullineri* is similar to that described for *N. cristata* (Bergh, 1905, pl. 18, figs. 7-8) where the basal penial spines are markedly longer than those immediately distal to them. This is in contrast to *N. milleri*, where the there are only small basal spines.

Family NOTODORIDIDAE Bergh, 1875

Notodoris Bergh, 1875

Notodoris serenae sp. nov.
(Figs. 7C; 12A, B; 13A-D)

Notodoris sp. Allen and Steene, 1994:195; Colin and Arneson, 1995:190, fig. 896; Gosliner, Behrens and Williams, 1996:172, fig. 610.

TYPE MATERIAL. — Holotype: CASIZ 107228, RVS 143, Belau, 6 Ocotober 1987, R. Van Syoc. Paratypes: CASIZ 107230, two specimens, 12 m depth, barrier reef wall, Madang Lagoon, Madang, Papua New Guinea, 13, 14 August 1989, T. M. Gosliner. CASIZ 076318, one specimen, 25-30 m depth, Cauayan Rock, N. Palawan Island, Philippines, 9 March 1984, A. J. Ferreira. CASIZ 107232, one specimen, dissected, RVS 138, Belau, 4 October 1987, R. Van Syoc. CASIZ 107229, four specimens, two dissected, Madang Lagoon, Madang, Papua New Guinea, August 1989, T. M. Gosliner. CASIZ 107231, 10 m depth, Wongat Island dropoff, 29 July 1989, S. Jebb. CASIZ 086690, one specimen, 15 m depth, Unjuran reeef, Flores, Indonesia, 29 April 1992, P. Fiene-Severns. CASIZ 073087, one specimen, Rasch Passage, Madang Lagoon, Madang, Papua New Guinea, 25 October 1986, G. Williamson.

ETYMOLOGY. — *Notodoris serenae* is named for Serena Jebb who found some of the first specimens of this species and is an enthusiastic supporter of this research.

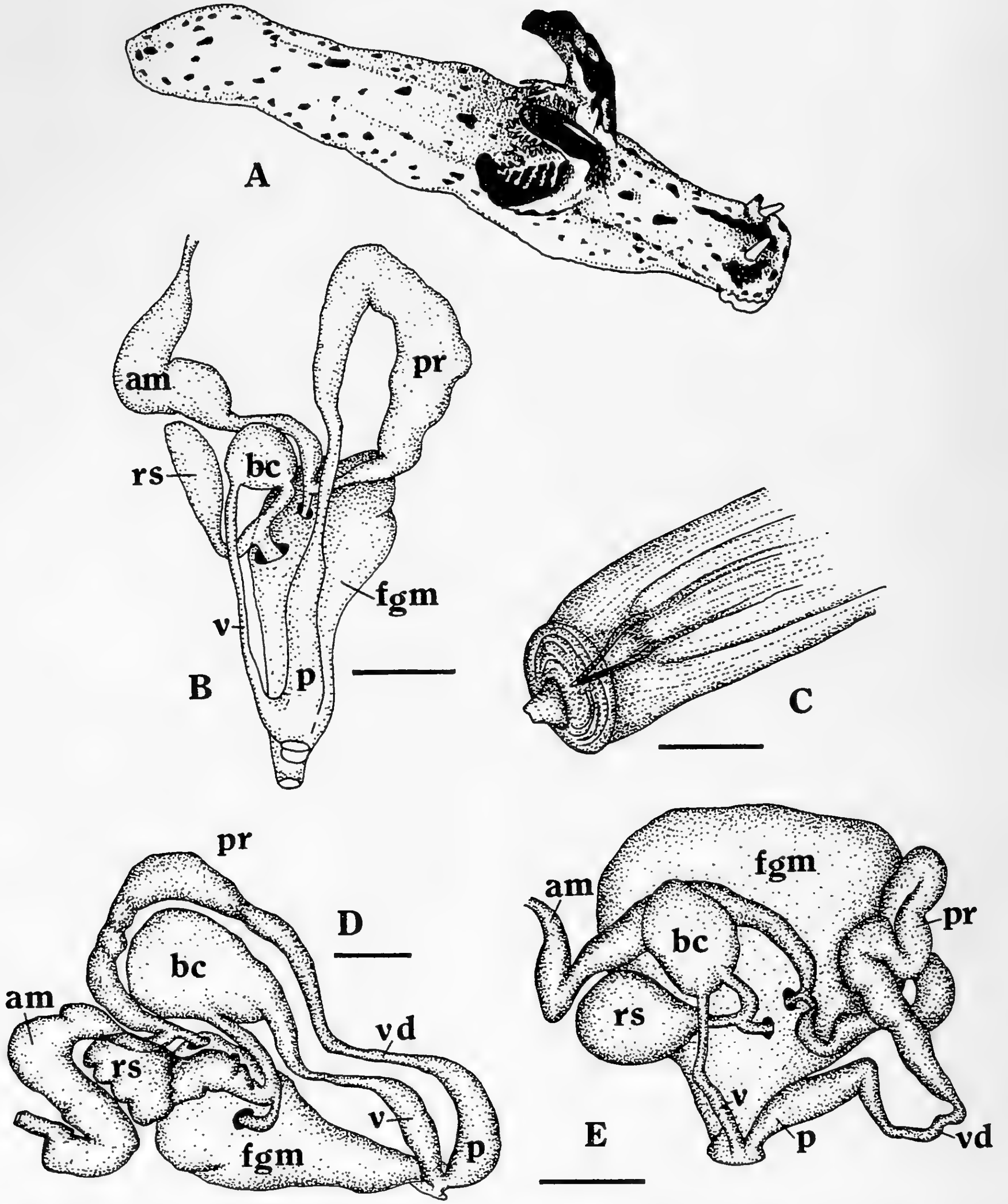

FIGURE 12. A. *Notodoris serenae* sp. nov., living animal. B. *Notodoris serenae* sp. nov., reproductive system, am = ampulla, bc = bursa copulatrix, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina, scale = 1.0 mm. C. *Notodoris serenae* sp. nov., detail of penial papilla, scale = 0.25 mm. D. *Notodoris minor* Eliot, 1904, reproductive system, lettering as in A, scale = 1.0 mm. E. *Notodoris gardineri* Eliot, 1908, reproductive system, lettering as in A, scale = 1.0 mm.

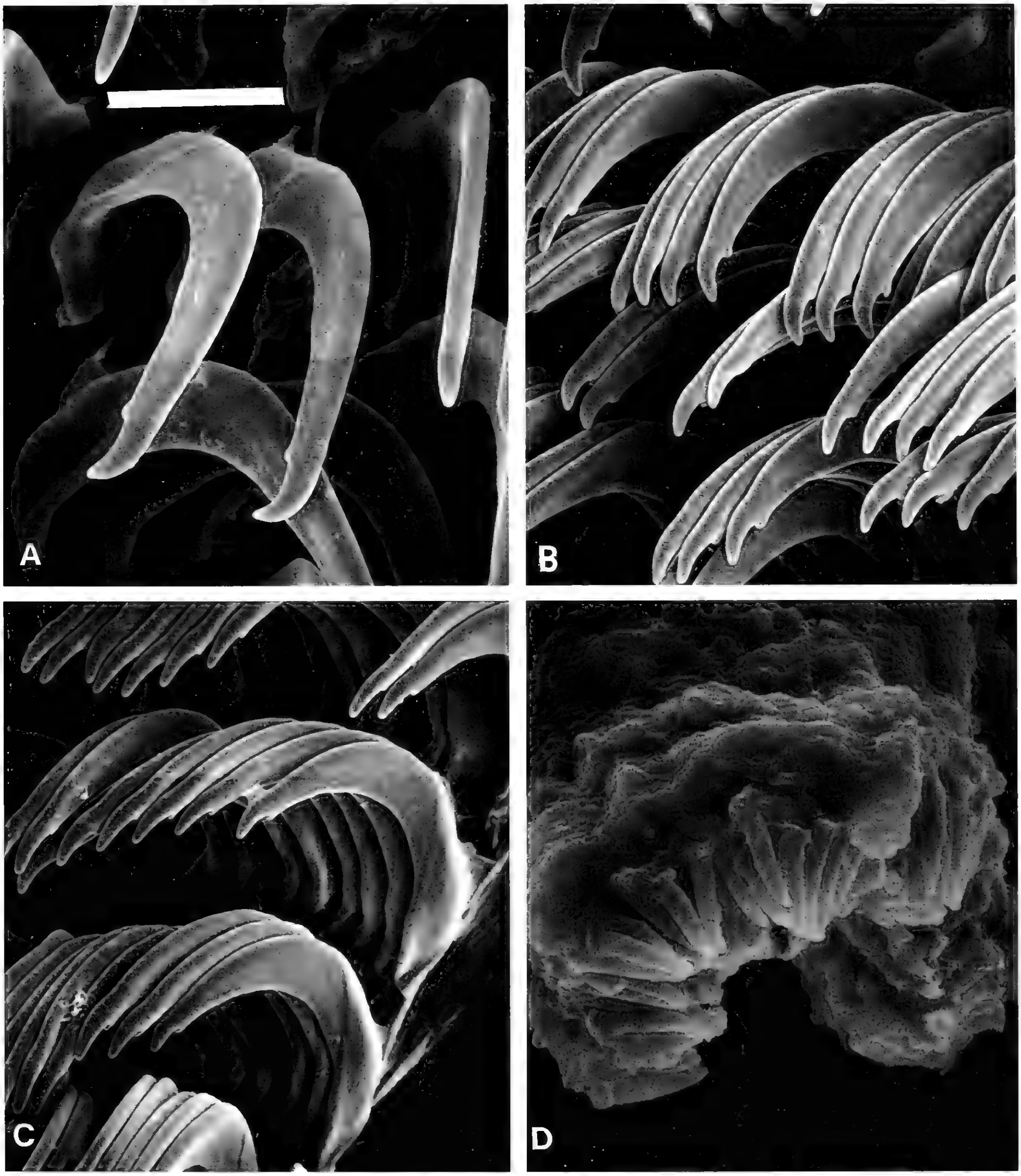

FIGURE 13. *Notodoris serenae* sp. nov. Scanning electron micrographs. A. Inner lateral teeth, scale = 43 µm. B. Middle lateral teeth, scale = 75 µm. C. Outer lateral teeth, scale = 75 µm. D. Penial armature, scale = 10 µm.

DISTRIBUTION. — Thus far this species is known from Papua New Guinea, Indonesia, Malaysia, Philippines, Belau, Pohnpei and Okinawa (C. Carlson, present study and P. J. Hoff, pers. comm.).

NATURAL HISTORY. — *Notodoris serenae* is found in 10–15 m depths on the edges of the crest of barrier reefs. It feeds upon the calcareous sponge *Leucetta chagosensis* Dendy, 1913 (present study), not *L. primigenia* Haeckel, 1872, as erroneously indicated in Gosliner, Behrens and Williams (1996:172).

EXTERNAL MORPHOLOGY. — As in other species of *Notodoris*, *N. serenae* is firm bodied and limaciform. The preserved animals examined were up to 58 mm in length. The living animals, which reach 100 mm in length (Fig. 7C, 12A), are dull white to grey with randomly distributed and variably sized low black tubercles and markings. The foot is yellow throughout and its margin is visible dorsally and laterally when the animal is crawling. The gills are yellow or green with black tips. There are three large, firm, arching appendages surrounding the gills, the medial of which is shorter than the two laterals. A pattern of reticulating ridges adorn each appendage. The ridges are marked with black, becoming densest at their tips. The head is angular, accentuated by a series of ridges of irregular black-tipped tubercles. The rhinophores are simple, smooth and bright yellow. The head bears a raised medial ridge, which is black. It begins anterior to the rhinophores and continues posteriorly. It may continue as a broken series of tubercles. A series of irregular tubercles, each black-tipped, are situated laterally to each rhinophore. There is a separation between the head and foot forming a groove and two oral lappets on either side of the head. The genital aperture is situated on the right side of the body, immediately posteroventral to the rhinophores.

BUCCAL ARMATURE. — There is a thin chitinous labial cuticle devoid of rodlets or armature. Salivary glands are thin and strap-like. The radular formula in two specimens is 32 × 30–32.0.30–32. The teeth from the inner portion of the radula (Fig. 13A), middle (Fig.13B) and outer margin (Fig. 13C) are all evenly arched and hamate, with a single rounded denticle situated just below the primary cusp.

REPRODUCTIVE SYSTEM. — The arrangement of organs is triaulic (Fig. 12B). The preampullary duct is short and straight. It widens into the thick, curved ampulla, which again narrows and bifurcates. The short oviduct enters the female gland mass, which was not fully mature in the single large individual examined. The vas deferens expands into a thick, curved prostatic portion which narrows into a short, straight ejaculatory portion. This segment again widens into the penial sac. The tip of the penis bears a small cuticular tube that protrudes from the apex. Immediately proximal to the apex is an area of darkly staining cells (Fig. 12C) which contains minute penial spines visible under the light microscope at 1000× magnification. Scanning electron micrographs confirm the presence of these minute penial spines (Fig. 13D). The uterine duct emerges from the female gland mass and widens and joins the elongate duct of the pyriform receptaculum seminis. Together these ducts enter the posterior end of the small, spherical bursa copulatrix. From the other end of the bursa, the thin, straight vaginal duct connects with the penial sac just proximally of the genital aperture.

DISCUSSION. — The predominantly gray body color of *N. serenae* differs significantly from the common bright yellow color found in three other described members of this genus: *Notodoris gardineri* Eliot, 1908, *N. minor*, Eliot, 1904 and *N. citrina* Bergh, 1875. The presence of three elongate extrabranchial appendages and three multipinnate gills are also unique to *N. serenae*. The remaining species have three branchial lappets that overhang and protect the gills. In *N. minor* these lappets are simply rounded while in *N. gardineri* and *N. citrina* their margin is distinctly lobed. The lobes are deeper in *N. gardineri* than in *N. citrina*. These three species have arrangements of gills that differ markedly from those of *N. serenae*. In *N. gardineri* and *N. minor*, there are numerous small gills, while in *N. citrina*, there are seven quadripinnate gills (O'Donoghue, 1924).

The radular teeth of *Notodoris serenae* are more deeply bifid as in *N. gardineri* (O'Donoghue, 1924, figs. 63-64; Thompson, 1975, fig. 4; Yonow, 1993, fig. 8a, b) rather than having the more shallow lobes found in *N. minor* (Eliot, 1904, pl. 3, fig. 1g) and *N. citrina* (Bergh, 1875, pl. 9, 10). The radula of *N. citrina* is much narrower than that of the other species. Bergh (1875) indicated that there were only 14 teeth per half-row in *N. citrina* while in the other species there are 25–42 teeth per half-row.

The reproductive system has not been fully described for any other species of *Notodoris*. Thompson (1975) indicated that the penis of *N. gardineri* has small spines, but did not illustrate this feature. The arrangement of the bursa copulatrix and receptaculum seminis of *N. citrina* was illustrated by Bergh (1875). To compare the reproductive anatomy of *N. serenae* to other members of the genus, specimens of *N. minor* (CASIZ 068668) and *N. gardineri* (CASIZ 068693) from Papua New Guinea were dissected (Fig. 12 D and E, respectively). The general arrangement of organs is similar in all three species examined. In all cases, after merging with the duct of the receptaculum seminis, the uterine duct enters the wall of the bursa copulatrix rather than the base of the bursa. This configuration was also described for *N. citrina* (Bergh, 1875). In *N. gardineri*, there is a faint area near the subapical portion of the penis, which may bear spines. In *N. minor*, the penis is slightly more protruded and the penial spines are obvious, but minute. The penial spines found in the specimens of *N. serenae* examined here are larger than those of *N. gardineri*, but smaller than those of *N. minor*.

Thompson (1975) in his discussion of *N. gardineri*, stated that *N. citrina* and *N. minor* had not been found since their original descriptions and doubted the validity of three distinct species of *Notodoris*. Reexamination of additional material of these species and *N. serenae*, confirms the distinctness of four species of *Notodoris*. The characteristics employed by O'Donoghue (1924) to separate the species are indeed valid. Additionally, characteristics of the branchial lappets clearly distinguish the species, as do consistent differences in color pattern.

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THE ACANTHACEAE OF CALIFORNIA AND THE PENINSULA OF BAJA CALIFORNIA

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Twenty-four species in 10 genera of Acanthaceae are treated as occurring in the states of California (United States), Baja California (Mexico), and Baja California Sur (Mexico). Two species (*Carlowrightia arizonica* and *Justicia californica*) occur in southern California; four species (*C. arizonica*, *Holographis virgata*, *J. californica*, and *Ruellia californica*) occur in the state of Baja California; and all 24 species (*Aphanosperma sinaloensis*, *C. arizonica*, *C. pectinata*, *Dicliptera resupinata*, *Dyschoriste decumbens*, *Elytraria imbricata*, *Henrya insularis*, *Holographis virgata*, *J. austrocapensis*, *J. californica*, *J. candicans*, *J. hians*, *J. insolita*, *J. palmeri*, *J. purpusii*, *J. spicigera*, *R. californica*, *R. cordata*, *R. intermedia*, *R. inundata*, *R. leucantha*, *R. nudiflora*, *Tetramerium fruticosum*, and *T. nervosum*) occur in Baja California Sur. Twelve of the species are widespread in their overall distributions and six are endemic to Baja California Sur. Among the phytogeographic regions covered by this treatment, the Cape Region of southern Baja California Sur has the greatest number of species of Acanthaceae.

Occurrences of *Aphanosperma sinaloensis*, *Justicia candicans*, *Ruellia intermedia*, *R. inundata*, and *R. nudiflora* are documented from the peninsula of Baja California for the first time. *Siphonoglossa incerta* is treated in *Justicia* and a new name, *J. austrocapensis*, is provided for it. Based on minor morphological differences and an allopatric distribution, the varieties of *J. insolita* are elevated to the rank of subspecies. *Ruellia peninsularis* and *R. californica* have suballopatric distributions and differ primarily by a single pubescence character. They are treated as two subspecies of a single species. *Dicliptera formosa*, previously treated as a species endemic to Baja California Sur, is considered to be conspecific with *D. resupinata*. *Holographis virgata* comprises two subspecies, one of which comprises two varieties. All species are described and their geographic ranges are plotted on maps. Illustrations of macromorphological characteristics are provided for each genus and photographs of pollen are provided for each species. Chromosome numbers are reported for the first time for *Justicia insolita* subsp. *tastensis*, *J. palmeri*, and *Ruellia leucantha*.

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The Acanthaceae comprise some 4,000 species in about 275 currently recognized genera. The family is worldwide in distribution with most taxa occurring in the tropics. Plants occur in most tropical habitats except those at very high elevations (i.e., above 3,000 m). About 50 species of Acanthaceae occur in the United States, mostly in the southern tier of states (especially Texas, Florida, and Arizona). More than 350 species of the family are known from Mexico with major centers of diversity in southwestern Mexico (Nayarit through Guerrero) southeastern Mexico (Veracruz) and southern Mexico (Oaxaca and Chiapas). The region covered in this treatment consists of the southernmost portion of the state of California (i.e., the only part of the state in which Acanthaceae occur) in the United States, and the Mexican states of Baja California and Baja California Sur. The latter two states comprise the peninsula of Baja California, one of the most prominent and isolated physiographic features of western North America.

The Acanthaceae of California were most recently treated by Heckard (1993) and those of the peninsula of Baja California by Wiggins (1980). In order to resolve several taxonomic problems, to add species not previously documented from Baja California Sur, and to document more thoroughly the distributions of species in these regions, a regional taxonomic treatment of the family was undertaken.

The region under consideration here is generally understood to include all or portions of three broad phytogeographic regions: the California Floristic Province, the Sonoran Desert, and the Cape Region of southern Baja California Sur. In addition, the Sierra de la Giganta in Baja California Sur is treated here as a separate region (see discussion below). Treatment of the boundaries of phytogeographic regions in the peninsula of Baja California varies with authors and Figure 1 presents a rather traditional scheme incorporating information from Brown and Lowe (1980), Turner and Brown (1982), and Zippin and Vanderwier (1994).

One of the most conspicuous features of North American Acanthaceae is the apparent radiation of taxa into the arid regions of northern Mexico and the adjacent United States resulting in considerable local and regional endemism. For example, fifty percent of the species (17 of 34) of Acanthaceae occurring in the Chihuahuan Desert of north-central Mexico and south-central United States are endemic there (Daniel 1985). The region covered by this geographic treatment is dominated by one of these distinctive arid regions, the Sonoran Desert, which occurs from southeastern California southward along the gulf coast of Baja California to about lat. 30°N where it extends westward to the Pacific Ocean and continues southward to about lat. 24°N in Baja California Sur where it continues as isolated patches along the Gulf coast of the Cape Region to the southeastern tip of the peninsula (Fig. 1).

Sonoran Desert vegetation is characterized by a great diversity of life forms, especially arboreal elements, large cacti, and succulent plants. In many respects it is an arid expression of the adjacent tropical dry forests and thornscrub to the south from which it is undoubtedly derived. The tropical dry forests of western Mexico are particularly rich in species of Acanthaceae (Daniel 1993) and likely have served as sources for taxa that either persisted in or dispersed into the lands which, through increasing aridity over time, came to support a regional Sonoran Desert.

Of the six subdivisions of the Sonoran Desert, four occur in the region under consideration here (Fig. 1): Lower Colorado River Valley, Central Gulf Coast, Vizcaíno, and Magdalena subdivisions (Turner and Brown 1982). The latter two are restricted to the peninsula of Baja California. Each subdivision has a distinctive climatic pattern and vegetational physiognomy (Turner and Brown 1982). At least 14 species of Acanthaceae in our region occur in at least one subdivision of the Sonoran Desert.

The Lower Colorado River Valley is the largest and driest subdivision of the Sonoran Desert. It includes much of southeastern California and most of eastern Baja California. Vegetation tends to be open and simple in structure. Two species of Acanthaceae occur in the Lower Colorado River Valley subdivision in our region. These comprise the only two Acanthaceae known from California, *Carlowrightia arizonica* and *Justicia californica*.

In the peninsula of Baja California the Central Gulf Coast subdivision occurs as a relatively narrow and disconnected band along much of the Gulf coast. Its vegetation is commonly dominated by stem succulents and generally lacks a low shrub layer. All 14 species of Acanthaceae that occur in the Sonoran Desert in our region

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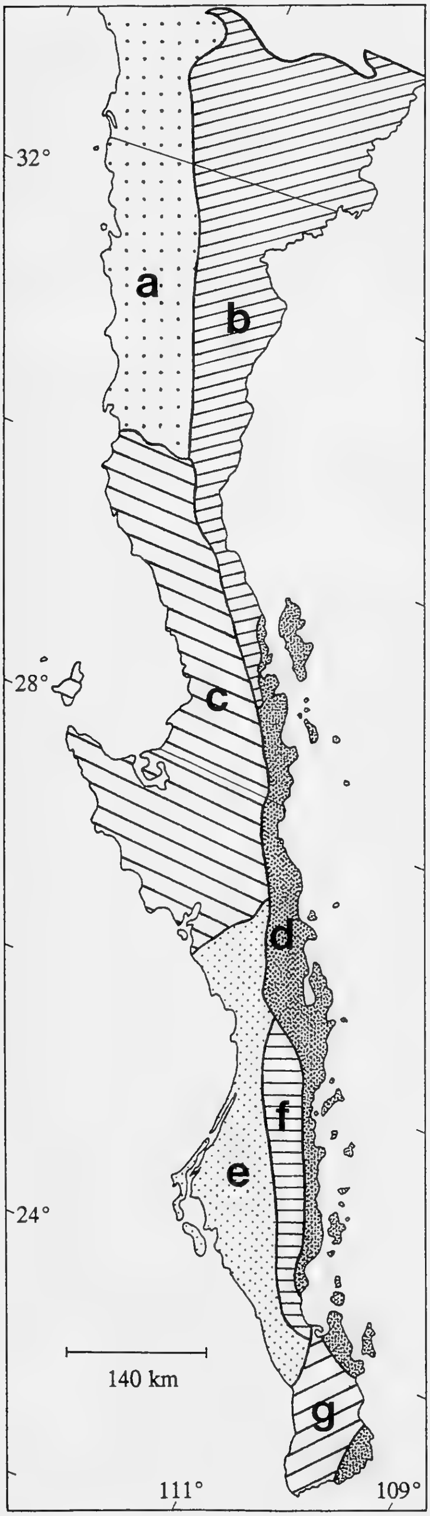
FIGURE 1. Map of southern California and the peninsula of Baja California with adjacent islands showing the distribution of major phytogeographic regions: California Floristic Province (a), Lower Colorado River Valley subdivision of the Sonoran Desert (b), Vizcaíno subdivision of the Sonoran Desert (c), Central Gulf Coast subdivision of the Sonoran Desert (d), Magdalena subdivision of the Sonoran Desert (e), Sierra de la Giganta (f), and Cape Region (g).



have been found in this subdivision. This number is considerably greater than that for any other subdivision of the Sonoran Desert in our region. All but four of these species also occur in the mainland (Sonoran) portion of this subdivision.

Most of the Vizcaíno subdivision of the west-central portion of the peninsula is low (less than 500 m) in elevation. Vegetationally, this subdivision contains many stem succulents but is dominated by fleshy-leaved plants. Near the Pacific coast, fog ameliorates the effects of low rainfall in the spring and summer resulting in a conspicuous covering of epiphytes on many plants. At least eight species of Acanthaceae occur here: *Carlowrightia arizonica*, *Dicliptera resupinata*, *Holographis virgata*, *Justicia californica*, *J. hians*, *J. palmeri*, *Ruellia californica*, and *Tetramerium fruticosum*. All of these species have relatively widespread distributions on the peninsula.

The Magdalena subdivision occupies the Pacific slopes and plains of the southern third of the peninsula. This subdivision has abundant, large cacti together with many small trees resulting in an equality of dominance between trees and large succulents (Shreve 1964). In the south, it intergrades and interdigitates with subtropical and tropical scrub of the Cape Region. At least seven species of Acanthaceae have been collected in this subdivision of the Sonoran Desert: *Dicliptera resupinata*, *Elytraria imbricata*, *Justicia californica*, *J. insolita*, *Ruellia californica*, *R. nudiflora*, and *Tetramerium fruticosum*. Most of these species have relatively widespread distributions on the peninsula.

The region of nondesert vegetation in the Cape Region and the Sierra de la Giganta of Baja California Sur is sometimes referred to as a phytogeographic "Cape Region" (e.g., Cody et al. 1983). Brown et al. (1979) refer to this phytogeographic region as the San Lucan biotic province [modified from Dice's (1943) larger region with the same name], a distinct biogeographic province of North America. Because of the floristic and vegetational differences between the Cape Region proper and the Sierra de la Giganta, and because numerous Acanthaceae are restricted to the former, these two regions are treated separately here.

Geographically and geologically the Cape Region is commonly delimited as that portion of the peninsula to the south and east of the La Paz

Fault, which runs approximately from Punta Coyote to Todos Santos near the northwestern foot of the mountains. This single, predominately granitic, fault block may have been an island in the Pliocene (Gastil et al. 1983). The region receives considerably more precipitation than areas to the north. Because of its separation from other areas of similar climate, the Cape Region remains today an isolated mountainous region. Vegetation of the Cape Region comprises two isolated regions of Sonoran Desert (Central Gulf Coast subdivision, which is discussed above), a large area of subtropical to tropical deciduous scrub and forest, and montane oak and pine-oak woodlands. Twenty-one of the 24 species of Acanthaceae occurring in our region inhabit the Cape Region; eight of these occur only there in our region; two species (*Justicia austrocapensis* and *J. purpusii*) are endemic to the Cape Region; and four total taxa of Acanthaceae are endemic there (i.e., the two species of *Justicia* mentioned above along with *J. insolita* subsp. *tastensis* and *Ruellia leucantha* subsp. *leucantha*). Although several species occurring in the Cape Region are found in portions of the Sonoran Desert there, none is restricted in distribution to these isolated desert regions. Indeed, the large number of Acanthaceae in the Cape Region is undoubtedly attributable to the wetter regions of scrub, forest, and montane woodland in which most of the species there are found.

Scrub vegetation similar to that of the Cape Region extends along the axis of the largely volcanic Sierra de la Giganta. This rugged montane region exhibits many similarities with adjacent regions of Sonoran Desert as well. It lacks coniferous woodlands at higher elevations, but does support scattered pinyon pines. At least 13 species of Acanthaceae are known from the Sierra de la Giganta, including *Ruellia cordata* which is endemic to the northwestern edge of this region.

That portion of the California Floristic Province in southwestern California and northwestern Baja California includes both coastal and montane communities that are sometimes treated as separate regions (e.g., Zippin and Vanderwier 1994). This region is characterized by a Mediterranean climate with winter rains and summer drought. Among Acanthaceae only the widespread *Justicia californica* is known from this region; it has been collected several times both near Lakeside in California and at Valle las Palmas in Baja California. According to R. Moran (pers. comm.), *J. californica* occurs naturally at both of these localities. Dr. Moran indicates that the southern portion of the California Floristic Province is drier than portions to the north and occasionally harbors plants more typical of the desert to the east. For example, Valle las Palmas has the only natural occurrence of palms (*Washingtonia*) west of the montane divide. The presence of *J. californica* at both of these sites likely represents either relatively recent incursions from the Sonoran Desert into regions of the California Floristic Province with ecologically suitable habitats or relictual colonies indicative of a formerly more widespread distribution. Further evidence of the apparent ability of *J. californica* to survive in portions of the California Floristic Province is the persistence of this species over many years in native plant gardens in various parts of southern California. The only two Acanthaceae known from California occur primarily (or exclusively in the case of *Carlowrightia arizonica*) in the Sonoran Desert to the east of the California Floristic Province and comprise the northernmost extent of the distribution of the family on the west coast of North America. This distribution suggests that the Mediterranean climate is an effective barrier to the northwestward advancement of Acanthaceae in North America.

Twelve of the 24 species of Acanthaceae occurring in the region covered by this revision are widespread in their overall distributions, that is, they occur in diverse regions of the United States and/or Mexico and/or elsewhere in Latin America. There are no endemic genera of Acanthaceae in our region; however, six of the 24 species of Acanthaceae (25%) occurring in the peninsula of Baja California are endemic there. These six species (*Justicia austrocapensis*, *J. hians*, *J. insolita*, *J. palmeri*, *J. purpusii*, and *Ruellia cordata*) are restricted to Baja California Sur, and two of them (*J. austrocapensis* and *J. purpusii*) occur only in the Cape Region. In order to compare the percentage of endemism of Acanthaceae with that noted by Wiggins (1980) for the entire vascular flora of the peninsula, infraspecific taxa must be considered. Eleven of the 28 taxa of Acanthaceae (39%) are endemic to the peninsula. This percentage is considerably higher than the 23% noted by Wiggins (1980) for the total flora. Four other species can be considered as near endemics, i.e., species with a distribution that is primarily peninsular but which are represented on the adjacent mainland by a single small population (*Tetramerium fruticosum*), by one subspecies that also occurs on the peninsula (*Holographis virgata* and *Ruellia californica*), or by a different subspecies (*Ruellia leucantha*). Two additional species (*Aphanosperma sinaloensis* and *Justicia californica*) are regional endemics (i.e., endemic to the southwestern United States and/or northwestern Mexico).

An interesting outcome of this study is the recognition of infraspecific taxa in four species, all of which are endemic to the peninsula of Baja California and adjacent regions of the Mexican mainland. Good evidence for geographically or elevationally distinct infraspecific taxa with minor morphological distinctions is not usually encountered among Acanthaceae elsewhere in Mexico. Several factors that might help to explain their presence here include: the geologic history of our region (including the peninsula's separation from the mainland, periods of insularity, etc.), the rugged physiography of a narrow and isolated peninsula that extends across nearly ten degrees of latitude, and the juxtaposition in our region of an array of ecological zones (and their displacements through time with changes in global climate and movements of the earth's crust). Both the endemic species and infraspecific taxa recognized in this treatment likely owe their origin and/or continued presence in the peninsula to a combination of these, and other, factors. Because we understand the processes of speciation and the genesis of infraspecific taxa so inadequately, one can only speculate as to the myriad environmental and evolutionary factors that have made this extensively collected region of Mexico ripe for recognition of infraspecific taxa in the Acanthaceae.

MATERIALS AND METHODS

The following geographic revision treats all Acanthaceae known to occur in the three politically delimited states of western North America noted above. Islands in the Pacific Ocean and the Gulf of California that comprise parts of these states are also included (Fig. 1). Islands comprising portions of other states (e.g., Isla Tiburón, in the Gulf of California, and the Islas Revillagigedo, in the Pacific Ocean) are excluded. Use of "Baja California" in this treatment refers only to the Mexican state of that name. When considering both Mexican states (i.e., Baja California and Baja California Sur) simultaneously, the phrase "peninsula of Baja California" is utilized.

More than 1,000 collections of Acanthaceae from California and the peninsula of Baja California were studied from the following institutions: CAS, DAV, DS, GH, HCIB, JEPS, LA, POM, RSA, SD, UC, and UCR. Selected collections from several additional herbaria were also studied (e.g., A, ARIZ, ASU, DES, DUKE, ENCB, F, G, K, LL, MEXU, MICH, MIN, MO, MSC, NY, TEX, US). Observations and collections were made by me during five field trips to the region between 1978 and 1994. The species descriptions are derived from those observations and the collections cited unless there is an indication that other materials were used to supplement them. Pollen was studied and photographed with a scanning electron microscope. Chromosome numbers were determined using the methodology described by Daniel and Chuang (1993). In addition to chromosome numbers reported herein, previously reported chromosome numbers are cited for each taxon and one or more references in which the numbers were reported are provided. Complete synonymies are provided for most taxa. In several cases (i.e., *Carlowrightia arizonica*, *Elytraria imbricata*, *Henrya insularis*, *Ruellia nudiflora*, and *Tetramerium nervosum*) where the taxa are widespread, many names have been applied to them, and a full synonymy has been recently published elsewhere, only names based on types from northwestern Mexico and the United States are included. In these instances a reference to the full synonymy is provided.

TAXONOMIC TREATMENT
ACANTHACEAE

Terrestrial (rarely aquatic) herbs or shrubs, less often trees or vines, vegetative and floral organs glabrous or pubescent with various types of eglandular (simple and compound), subglandular (i.e., lacking a conspicuous capitate gland at apex but apically enlarged), and glandular trichomes, often beset with cystoliths visible in epidermis (these absent in *Elytraria* and *Holographis*) and sometimes beset with sessile lenticular glands mostly 0.05–0.2 mm in diameter (glandular punctate). Young stems with nodes usually swollen. Leaves opposite and decussate or sometimes quaternate, simple, estipulate, sessile to petiolate, margin usually entire. Inflorescence in leaf axils (axillary) or terminating shoots (terminal), cymose (e.g., dichasia solitary in leaf axils) or thyrsoid (i.e., with the main axis indeterminate and with lateral axes determinate), the basic unit a variably reduced or expanded dichasium, dichasia borne in axils of leaves or bracts, alternate (= solitary) or opposite (= paired) at nodes, sessile or pedunculate, 1–many-flowered, when in axils of bracts then usually forming dichasiate spikes (i.e., dichasia and flowers sessile to subsessile), racemes (i.e., dichasia sessile to subsessile and flowers pedicellate), or thyrses (i.e., dichasia pedunculate), these inflorescences sometimes branched and then forming panicles. Bracts large and brightly colored or small and green. Flowers sessile or pedicellate, usually subtended by 2 bracteoles, complete, bisexual, chasmogamous and often cleistogamous. Calyx synsepalous, comprising 5 sepals, usually deeply 4–5-lobed, lobes equal to unequal in length. Corolla sympetalous, comprising 5 petals, tube cylindric or funnelform (i.e., gradually or abruptly expanded distally into a ± distinct throat), sometimes twisted 180° (i.e., corolla resupinate) or 360°, limb subactinomorphic to zygomorphic, commonly bilabiate with an upper lip of 2 lobes and a lower lip of 3 lobes, corolla lobes imbricate (including cochlear and quincuncial) or contorted in bud. Stamens epipetalous, included in corolla tube or exserted from mouth of corolla, usually 2 or 4 and didynamous, filaments free or connate in pairs proximally, anthers 1-thecous or 2-thecous, thecae usually dehiscing by longitudinal slits, sometimes with basal or apical appendages, thecae of a pair parallel to perpendicular, collaterally attached to filament to superposed to widely separated by a modified connective, pollen extremely diverse, spheric to prolate, 2–many-aperturate (apertures simple or compound) or inaperturate, staminodes 0–3, comprising minute projections or sterile filaments. Nectariferous disk usually present around base of ovary, annular. Gynoecium 2-carpellate, ovary superior, generally 2-locular, placentation usually axile, ovules 2–many in each locule, style simple, terminal, filiform, included within corolla tube or exserted from mouth of corolla, stigma funnelform, 2-lobed, or with one lobe suppressed, 1 or both lobes sometimes recurved or recoiled. Fruit usually a loculicidal, explosively dehiscent, stipitate or estipitate, 2-valved capsule, septa sometimes separating from inner wall of mature capsule. Seeds usually 2–many, each usually subtended by a prominent hook-shaped retinaculum (retinacula borne along septa, lacking or papilliform in *Elytraria*), globose to lenticular, often asymmetrically notched at base, glabrous or pubescent, trichomes often hygroscopic or becoming mucilaginous when wet, surfaces smooth or variously ornamented. (x = 7).

KEY TO GENERA OF ACANTHACEAE IN CALIFORNIA AND BAJA CALIFORNIA

1. Leaves alternate, often crowded at stem apices; inflorescence borne on scapes covered with coriaceous and clasping scales; corollas 4–8.5 mm long; stigma touch-sensitive; capsule 2.8–4.1 mm long; seeds irregularly blocky, borne on papilliform placentae (hooklike retinacula lacking) . . . . *Elytraria*
1. Leaves opposite, usually ± evenly distributed along stems; inflorescence not borne on scaly scapes; corollas 5.5–90 mm long; stigma not touch-sensitive; capsule 4.4–24 mm long; seeds subglobose to lenticular, borne on hooklike retinacula.
    2. Fertile stamens 4.
        3. Cystoliths absent; corolla 9–14 mm long, strongly bilabiate, lobes imbricate in bud; anthers 1-thecous; pollen 3-colpate. . . . . *Holographis*
        3. Cystoliths present; corolla 15–90 mm long, subactinomorphic, lobes contorted in bud; anthers 2-thecous; pollen otherwise.
            4. Corolla 15–17 mm long; calyx tube with weak (i.e., rupturing when capsule matures) hyaline regions proximal to sinuses of lobes; thecae basally awned; pollen 3-colporate, mesocolpia multi-striate with pseudocolpi . . . . *Dyschoriste*

4. Corolla 20–90 mm long; calyx lacking weak hyaline regions; thecae lacking basal awns; pollen 3-porate, exine coarsely reticulate .... *Ruellia*

2. Fertile stamens 2.

5. Stems hexagonal in cross-section; inflorescence of axillary bracteate cymes bearing (1–) 3 (–5) pedunculate cymules; cymules consisting of 1 or more flowers subtended by an involucre of 2 or more pairs of bracteoles; outer pair of cymule bracteoles cordate to deltate, conspicuous and larger than inner pair(s); septa with attached retinacula separating from inner capsule wall at maturity and protruding prominently from each valve of capsule, the mature capsule conspicuously ruptured near base of head; corolla resupinate 180° .... *Dicliptera*

5. Stems terete to quadrate-alate in cross-section; inflorescence various but not as described above; cymules never present; flowers subtended by 1 pair of bracteoles; retinacula remaining attached to inner capsule wall at maturity or separating slightly near base of head (i.e., *Henrya* and *Tetramerium*) but not protruding prominently from each valve of capsule, mature capsule not or barely ruptured near base of head; corolla not resupinate.

6. Upper lip of corolla rugulate (i.e., with a stylar furrow); stamens appressed to upper lip of corolla, anthers dehiscing toward lower lip (i.e., flower nototribal); thecae sometimes unequally inserted and sometimes with basal appendages; pollen 2–4 aperturate, apertures flanked on each side by 1–several rows of ± circular insulae and/or peninsulae (i.e., lacking pseudocolpi) .... *Justicia*

6. Upper lip of corolla not rugulate (i.e., lacking a stylar furrow); stamens appressed to lower lip of corolla, anthers dehiscing toward upper lip (i.e., flower stenotribal); thecae equally to subequally inserted and lacking basal appendages; pollen 3-aperturate, apertures flanked on each side by a solid band of exine and a pseudocolpus (i.e., 6-pseudocolpate).

7. Capsules completely reflexed at maturity, expanded and truncate (to subemarginate) at apex, base of stipe covered with uncinate trichomes; seeds fused to and permanently retained within capsule valves; pollen with 3-pronged polar apertures .... *Aphanosperma*

7. Capsules erect at maturity, narrowed and acute at apex, base of stipe lacking uncinate trichomes; seeds free from capsule valves and ejected therefrom at maturity; pollen lacking polar apertures.

8. Either bracts or bracteoles conspicuous, concealing calyx; capsule 4.5–6.5 mm long, septa with attached retinacula separating slightly from inner wall of mature capsule near base of head; seeds 1.3–2 mm long.

9. Bracteoles fused, if at all, only at base for a distance up to 1 mm, not forming an involucre; bracts longer than bracteoles; seeds 4, lacking trichomes; pollen with colpi narrow, not or barely exceeding width of centrally positioned ora .... *Tetramerium*

9. Bracteoles fused along 1 side from base to near apex, forming a conspicuous involucre; bracts shorter than bracteoles; seeds 2, pubescent with stiff, interwoven, hygroscopic trichomes to 0.5 mm long; pollen with colpi broad, far exceeding width of centrally positioned ora.................... *Henrya*

8. Neither bracts nor bracteoles conspicuous, not concealing calyx; capsule 6.5–14 mm long, septa with attached retinacula remaining attached to inner wall of mature capsule; seeds 2.5–4.5 mm long...................... *Carlowrightia*

APHANOSPERMA

Aphanosperma T. F. Daniel, Amer. J. Bot. 75:547. 1988. TYPE. — *Aphanosperma sinaloensis* (Leonard & Gentry) T. F. Daniel.

Erect perennial herbs to shrubs with cystoliths. Older stems with epidermis exfoliating. Leaves opposite, petiolate, margin entire. Inflorescence of dichasiate spikes; dichasia (alternate to) opposite, 1-flowered, sessile, subtended by a bract. Bracts and bracteoles small, green, inconspicuous, their margins entire. Flowers homostylous, sessile to subsessile, subtended by 2 homomorphic bracteoles. Calyx deeply 5-lobed, lobes equal to subequal in size. Corolla cream to white with purple markings on upper lip, tube subcylindric, shorter than limb, limb bilabiate (although sometimes appearing nearly regular), upper lip comprising 2 fused lobes, emarginate at apex, lower lip 3-lobed. Stamens 2, inserted at apex of corolla tube, exserted from mouth of corolla, anthers 2-thecous, thecae equal in size, subsagittate to subparallel, equally to subequally inserted on filament, lacking basal appendages, dehiscing toward upper lip of corolla (i.e., flower stenotribal); pollen (Fig. 2a, b) prolate, 3-colporate, 6-pseudocolpate, pseudocolpi 2 per mesocolpium, poles sometimes with a 3-pronged aperture, arms aligned with colpi and extending from pole toward equator, exine reticulate; staminodes 0. Style exserted from mouth of corolla, stigma 2-lobed. Capsule stipitate, cuneiform, reflexed at maturity, stipe densely pubescent at base with uncinate trichomes, head truncate to ± emarginate at apex, retinacula not visible in mature capsule. Seeds 2, permanently invested in capsule valves. ($x = 18$).

A single species from tropical dry forests in northwestern Mexico is known.

REFERENCE. — DANIEL, T. F. 1988. *Aphanosperma*, a new genus of Acanthaceae from Mexico with unusual diaspores. Amer. J. Bot. 75:545-550.

1. **Aphanosperma sinaloensis** (Leonard & Gentry) T. F. Daniel, Amer. J. Bot. 75:548. 1988. *Carlowrightia sinaloensis* Leonard & Gentry, Brittonia 6:327. 1948. TYPE. — MEXICO. **Sinaloa:** slope at Cerro Prieto, vicinity of Culiacán, 30 Nov 1944, *H. Gentry 7111* (holotype: US!; isotypes: CAS!, DES!, DS!, F!, GH!, MICH!, NY!, RSA!, UC!).

Erect perennial herbs to shrubs to 1 m tall. Young stems subterete to subquadrate, striate, pubescent with a mixture of erect to flexuose glandular and eglandular trichomes 0.05–0.8 mm long, trichomes ± evenly disposed to mostly concentrated in 2 vertical lines, mature stems becoming glabrate as the epidermis exfoliates in thin papery strips. Leaves petiolate, petioles to 45 mm long, blades lance-ovate to ovate to subcordate (rarely elliptic to obovate), (10–) 25–140 mm long, (5–) 15–75 mm wide, 1.3–2.6 times longer than wide, acute to truncate to subcordate at base, (rounded to) acute to acuminate at apex, surfaces sparsely pubescent with mostly flexuose to antrorse eglandular trichomes, margin entire. Inflorescence of terminal and axillary (from axils of distal, often considerably reduced, leaves) slender dichasiate spikes forming a terminal leafy panicle; spikes alternate or usually opposite, 1 (–2) per axil, to 200 mm long, pedunculate, rachis pubescent with glandular and eglandular trichomes 0.05–0.30 mm long and sometimes with an overstory of straight to flexuose eglandular trichomes 0.4–0.7 mm long as well; dichasia (alternate to) opposite, 1–2-flowered, subtended by a bract (or proximalmost ones sometimes borne in axils of reduced distal leaves). Flowers sessile to subsessile (i.e., borne on pedicels to 0.5 mm long). Bracts triangular to subulate, 1–4 mm long, 0.5–1 mm wide, pubescent like rachis, eglandular, or nearly glabrous. Bracteoles triangular to subulate, 0.5–2.5 mm long, 0.2–0.5 mm wide, pubescent like bracts or nearly glabrous. Calyx 1.5–3 mm long (sometimes accrescent, up to 4.5 mm long, in fruit), lobes subulate, 1.5–2.5 mm long, pubescent like bracts. Corolla cream (with a white chevron outlined and streaked with maroon on the upper lip) on the inner surface, white (sometimes with a maroon tinge) on the outer surface, 5.5–10 mm long, externally pubescent with erect eglandular trichomes to 0.3 mm long, tube 1.8–2.6 mm long, upper lip obovate, 4–7.5 mm long, 2–2.8 mm wide, emarginate and usually reflexed at apex, the chevron papillate, lower lip 4–7.5 mm long, lateral lobes elliptic to obovate, 4–7.5 mm long, 1.5–4 mm wide, often reflexed at apex, lower-central lobe elliptic, 4–7 mm long, 1.8–3 mm wide, reflexed at apex. Stamens 3.7–6.5 mm

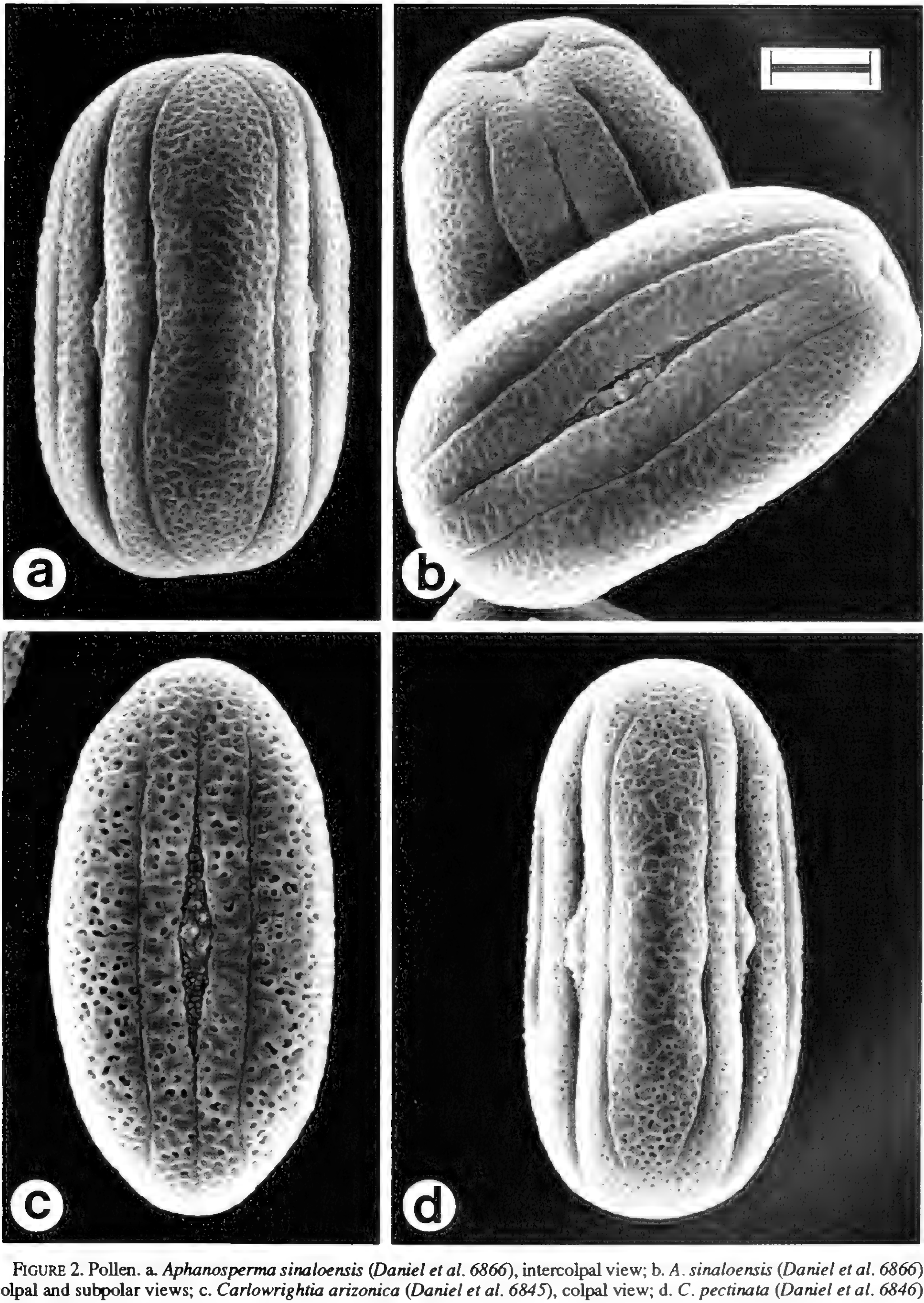


FIGURE 2. Pollen. a. *Aphanosperma sinaloensis* (*Daniel et al. 6866*), intercolpal view; b. *A. sinaloensis* (*Daniel et al. 6866*), colpal and subpolar views; c. *Carlowrightia arizonica* (*Daniel et al. 6845*), colpal view; d. *C. pectinata* (*Daniel et al. 6846*), intercolpal view. Scale for a–d = 7.5 µm.

long, filaments white, sparsely pubescent proximally, glabrous distally, thecae dark maroon (turning blackish), 0.7–0.9 mm long, glabrous. Style 4–8 mm long, glabrous, stigma lobes 0.2 mm long. Capsule 9–14 mm long, stipe 6–8 mm long, densely pubescent near base with eglandular apically hooked trichomes 0.2–0.3 mm long, glabrous or pubescent with retrorse trichomes to 0.2 mm long distally, head 4–5 mm long, nearly glabrous to densely pubescent with retrorse eglandular trichomes to 0.2 mm long. Seeds 2, seed coat fused to inner wall of capsule except for a small portion across the slight opening of the valve, that portion tuberculate with subconic tubercles. (*n* = 18, Daniel et al. 1990). Fig. 3.

PHENOLOGY. — Flowering and fruiting: December (elsewhere: October–March).

DISTRIBUTION AND HABITAT. — Western Mexico (Baja California Sur, Sinaloa, Sonora); in our region the species is known only from the western escarpment of the Sierra de la Laguna in the Cape Region (Fig. 4), where plants occur in floodplains and on rocky slopes in tropical deciduous forest at 450–500 m elevation.

ADDITIONAL SPECIMEN EXAMINED. — MEXICO. **Baja California Sur**: Rancho La Burrera, W slope of Sierra de la Laguna, ca. 22 km NE of Todos Santos, ca. 23°31′N, 110°02′W, *T. Daniel et al. 6866* (BR, CAS, ENCB, HCIB, K, MEXU, MICH, MO, SBBG, US).

This is the first report of *Aphanosperma* from the peninsula of Baja California. The region in which it was found (Rancho La Burrera) is a well-collected area of Baja California Sur; more than forty collections of Acanthaceae have been made there in this century. The region has excellent examples of tropical deciduous forest that are reminiscent of some of those in southern Sonora and Sinaloa where this species also occurs. Additional species of Acanthaceae that are known from the dry forests of northwestern Mexico might also eventually be found in the Cape Region of Baja California Sur.

Aphanosperma is a monotypic genus with flowers similar to those of some species of *Carlowrightia* and with unique capsules. Aspects of the reproductive biology of this species were discussed by Daniel (1988). The above description includes data from specimens collected in Sinaloa and Sonora. Our plants differ from those on mainland Mexico by their generally smaller corollas (5.5–6.8 vs. 7–10 mm long), shorter stamens (3.7–4.3 vs. 4.5–6.5 mm long), and pollen with a polar aperture (vs. lacking a polar aperture). Vesture of the head of the capsule varies from densely pubescent to nearly glabrous among plants from the single population sampled in Baja California Sur.

CARLOWRIGHTIA

Carlowrightia A. Gray, Proc. Amer. Acad. Arts 13:364. 1878. nom. cons. LECTOTYPE (Bremekamp, Ind. Nom. Gener. Card 01197. 1956). — *Carlowrightia linearifolia* (Torr.) A. Gray (≡ *Schaueria linearifolia* Torr.).

Cardiacanthus Nees & S. Schauer in A. DC., Prodr. 11:331. 1847. nom. rej. TYPE. — *Cardiacanthus neesianus* S. Schauer ex Nees. (≡ *Carlowrightia neesiana* (S. Schauer ex Nees) T. F. Daniel).

Croftia Small, Fl. s.e. U. S. 1088. 1903, (not *Croftia* King & Prain, 1896). TYPE. — *Croftia parvifolia* (Torr.) Small (≡ *Schaueria parvifolia* Torr.).

Erect to ascending or decumbent perennial herbs or shrubs with cystoliths. Older stems with epidermis exfoliating. Leaves opposite (in ours, elsewhere rarely subopposite), sessile or petiolate, margin entire (to sinuate). Inflorescence of dichasia in leaf axils, or, more commonly, of dichasiate spikes, racemes, thyrses, or panicles; dichasia alternate or opposite, 1–3 (or more)-flowered, sessile or pedunculate, subtended by a leaf or bract. Bracts and bracteoles small, green, inconspicuous, margin entire. Flowers homostylous, subtended by 2 homomorphic bracteoles, sessile or pedicellate. Calyx deeply 5-lobed, lobes homomorphic. Corolla white to cream to yellowish to rose-purple to blue, usually with yellow and maroon or purple markings on upper lip, tube cylindric to subcylindric, shorter than limb, throat indistinct, limb pseudopapilionaceous (in ours, elsewhere also bilabiate to subactinomorphic), upper lip comprising 2 fused lobes, (entire to) emarginate at apex, lower lip consisting of 2 similar lateral lobes and a lower-central lobe that is either similar in form to lateral lobes or ± recurved or conduplicate-keeled and enclosing stamens and distal portion of style during anthesis, corolla lobes imbricate in bud.

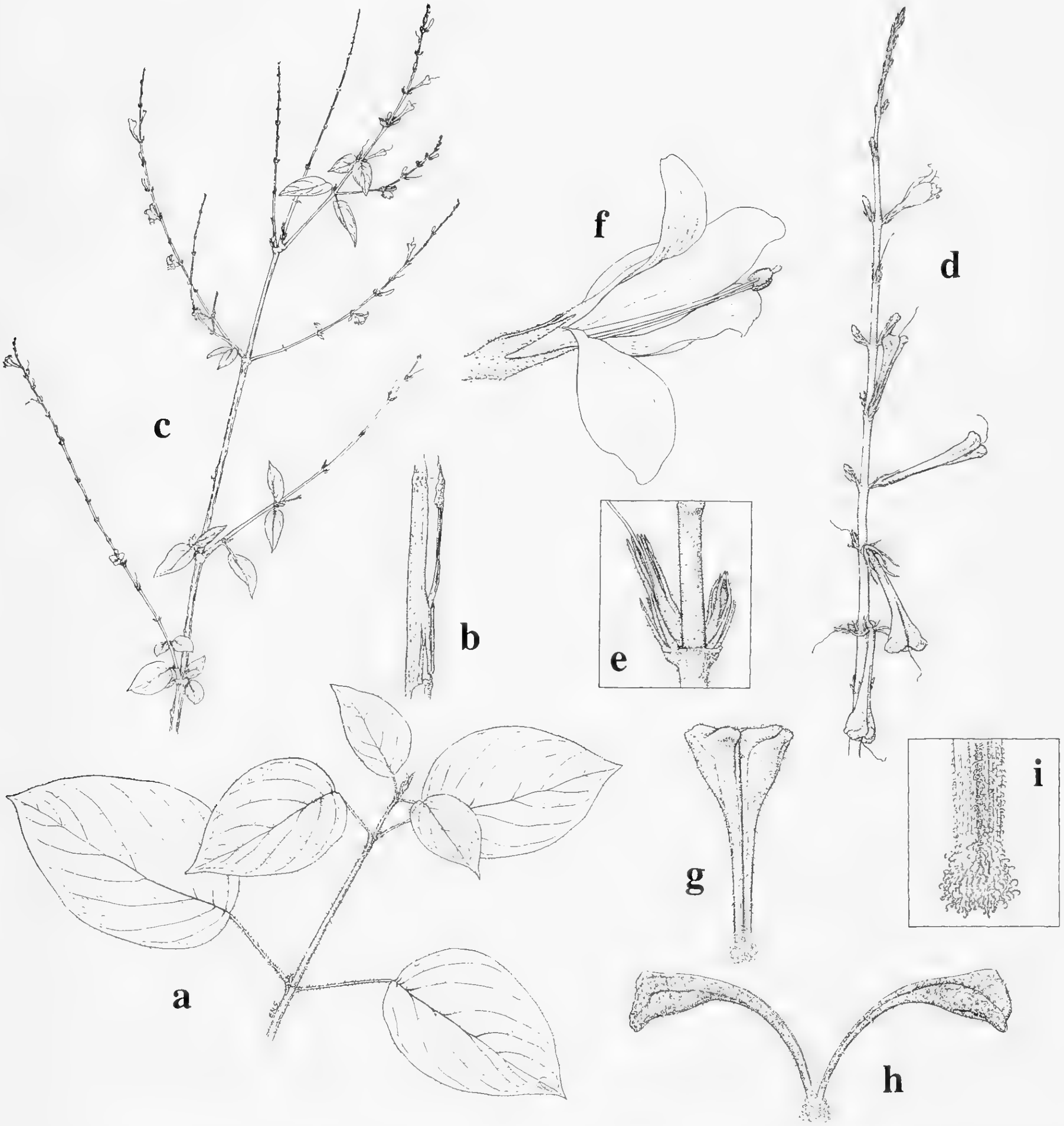


FIGURE 3. *Aphanosperma sinaloensis*. (all from *Daniel 4070cv*). a. vegetative shoot, × 0.5; b. mature stem with exfoliating epidermis, × 1.2; c. distal portion of shoot with inflorescences, × 0.4; d. inflorescence showing progressive reflexing of capsules with age, × 1.3; e. inflorescence node, × 6.5; f. flower, × 6; g. undehisced capsule, × 2.5; h. dehisced capsule with valves attached by uncinate trichomes at base of stipe, × 2.5; i. base of stipe, × 11. Drawn by Carolyn Rendu.

Stamens 2, inserted in distal portion of corolla tube, exserted from mouth of corolla, anthers 2-thecous, thecae equal in size, parallel or subsagittate, subequally inserted on filament, lacking basal appendages, dehiscing toward upper lip of corolla (i.e., flowers stenotribal); pollen (Fig. 2c, d) prolate to subspheric, 3-colporate, 6-pseudocolpate, pseudocolpi 2 per mesocolpium, exine reticulate; staminodes 0. Style exserted from mouth of corolla, stigma 2-lobed. Capsule stipitate, head flattened to nearly spheric, circular to ovate-elliptic in outline, retinacula present, septae with attached retinacula remaining attached to inner wall of mature capsule. Seeds

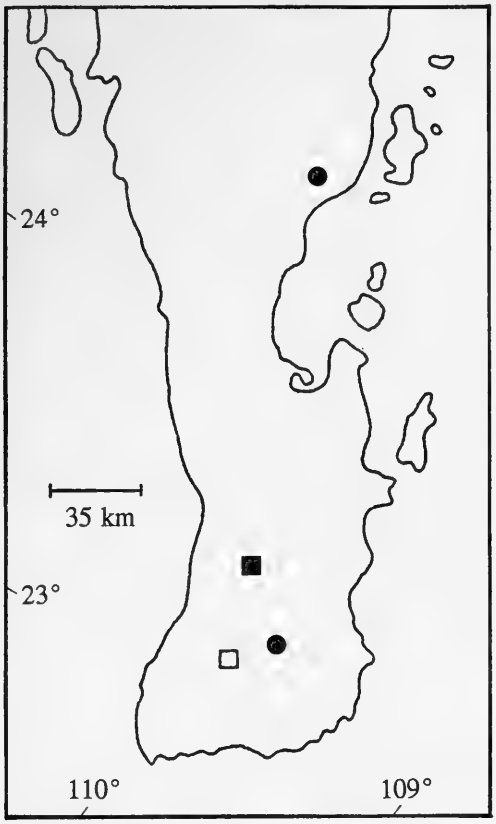


FIGURE 4. Distribution of *Aphanosperma sinaloensis* (square), *Dyschoriste decumbens* (open square), and *Justicia spicigera* (circles) in southern Baja California Sur.

2–4, homomorphic or heteromorphic, flat to concavoconvex, smooth or variously ornamented, lacking trichomes. ($x = 18$).

Twenty-four species are recognized in this New World genus. They occur from the southwestern United States throughout Mexico to northwestern Costa Rica and disjunctly to southwestern Ecuador. With 23 species, Mexico is the center of diversity for *Carlowrightia*. Seven species occur in the United States.

REFERENCES.—DANIEL, T. F. 1983. *Carlowrightia* (Acanthaceae). Fl. Neotrop. Monogr. 34:1–116; DANIEL, T. F. 1988. Taxonomic, nomenclatural, and reproductive notes on *Carlowrightia* (Acanthaceae). Brittonia 40:245–255.

Key to Species of *Carlowrightia*

1. Leaf blades petiolate, ovate to elliptic, 1.6–2.5 times longer than wide, margin flat; lower-central lobe of corolla conduplicate-keeled, enclosing stamens and style; thecae maroon turning black; capsule glabrous, head 5.5–7.5 mm long; seeds 4, homomorphic . . . . *C. arizonica*
1. Leaf blades sessile to subsessile, linear to narrowly elliptic-lanceolate, 6–29 times longer than wide, margin revolute; lower-central lobe of corolla neither conduplicate nor keel-like, not enclosing stamens and style; thecae golden yellow; capsule pubescent (sometimes only sparsely so at apex), head 3.5–5.5 mm long; seeds 2–4, the third and fourth seeds (when present) usually markedly different in form from others (i.e., partially conduplicate and with a conspicuous pectinate margin) . . . . *C. pectinata*

1. Carlowrightia arizonica A. Gray, Proc. Amer. Acad. Arts 13:364. 1878. TYPE.—UNITED STATES. **Arizona**: Pinal Co., near Camp Grant, 1867, *E. Palmer 165* (holotype: GH!).

Carlowrightia cordifolia A. Gray, Proc. Amer. Acad. Arts 21:406. 1886. TYPE.—MEXICO. **Chihuahua**: mountains above Batopilas, 1885, *E. Palmer 224* (holotype: GH!; isotypes: K!, NY!, US!).

Carlowrightia glabrata Fernald, Bot. Gaz. (Crawfordsville) 20:536. 1895. TYPE.—MEXICO. **Sinaloa**: Villa Union, Jan 1893, *F. Lamb 420* (lectotype, designated in Fl. Neotrop. Monogr. 34:76. 1983: GH!; isolectotypes: DS!, F!, G!, MO!, MSC!, NY!, US!).

Carlowrightia californica Brandegee, Zoe 5:172. 1903. TYPE.—MEXICO. **Baja California Sur**: Comondú, 22 Mar 1889, *T. Brandegee s.n.* (holotype: UC!).

Carlowrightia californica var. *pallida* I. M. Johnst., Proc. Calif. Acad. Sci., ser. 4, 12:1169. 1924. TYPE.—MEXICO. **Baja California**: San Esteban Island, 20 Apr 1921, *I. Johnston 3195* (holotype: CAS!; isotypes: GH!, US!).

See Daniel (1995) for a complete listing of synonyms for this species.

Erect to ascending perennial herbs to shrubs to 1 m tall. Young stems subterete to subquadrate, usually multistriate, variously pubescent with eglandular and sometimes glandular trichomes (see discussion). Leaves (plants sometimes leafless or nearly so during anthesis) petiolate, petioles to 32 mm long, blades ovate to elliptic, 8–69 mm long, 5–35 mm wide, 1.6–2.5 times longer than wide, (rounded to) acute to acuminate at apex, acute to rounded to truncate to cordate at base, surfaces pubescent with eglandular and sometimes glandular trichomes, 2 or more orders of venation evident, margin flat. Inflorescence of axillary and terminal spicate axes or panicles of spicate axes, rachises variously pubescent with glandular and often eglandular trichomes (see discussion); dichasia sessile in axils of reduced leaves or bracts, solitary or opposite at nodes; flowers 1–3 per dichasium, sessile. Bracts (ovate to) lanceolate to subulate, 2–4 (–5) mm long, 0.6–1.7 mm wide, abaxial surface pubescent like rachis or pubescent with eglandular trichomes additionally or exclusively. Bracteoles linear to subulate, 1.5–3.6 mm long, 0.3–0.7 mm wide, abaxial surface pubescent like bracts. Calyx 2–4.6 mm long, abaxially pubescent like rachis (and sometimes with eglandular trichomes near apex of lobes when eglandular trichomes are absent from rachis), lobes subulate, 1.3–3.7 mm long. Corolla pseudopapilionaceous, cream to white with maroon and yellow markings on inner surface of upper lip (and sometimes with a yellowish region on outer surface of lower-central lobe), 10–19 mm long, externally pubescent with erect to flexuose eglandular trichomes, tube 2–7 mm long, upper lip obovate to spatulate, 6–13 mm long, 2.2–6.7 mm wide, lower lip 7–13.5 mm long, lobes heteromorphic, lateral lobes ovate-elliptic, 5.5-13 mm long, 2.4–7.5 mm wide, lower-central lobe conduplicate-keeled, enclosing stamens and style, 6–14 mm long, 2–5 mm wide. Stamens 4.5–9 mm long, thecae maroon turning black, 0.5–1.4 mm long. Style 7.5–15 mm long, glabrous. Capsule 9.5–14 mm long, glabrous, stipe 4–6.5 mm long, head flattened, 5.5–7.5 mm long. Seeds 4, homomorphic, flat, 3.5–4.5 mm long, 3–3.8 mm wide, surfaces nearly smooth to papillose, margin papillose-dentate. (*n* = 18, Daniel et al. 1984).

PHENOLOGY. — Flowering and fruiting: October–June.

DISTRIBUTION AND HABITAT. — Southwestern United States (Arizona, California, Texas), Mexico (Baja California, Baja California Sur, Chiapas, Chihuahua, Coahuila, Colima, Guerrero, Jalisco, México, Michoacán, Nayarit, Oaxaca, Puebla, San Luis Potosí, Sinaloa, Sonora), Guatemala, Nicaragua, and Costa Rica; in our region (Fig. 5) the species is abundant in the Cape Region and has been collected much less frequently northward in the Sierra de la Giganta and the Sonoran Desert (Lower Colorado River Valley, Vizcaíno, and Central Gulf Coast subdivisions); the species is not known from the Magdalena subdivision of the Sonoran Desert and is very rare in the Vizcaíno subdivision; plants occur along watercourses, on rocky slopes and rocky or sandy plains, and in artificially disturbed areas (e.g., roadcuts) in desertscrub, thornscrub, tropical deciduous forest, and oak woodland at 3–750 (–1100) m elevation.

ADDITIONAL SPECIMENS EXAMINED. — UNITED STATES. **California**: San Diego Co: Anza Borrego Desert State Park, Borrego Palm Canyon, ca. 2 km NW of Borrego Springs, *M. Bourell 3509* (CAS).

MEXICO. **Baja California**: San Julio, *T. Brandegee s.n.* (UC); along Hwy 5, 5.9 mi S of La Ventana, *T. Daniel 1545* (ASU, CAS); 7 mi W of San Francisquito Bay, *C. Harbison 41674* (DS, SD); Mpio. Ensenada, San Borja, 28°46′N, 113°55′W, *P. Tenorio L. & C. Romero de T. 13095* (CAS); Cañón de Guadalupe, above resort area, ca. 32°09′N, 115°48′W, *R. Thorne et al. 61769* (RSA); 14 mi N of Los Angeles, *I. Wiggins 5427* (DS, MICH, UC, US); W margin of San Felipe Desert, El Cajón, SW of San Felipe, *I. Wiggins 9837* (DS). **Baja California Sur**: San José del Cabo, *A. Anthony 351* (DS, F, GH, MO, UC, US); near San José, *Bailey Herbarium 220* (F); N Sierra de la Giganta, on track to San José Comondú, 23 mi S of rd to San Isidro, 11 mi W of Hwy 1, ca. 26°15′N, 111°45′W, *S. Boyd & T. Ross 5925* (RSA); W side Cape Region, *T. Brandegee s.n.* (GH, UC); Comondú, *T. Brandegee s.n.* (UC); Sierra de Laguna, *T. Brandegee s.n.* (UC); 2.6 mi S of Todos Santos on hwy. to Cabo San Lucas, *D. Breedlove & D. Axelrod 43135* (CAS); 23 km S de San José del Cabo, carr. a Cabo San Lucas, 22°55′N, 109°52′W, *A. Campos V. et al. 4504* (CAS); 12 km NW of San Bartolo, 23°46′N, 109°50′W, *A. Carter 2656* (DS, LL, UC); Sierra de la Giganta, Arroyo Gabilán, ca. 25°55′N, 111°23′W, *A. Carter 4072* (UC); Sierra de la Victoria, between "Tapon" and Rancho Poza Larga, Arroyo de San Francisquito, ca. 23°29–31′N, 109°47–55′W, *A. Carter & R. Ferris 3378* (DS, UC); Sierra de la Victoria, La Spila, Arroyo Santa Rita, 23°29–31′N, 109°47–55′W, *A. Carter & R. Ferris 3410* (DS, SD, UC); Sierra de la Giganta, between La Victoria and portezuelo to the E, ca. 25°52′N, 111°25′W, *A. Carter & R. Ferris 3918* (UC); Sierra de la Giganta, Valle de

Los Encinos (S side of Cerro Giganta), ca. 26°04′N, 111°34′W, *A. Carter & R. Ferris 4023* (UC); 13 km E of Cabo San Lucas, *A. Carter et al. 2250* (DS, UC, US); Cape Region, opposite dam above Boca de la Sierra, ca. 23°21′N, 109°49′W, *A. Carter et al. 5799* (CAS, UC); La Paz, *Collins et al. 63* (US); 2 mi N of Miraflores, *L. Constance 3181* (CAS, DS, F, GH, LL, MICH, MO, NY, SD, UC, US); Cape San Lucas, 1 mi from beach, *T. Craig 755* (POM); S end of Bahía Coyote, across from Rancho El Coyote, 16.7 mi S of Puenta Mulegé, ca. 26°42′N, 111°55′W, *T. Daniel 207* (CAS, DUKE, F, GH, MEXU, MICH, MO, NY, UC, US); Isla Bargo in Bahía Coyote, ca. 26°42′N, 111°55′W, *T. Daniel 209* (ENCB, MEXU, MICH); along Hwy 1, 4.1 mi E of San Ignacio, *T. Daniel 1882* (CAS); near jct Hwy 1 and rd to Sta. Marta, near Alfredo V. Bonfil, ca. 27°22′N, 112°43′W, *T. Daniel & M. Butterwick 6774* (CAS); Arroyo La Huerta, near Hwy 286 between La Paz and San Juan de los Planes, 2.7 km E of La Huerta, ca. 24°03′N, 110°09′W, *T. Daniel & M. Butterwick 6835* (CAS, HCIB, MEXU); along rd to Microondas San Antonio, 2.7 km S of San Antonio, ca. 23°47′N, 110°04′W, *T. Daniel & M. Butterwick 6867* (CAS, HCIB); along rd from Hwy 1 across Cape Region mts to Hwy 19, ca. 1 km W of Hwy 1, ca. 23°14′N, 109°45′W, *T. Daniel & M. Butterwick 6897* (CAS, MEXU); along rd from Hwy 1 across Cape Region mts to Hwy 19, ca. 3.5 km NE of San Pedro de la Soledad, ca. 23°15′N, 109°57′W, *T. Daniel & M. Butterwick 6944* (CAS, HCIB); along Hwy 11, 2.1 mi S of ferry terminal at Pichilingue, *T. Daniel et al. 2470* (ASU, CAS); along Hwy 1, 4.4 mi NW of El Triunfo, *T. Daniel et al. 2487* (ASU); near Hwy 1 SE of San Bartolo, 28.2 mi SE of El Triunfo, *T. Daniel et al. 2513* (ASU); along Hwy 19 just S of Microondas El Carrizal, ca. 5.6 km S of jct Hwy 1 S of San Pedro, ca. 23°50′N, 110°14′W, *T. Daniel et al. 6845* (CAS, K, MEXU, SBBG, US); Rancho La Burrera, W slope of Sierra de la Laguna, ca. 22 km NE of Todos Santos, ca. 23°31′N, 110°02′W, *T. Daniel et al. 6855* (CAS); Punta Frailes, *E. Dawson 1133* (MICH, RSA), *1146* (RSA); San José del Cabo, *E. Dawson 1196* (F, MICH, RSA); Cape San Lucas, *E. Dawson 6422* (RSA); 2 mi S of San Pedro along Rte. 19 toward Todos Santos, *T. Elias 10721* (RSA); Isla Cerralvo, lado S de la isla, 1 km de la playa, *G. Flores F. 540* (RSA); Cape District, El Triumfo, *H. Gentry 4331* (DES, DS, GH, MO, UC); Rancho La Huerta area, ca. 12 km SE of La Paz toward San Juan de los Planes, ca. 24°02′N, 110°09′W, *D. Harder & W. Appleby 1092* (RSA); 16 km N of La Paz, 2 km S of Pichilingue, *J. Henrickson 2185* (MICH, RSA); Ceralbo Island, Ruffo's Ranch, *I. Johnston 4052* (CAS); Miraflores, *M. Jones 24170* (A, F, GH, LA, MICH, MO, NY, POM, SD, UC, US); Todos Santos, *M. Jones 24199* (F, GH, MO, POM); Laguna Mts, 14 mi E of Todos Santos, *M. Jones 24200* (NY, POM); ramal a Los Naranjos, ca. 7 km W of Hwy 1, 23°10′N, 109°45′W, *G. Levin 1748* (SD); Cerralvo Island, middle of S coast, 24°09′N, 109°54′W, *R. Moran 3573* (A, DS, LL, SD, UC); San José Island, N side of Amartajada Bay near village, 24°55′N, 110°38′W, *R. Moran 3798* (DS);Carmen Island, Ballandra Bay, 26°00′N, 111°10′W, *R. Moran 3929* (DS); Cape Region, Arroyo de los Pozos, 24°11′N, 110°12′W, *R. Moran 6883* (SD); Cape Region, 11 km N of Santa Anita, ca. 23°15′N, 109°42′W, *R. Moran 6929* (CAS, DS, SD); Cape Region, Arroyo San Bernardo, ca. 3 km above Boca de la Sierra, ca. 23°23′N, 109°49′W, *R. Moran 7087* (CAS, DS, GH, SD, TEX); Cape Region, 12 km SE of San Pedro, ca. 23°50′N, 110°11′W, *R. Moran 7131* (CAS, DS, ENCB, GH, RSA, SD, US); Cape Region, S fork of Cañón San Pedro, ca. 23°19′N, 109°55′W, *R. Moran 7414* (CAS, DS, ENCB, GH, SD, US); San Marcos Island, Arroyo de los Chivos, 27°15′N, 112°06′W, *R. Moran 8988* (SD); Cerralvo Island, Arroyo Aguaje, ca. 24°18′N, 100°55′W, *R. Moran 9458* (DS, SD); La Paz, *E. Palmer 107* (GH, US); Cape District, Santiago, 3 mi S of Caduano, *R. Peters 18* (UC); ca. 1 mi up hillside S of main arroyo, 3.5 mi E of San Bartolo, *D. Porter 286* (CAS, DS, GH); Cape Region, San Felipe, *C. Purpus 508* (GH, UC); 4 mi NW of El Triumfo, *J. Reeder & C. Reeder* 6746 (ARIZ); Cape San Lucas, *J. Rose 16417* (US); San José del Cabo, *J. Rose 16912* (US); 28.7 km N of Cabo San Lucas toward Todos Santos, ca. 23°05′N, 110°05′W, *A. Sanders et al. 3443* (CAS, RSA, UCR); 16 mi S of La Paz, *F. Shreve 7205* (DS, MICH, US); between Todos Santos and Cabo San Lucas; ca. 4 mi N of the Cape, *R. Spjut 5405* (CAS); Arroyo San Lázaro, from its mouth (ca. 10 mi NW of San José del Cabo) to 3 mi upstream, *J. Thomas 7775b* (DS), *7775c* (DS); ca. 10 mi W of La Paz, *R. Turner et al. 77-82* (ARIZ); 8 mi SE of San Antonio, 23°45′N, 109°50′W, *G. Webster 19505* (SD); 17 mi S of La Paz, *J. Whitehead 850* (DS); N of Comondú, *I. Wiggins 5481* (DS); between La Paz and San Pedro, *I. Wiggins 5596* (DS, MICH, UC, US); 4 mi E of La Paz along rd to Las Cruces, *I. Wiggins 14479* (CAS, DS, UC); 39.5 mi S of La Paz on rd to Todos Santos, *I. Wiggins 14498* (DS,

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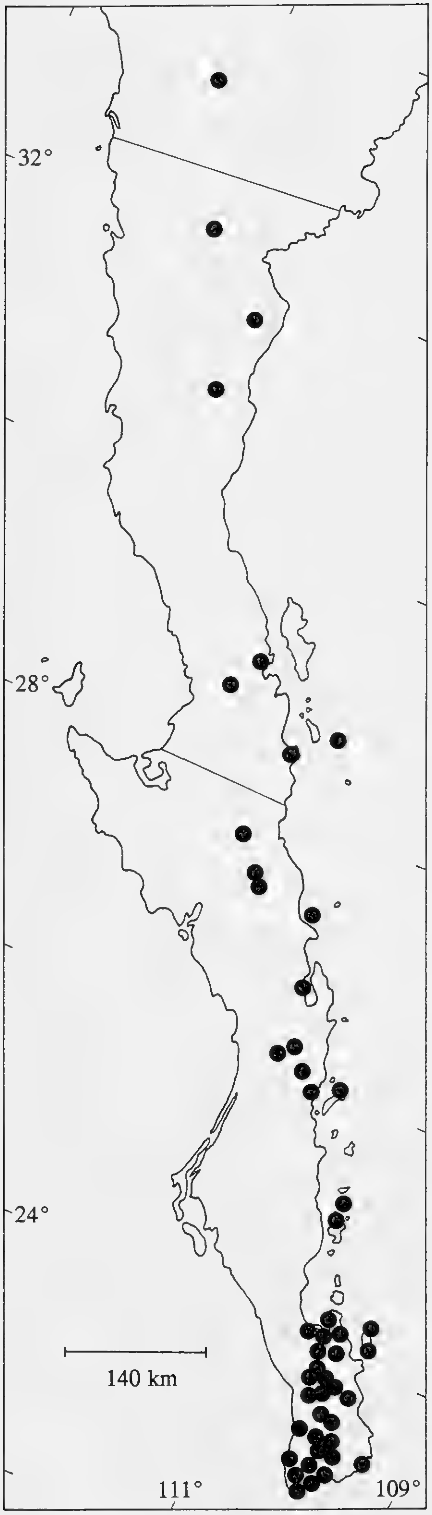
FIGURE 5. Distribution of *Carlowrightia arizonica* in California, Baja California, and Baja California Sur.



GH, TEX); 3.4 mi S of El Valle Perdido on rd to La Junta, ca. 23°41′N, 110°06′W, *I. Wiggins 15383* (DS, UC); 15.5 mi SE of La Paz, on rd to Las Cruces, *I. Wiggins 15669-B* (DS); 10 mi SE of La Paz along rd to Los Planes, *I. Wiggins 15685* (DS, CAS); Isla San Diego, ca. 25°12′N, 110°40′W, *I. Wiggins 17821* (DS); along rd to Los Planes, 5.5 mi SE of La Paz, *I. Wiggins et al. 440* (DS, UC).

Daniel (1983a, 1984, 1988, 1995) discussed some of the morphological variation, and its geographic basis, in this widely distributed species. Since publication of a monograph of the genus (Daniel 1983a) *Carlowrightia arizonica* has been collected in the northeastern portion of Baja California and in southern California. The description above is derived from specimens collected in California and the peninsula of Baja California only. Five forms can be readily distinguished from among collections occurring in these regions. All but one are restricted to the Cape Region of Baja California Sur. Most of these forms do not correspond well to plants treated by Wiggins (1980) as *C. arizonica*, *C. californica*, and *C. cordifolia*.

Form A. Young stems evenly puberulent with retrorse eglandular trichomes 0.05–0.1 (–0.2) mm long; inflorescences of unbranched spikes; and rachises pubescent with subglandular to glandular (rarely absent) and eglandular trichomes. This is the most widespread form with plants occurring from southern California southward throughout most of the peninsula of Baja California to the Cape. The type of *C. californica* conforms to this form and most specimens corresponding to this form have been so annotated. The following collections are representative of this form: *Anthony 351*; *Brandegee s.n.* (19 Apr 1889); *Breedlove & Axelrod 43135*; *Carter 4023, 4072*; *Daniel 1882, 2470*; *Harbison 41674*; *Jones 24199*; *Moran 3798, 3929*; *Tenorio L. & Romero de T. 13095*; *Wiggins 5427, 9837, 17821.*

An extreme expression of this form from Isla San Esteban in the Gulf of California was described as *C. californica* var. *pallida*. In these plants the stems are so densely pubescent that the epidermis is not visible and they appear very pale in color. Collections from hills near Bahía Concepción (*Daniel 207, 209*) resemble Johnston's type specimen from Isla San Esteban. Additional information on plants grown from seeds of

Daniel 207 was provided by Daniel (1983a). Collections from southern California (*Bourell 3509*), northeastern Baja California (*Daniel 1545*), and northeastern Baja California Sur (*Daniel & Butterwick 6774*) approach the density of cauline pubescence evident in Johnston's type specimen.

Form B. Young stems pubescent with (flexuose to) retrorse eglandular trichomes 0.05–0.3 (–0.5) mm long (or up to 0.8 mm long at nodes) and sometimes with erect inconspicuous glandular trichomes 0.05–0.1 mm long as well, the internodal trichomes ± concentrated in 2 lines; inflorescences of unbranched (or rarely once-branched at the base) spikes; and rachises pubescent with subglandular, glandular, and usually eglandular trichomes. This form occurs only in the Cape Region (i.e., vicinity of La Paz and southward) and is represented by the following collections: *Brandegee s.n.* (Nov. 1902); *Campos V. et al. 4504*; *Carter et al. 2250*; *Daniel & Butterwick 3865*; *Daniel et al. 6845*; *Gentry 4331*; *Moran 7131*; *Sanders et al. 3443*; *Shreve 7205*, *Spjut 5405*; *Whitehead 850*, *Wiggins 14479*, *14498*, *15669-B*, *15685*; *Wiggins et al. 440*. Wiggins identified material here referred to this form as both *C. californica* and *C. cordifolia*.

Form C. Young stems ± evenly (or soon bifariously) pubescent with (erect to) flexuose to retrorse eglandular trichomes 0.3–1 mm long and sometimes with an understory of subglandular to glandular trichomes 0.05–0.1 mm long as well; inflorescences of mostly unbranched spikes (or in *Constance 3181*, the inflorescences appear to branch several times); and rachises pubescent with subglandular, glandular, and usually some eglandular trichomes. The form occurs primarily in the Cape Region south of latitude 24°N, but is also known from the Sierra de la Giganta at ca. lat. 25°53′N as well. The following collections are representative of this form: *Brandegee s.n.* (27 Jan. 1890); *Carter 2656*; *Carter & Ferris 3918*; *Constance 3181*; *Daniel & Butterwick 6867*, *6897*, *6944*; *Daniel et al. 2487*, *2513*, *6855*; *Jones 24170*; *Moran 6929*, *7131*; *Thomas 7775b*, *7775c*; *Wiggins 5596*, *15383*. *Purpus 508* (UC) contains a shoot of Form A and one of Form C.

Form D. Young stems evenly pubescent with erect to flexuose glandular and eglandular trichomes 0.3–1 mm long; inflorescences of much branched (the branching mostly dichotomous) spikes; and rachises pubescent with subglandular and glandular trichomes. It occurs in the Cape Region south of latitude 24°N and has usually been identified as *C. californica*. The following collections are representative of this form: *Carter & Ferris 3378*, *3410*; *Carter et al. 5799*; *Moran 7087*, *7414*; and *Porter 286*.

Form E. Young stems evenly pubescent with retrorse eglandular trichomes 0.05–0.1 mm long; inflorescences of much branched spikes; and rachises pubescent with subglandular, glandular, and eglandular trichomes. This is the most restricted of the forms, occurring only on Cerralvo Island in the southern portion of the Gulf of California. It is represented by the following collections: *Flores F. 540*; *Johnston 4052*; *Moran 3573*, *9458*.

Information on the reproductive biology and pollination ecology of this species was provided by Daniel (1983a).

Carlowrightia arizonica is treated in section *Pseudopapilionaceae* T. F. Daniel (Daniel 1983a) where it appears to be most similar to *C. neesiana* (S. Schauer ex Nees) T. F. Daniel, a species of eastern and southern Mexico with more glandular pubescence.

2. Carlowrightia pectinata Brandegee, Proc. Calif. Acad. Sci., ser. 2, 3:160. 1891. TYPE. — MEXICO. **Baja California Sur**: San José del Cabo, 24 Sep 1890, *T. Brandegee 452* (holotype: UC!; isotypes: F!, GH!, US!).

Carlowrightia fimbriata Brandegee, Proc. Calif. Acad. Sci., ser. 2, 3:161. 1891. TYPE. — MEXICO. **Baja California Sur**: San Pedro, 29 Oct 1890, *T. Brandegee 453* (holotype: UC!; isotypes: CAS!, F!, G!, GH!, MIN!, US!).

Carlowrightia lanceolata Leonard, Kew Bull. 1938:66. 1938. TYPE. — MEXICO. **México**: Distr. Temascaltepec, Tejupilco, 21 Dec 1932, *G. Hinton 2672* (holotype: K; isotypes: ENCB!, F!, G!, GH!, MO!, NY!, TEX!, RSA!, US!).

Erect to ascending perennial herbs to shrubs to 1 m tall. Young stems quadrate, glabrous or bifariously pubescent with retrorse to retrorse-appressed eglandular trichomes 0.05–0.2 (–0.5) mm long (strigillose), the nodes frequently pubescent with flexuose eglandular trichomes to 0.8 mm long. Leaves sessile (to subsessile with petioles to 1 mm long), blades linear to narrowly elliptic-lanceolate, (5–) 30–85 mm long, 0.5–13 mm wide, 6–29 times longer than wide, long-acuminate at apex, acute to long-attenuate at base, surfaces glabrous (or strigillose on adaxial surface), only midvein evident on most leaves (at least adaxially; several orders of venation evident on wider leaves), margin revolute. Inflorescence of numerous spicate axes from axils of distal (sometimes greatly reduced) leaves, collectively forming a ± leafy, often dichotomously branched, panicle to 40 cm long, rachises glabrous or pubescent with straight glandular (and sometimes eglandular as well) trichomes 0.05–0.2 mm long (glandular puberulent); dichasia sessile or rarely short (to 0.5 mm long) pedunculate in the axil of a bract, solitary or opposite at nodes; flowers 1 (–2) per dichasium, sessile to short (to 1 mm long) pedicellate. Bracts linear to subulate, 0.8–5 mm long, 0.2–1 mm wide, abaxial surface glabrous or glandular puberulent. Bracteoles linear to subulate, 0.8–2.2 mm long, 0.3–0.5 mm wide, abaxial surface glabrous or glandular puberulent. Calyx 2–3.5 mm long, abaxially glabrous or glandular puberulent, lobes subulate, 1.5–3 mm long. Corolla subactinomorphic, bright yellow (rarely light purplish), 7.5–12 mm long, externally pubescent (rarely glabrous) with trichomes 0.2–0.4 mm long, tube 1.7–2.5 mm long, upper lip oblanceolate-obovate to spatulate, 5.5–8.5 mm long, 1.8–2.5 mm wide, lower lip 6–8 mm long, lobes homomorphic, obovate to elliptic, 5–9.5 mm long, 1.5–4.5 mm wide. Stamens 5–8 mm long, thecae golden yellow, 1–1.3 mm long. Style 6–7.5 mm long, glabrous. Capsules 6.5–9 mm long, pubescent (often sparsely so at apex only) with eglandular trichomes 0.2–0.3 mm long, stipe 3–5 mm long, head spheric to partially flattened, 3.5–5.5 mm long. Seeds 2–4 per capsule, concavoconvex, 2.5–3.5 mm long, 2.3–3 mm wide, tuberculate with prominent conical tubercles on concave side, smooth to papillose on convex side, margin entire or dentate, teeth widely scattered or restricted to the base, usually with retrorse barbs (third or fourth seeds, when present, partially conduplicate with exaggerated winglike marginal teeth). (*n* = 18, Daniel et al. 1990). Fig. 6.

PHENOLOGY. — Flowering: December–May; fruiting: December–March.

DISTRIBUTION AND HABITAT. — Western Mexico (Baja California Sur, Colima, México, Oaxaca, Sinaloa, and Sonora); in our region the species is known only from the Cape Region and the Sierra de la Giganta in Baja California Sur (Fig. 7); plants occur in and along watercourses and on slopes in thornscrub and tropical deciduous forest at 200–750 m elevation.

ADDITIONAL SPECIMENS EXAMINED. — MEXICO. **Baja California Sur**: San José del Cabo, *T. Brandegee s.n.* (UC); brecha a Alvaro Obregón, 7.5 km de la carr. La Paz–El Triunfo, 23°52′N, 110°08′W, *A. Campos V. et al. 4517* (CAS); Sierra de la Giganta, between La Esperanza and Arroyo Peloteado (near Rancho El Potrero), ca. 25°49′N, 111°27′W, *A. Carter 4371* (MICH, RSA, UC); Sierra de la Giganta, Cerro Gabilán, S of Portezuelo de Gabilán, ca. 25°51′N, 111°25′W, *A. Carter 5052* (SD, UC); Sierra de la Giganta, Cerro Gabilán, S of Portezuelo de Gabilán, ca. 25°51′N, 111°25′W, *A. Carter 5052a* (MICH, UC); Sierra de la Giganta, Cañada del Quemado, NE end of Valle de Los Encinos (S side of Cerro Giganta), ca. 26°05′N, 111°33′W, *A. Carter & R. Moran 5313* (UC); along Hwy 19 just S of Microondas El Carrizal, ca. 5.6 km S of jct Hwy 1 S of San Pedro, ca. 23°50′N, 110°14′W, *T. Daniel et al. 6846* (BR, CAS, HCIB, MEXU, MICH, SBBG, US); Rancho San Andreas, Sierra de las Palmas, *H. Gentry & Fox 11810* (LL); Cape Region, 4.5 km W of La Palmilla, ca. 23°01′N, 109°45′W, *R. Moran 7071* (CAS, DS, SD); San José del Cabo, *C. Purpus 418* (MO, UC); San Jose del Cabo, *J. Rose 16429* (NY, US); between La Paz and San Pedro, *I. Wiggins 5597* (DS).

Considerable variation in color of the corolla is evident from throughout the range of this species. Most collections from our region note a yellowish corolla, but data on *Moran 7071* notes "orchid" (i.e., light reddish purple) colored corollas and a dried corolla on this collection at DS is indeed purple.

Carlowrightia pectinata is treated in section *Tuberculosperma* T. F. Daniel (Daniel 1983a) where it appears most similar to *C. albiflora* T. F. Daniel and *C. parvifolia* Brandegee, species of Tamaulipas and the Chihuahuan Desert respectively.

DICLIPTERA

Dicliptera Juss., Ann. Mus. Natl. Hist. Nat. 9:267. 1807, nom. cons. TYPE. — *Dicliptera chinensis* (L.) Juss. (≡ *Justicia chinensis* L.).

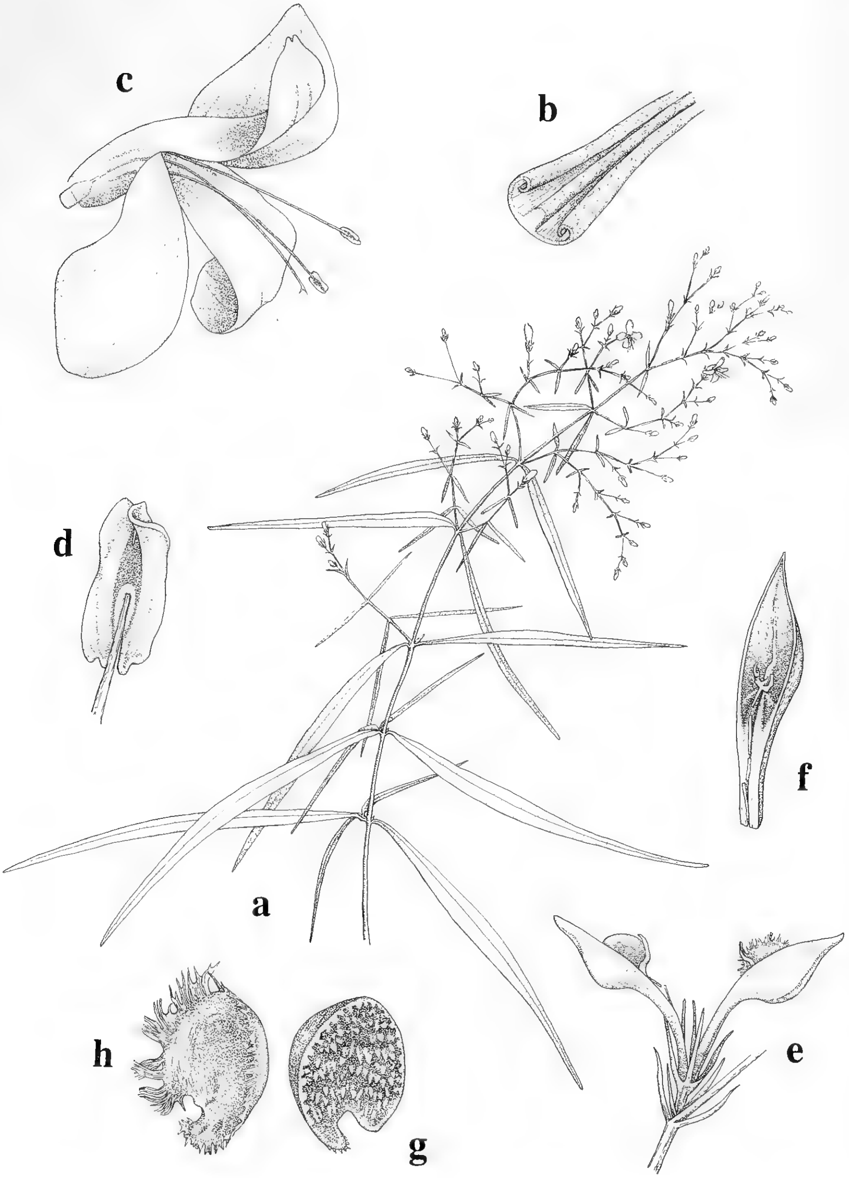


FIGURE 6. *Carlowrightia pectinata*. (a, b from *Van Devender et al. 93-1449*, c–h from *Daniel 3345*). a. habit, × 0.5; b. portion of sectioned leaf, × 10; c. flower with calyx removed, × 5; d. anther, × 19; e. inflorescence node with capsule, × 3; f. capsule valve, × 4; g. concavoconvex seed, × 7.5; h. partially conduplicate seed with marginal teeth, × 7.5. Drawn by Jenny Speckels.

Diapedium K. D. Koenig, Ann. Bot. 2:189. 1805 ("1806"), nom. rej. TYPE. — *Diapedium chinense* (L.) K. D. Koenig (≡ *Justicia chinensis* L.).

Solenochasma Fenzl in J. Jacq., Ecl. pl. rar. 2:1. 1844. TYPE. — *Solenochasma assurgens* (L.) Fenzl (≡ *Justicia assurgens* L.).

Dactylostegium Nees in Mart., Fl. bras. 9:162. 1847. TYPE. — *Dactylostegium sparsiflorum* Nees.

Erect to ascending or decumbent perennial herbs or shrubs with cystoliths. Young stems ± distinctly 6-angled in cross-section. Leaves opposite, petiolate, margin entire to subsinuate. Inflorescence of axillary cymes (= modified dichasia ?) bearing 1 or more, bracteolate cymules; cymes alternate or opposite, subtended by paired bracts, sessile or pedunculate in leaf axils or in axils of inflorescence bracts forming a terminal spikelike thyrse or panicle of thyrses; cymules sessile or pedunculate, comprising an involucre of several pairs of bracteoles, outermost pair usually conspicuous and larger than inner, often hyaline, pair(s), cymule bracteoles of a pair equal or unequal in size. Flowers 1–several per cymule, homostylous, sessile. Calyx deeply 5-lobed, usually reduced (shorter than outer cymule bracts in ours) and hyaline, lobes equal to subequal. Corolla often resupinate (i.e., tube twisted 180°, elsewhere sometimes twisted 360°), pink to purple, red, or whitish (elsewhere also blue), often with pink to purple markings, tube cylindric to gradually expanded distally but lacking a distinct throat (in ours), limb bilabiate, upper lip entire to emarginate, lower lip entire to shallowly 3-lobed (normal position of lips reversed when corolla resupinate), corolla lobes imbricate in bud. Stamens 2, inserted in proximal or distal 1/2 of corolla tube, exserted from mouth of corolla or rarely included in corolla tube, anthers 2-thecous, thecae equal to subequal in size, parallel to perpendicular, equally to unequally inserted on filament, lacking basal appendages (in ours; elsewhere rarely with lower theca minutely appendaged at base), dehiscing toward lower lip (i.e., flower nototribal) in species with corollas either not resupinate or twisted 360°, dehiscing toward upper lip (i.e., flower stenotribal) in species with resupinate corollas; pollen (Fig. 8a, b) perprolate to prolate, 3-colporate, 6-pseudocolpate, pseudocolpi 2 per mesocolpium, exine reticulate; staminodes 0. Style exserted from mouth of corolla or rarely included in corolla tube, stigma 2-lobed, lobes equal. Capsule substipitate to stipitate, head ellipsoid to obovoid, retinacula present, septa with attached retinacula separating elastically and rising from inner wall of mature capsule. Seeds 2–4, homomorphic, subreniform to lenticular. ($x = 40$ in New World taxa, $x = 13$ or 15? in Old World taxa).

Although about 300 species have been described from tropical and temperate regions of the world, the number of species usually given is about one-half that number or fewer. The genus is in need of critical taxonomic study. About 15

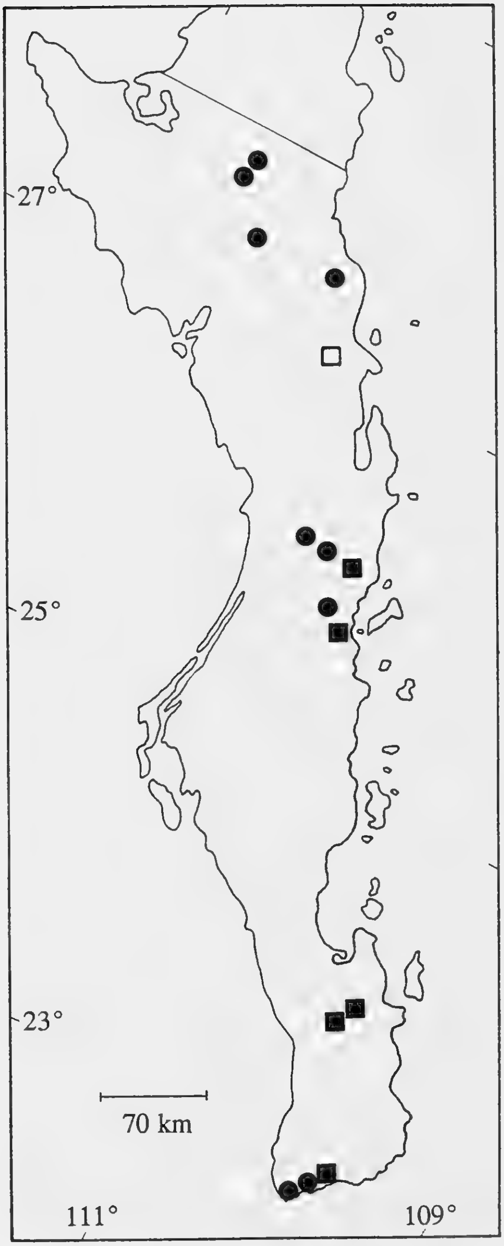


FIGURE 7. Distribution of *Carlowrightia pectinata* (squares), *Justicia candicans* (open square), and *J. hians* (circles) in the peninsula of Baja California.

species occur in Mexico and three occur in the United States.

1. Dicliptera resupinata (Vahl) Juss., Ann. Mus. Natl. Hist. Nat. 9:268. 1807. *Justicia sexangularis* Cav., Icon. 3:2. 1795, non L. (1753). *Justicia resupinata* Vahl, Enum. pl. 1:114. 1804. *Diapedium resupinatum* (Vahl) Kuntze, Revis. gen. pl. 2:485. 1891. TYPE. — Not designated (see discussion below).

Dicliptera pseudoverticillaris A. Gray, Proc. Amer. Acad. Arts 20:308. 1885. TYPE. — MEXICO. **Sonora**: valley of the Altar, 2 Apr 1884, *C. Pringle 27* (lectotype, designated here: GH!).

Dicliptera torreyi A. Gray, Proc. Amer. Acad. Arts 20:309. 1885. *Diapedium torreyi* (A. Gray) A. Heller, Cat. N. Amer. pl. 7. 1898. TYPE. — UNITED STATES. **Arizona**: unspecified collections of Thurber, Wright, Schott, Rothrock, Lemmon, and Pringle were cited (syntypes, see discussion below).

Dianthera sexangularis Sessé & Moc., Pl. nov. Hisp. 5. 1887. TYPE. — Icones Florae Mexicanae no. 22. Original plate preserved at Hunt Institute for Botanical Documentation, Pittsburgh, Pennsylvania, USA (lectotype, designated here), see discussion.

Dicliptera formosa Brandegee, Proc. Calif. Acad. Sci., ser. 2, 3:162. 1891. TYPE. — MEXICO. **Baja California Sur**: summit of Sierra de San Francisquito, 20 Oct 1890, *T. Brandegee 455* (holotype: UC!; isotypes: GH!, NY).

Dicliptera resupinata var. *orbicularis* B.L. Rob. & Seaton, Proc. Amer. Acad. Arts 28:114. 1893. TYPE. — MEXICO. **Jalisco**: barranca near Guadalajara, Oct 1891, *C. Pringle 5169* (holotype: GH; isotype: MEXU!).

Ascending to erect annual to perennial herbs to 5 (–8) dm tall. Young stems hexagonal, nearly glabrous or pubescent (especially just proximal to nodes) with flexuose to retrorse to retrorsely appressed eglandular trichomes 0.1–0.4 mm long, the trichomes restricted to ridges, or ± densely and evenly pubescent with erect to downward-pointing to retrorse eglandular trichomes 0.2–1.2 mm long (see discussion). Leaves (plants sometimes leafless or nearly so during anthesis) petiolate, petioles to 35 mm long, blades ovate to lanceolate, 11–95 mm long, 3–44 mm wide, 1.6–6.7 times longer than wide, acute to acuminate to attenuate at apex, rounded to acute to subtruncate at base, surfaces pubescent with eglandular trichomes, trichomes sometimes restricted to major veins. Inflorescence of subsessile to pedunculate cymules and/or cymes of cymules from leaf axils, cymules and/or cymes (alternate to) opposite, 1–2 per axil, cymes consisting of (1–) 3 (–5) cymules, terminal (i.e., central) cymule of cymes sometimes modified into a branch bearing pedunculate cymules or cymes of cymules in axils of leaves or reduced leaflike bracts, peduncles of cymes 0.05–7 (–28) mm long, pubescent with cauline type trichomes, paired bracts subtending cymes subulate to linear to lanceolate to oblanceolate (to ovate), often curved, 2–11 (–13) mm long, 0.2–2 (–4.5) mm wide, abaxial surface glabrous, or with a few antrorse eglandular trichomes 0.1–0.2 mm long, or covered with erect to antrorse eglandular trichomes 0.2–0.6 mm long, margin ciliate with erect to antrorse eglandular trichomes 0.1–0.6 mm long (solitary cymules in axils of leaves or bracts usually not subtended by paired bracts); cymules pedunculate, peduncles 1.5–51 mm long, pubescent (often more densely so) with cauline type trichomes. Outer cymule bracteoles sometimes tinged with maroon at margin and apex, cordate to deltate, 5–18 (–24) mm long, equal to subequal (i.e., one up to 1.2 times longer than the other), 4–15 (–20) mm wide, (acute to rounded to truncate to) emarginate at apex, abaxial surface glabrous, or pubescent with a few antrorse eglandular trichomes 0.1–0.2 mm long, or pubescent with erect to flexuose to antrorse eglandular trichomes 0.1–0.7 mm long. Inner cymule bracteoles elliptic to lance-ovate, 1.5–3.5 (–4.5) mm long, 0.8–1.5 mm wide, abaxial surface glabrous or pubescent like outer cymule bracteoles. Calyx 2–3.5 (–4.8) mm long, abaxially pubescent with antrorse to antrorsely appressed eglandular trichomes 0.2–0.4 mm long, lobes triangular to lanceolate to lance-ovate, 1–3 (–3.8) mm long. Corolla resupinate 180°, pink to purplish red with a white region bordered by darker pink markings on upper lip, 12–26 (–30) mm long, externally pubescent with erect to flexuose to retrorse eglandular trichomes 0.1–0.2 (–0.5) mm long, tube 6–11 (–17) mm long, 1.1–1.7 (–2.5) mm in diameter near midpoint, upper lip curved to recurved, 6–15 (–18) mm long, 3-lobed at apex, lobes 0.6–2 mm long, lower lip 6–15 (–18) mm long, entire to emarginate at apex. Stamens 5.5–15 (–22) mm long,

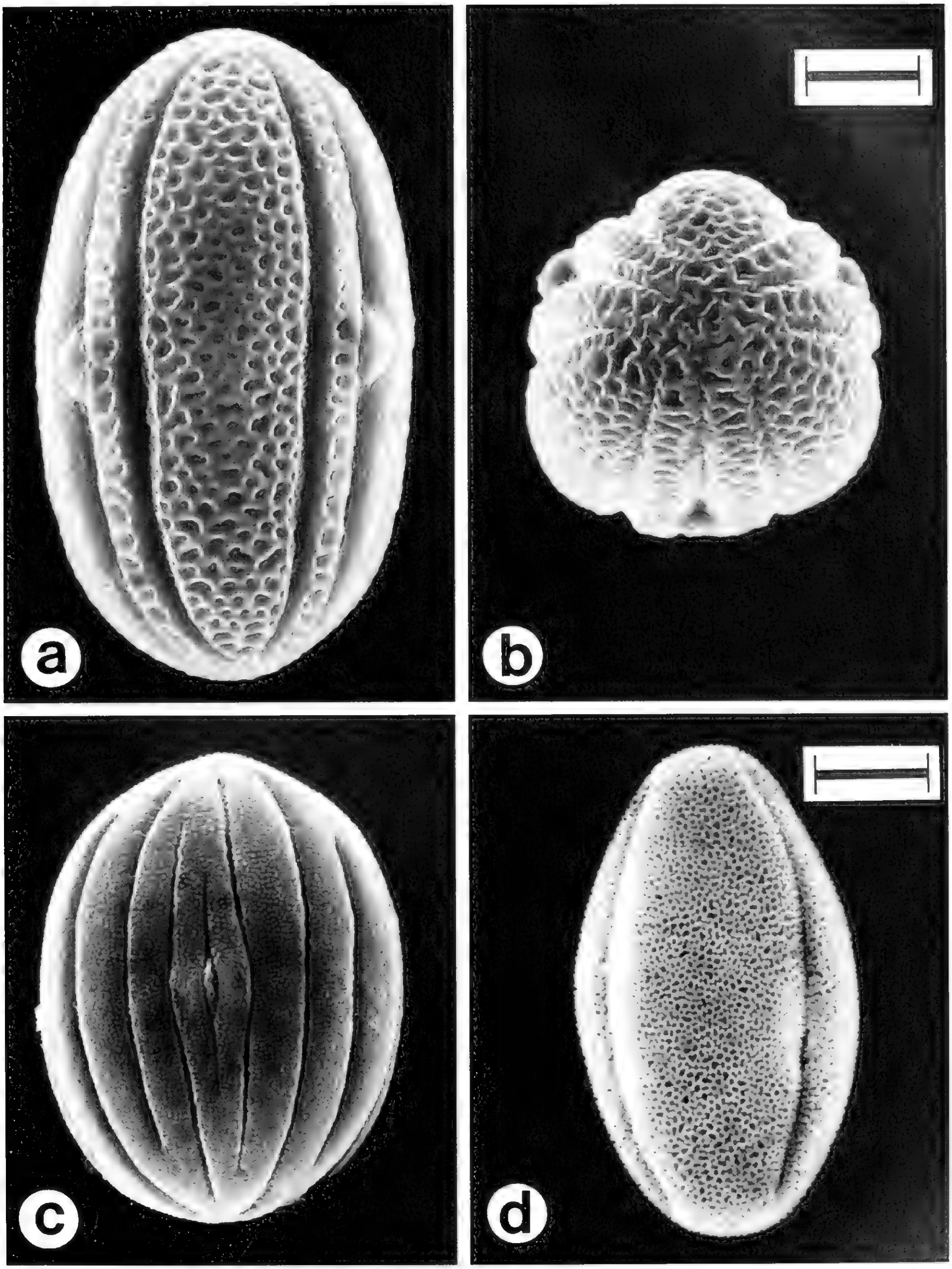


FIGURE 8. Pollen. a. *Dicliptera resupinata* (*Daniel et al. 6865*), intercolpal view; b. *D. resupinata* (*Daniel et al. 6865*), polar view; c. *Dyschoriste decumbens* (*Jones 24437*), colpal view; d. *Elytraria imbricata* (*Porter 297*), intercolpal view. Scale for a and b = 7.5 µm; scale for c and d = 10 µm.

inserted near apex of corolla tube (or in distal 1/2 of tube), filaments distally pubescent with eglandular trichomes, thecae 0.5–1.1 (–1.6) mm long, equal in length, parallel to subperpendicular, superposed (contiguous or with a gap up to 0.1 mm long) or unequally inserted (overlapping by up to 0.4 mm), dehiscing toward upper lip. Style 10.5–22 (–32) mm long, sparsely pubescent (at least proximally) with eglandular trichomes, stigma lobes 0.2–0.3 mm long. Capsule 4.4–7.5 (–9) mm long, glabrous, stipe 0.5–1.5 mm long. Seeds subreniform, 1.3–2.6 mm long, 1.8–3 mm wide, surface covered with tubercles bearing retrorse barbs (or these becoming low rounded encrustations). (n = 40, Daniel et al. 1990). Fig. 9.

PHENOLOGY. — Flowering and fruiting: September–May.

DISTRIBUTION AND HABITAT. — Southwestern United States (Arizona, New Mexico) and western Mexico (Baja California Sur, Chihuahua, Colima, Guerrero, Jalisco, Michoacán, Sinaloa, Sonora, Zacatecas); in our region the species is known from the Cape Region, the Sierra de la Giganta, and much of the Sonoran Desert (Central Gulf Coast, Vizcaíno, and Magdalena subdivisions) in Baja California Sur (Fig. 10); plants occur along watercourses, on rocky slopes, and in artificially disturbed areas (e.g., roadsides) in desertscrub, thornscrub, tropical deciduous forest, and oak woodland from near sea level to 1900 m elevation.

LOCAL NAME. — "Huachichila" (*Peters 21*).

ADDITIONAL SPECIMENS EXAMINED. — MEXICO. **Baja California Sur**: N Sierra de la Giganta, S of Mulegé, base of Mesa San Felipe, 1.7 mi S of rd to San Isidro, 11 mi W of Hwy 1, ca. 26°20′N, 111°46′W, *S. Boyd & T. Ross 5898* (RSA); N Sierra La Giganta, S of Mulegé, on track to San José Comondú, 23 mi S of rd to San Isidro, 11 mi W of Hwy 1, ca. 26°15′N, 111°45′W, *S. Boyd & T. Ross 5924* (CAS, RSA, UCR); Agua Caliente, *T. Brandegee 454* (UC), *s.n.* (DS); Sierra de la Laguna, *T. Brandegee 455* (UC), *s.n.* (UC); El Taste, *T. Brandegee s.n.* (UC); Cape Region, *T. Brandegee s.n.* (UC); San José del Cabo, *T. Brandegee s.n.* (UC, GH); Comondú Viejo, *T. Brandegee s.n.* (UC); Saucito, *T. Brandegee s.n.* (GH, POM, UC); Sierra El Taste, *T. Brandegee s.n.* (UC); Río del Salada along rd from Puerto Chale to Santa Rita, *D. Breedlove & D. Axelrod 43122* (CAS); Sierra La Laguna, interior valley (La Laguna) S of Pico La Aguja, *D. Breedlove & D. Axelrod 43365* (CAS); brecha a Alvaro Obregón, 7.5 km de la carr. La Paz–El Triunfo, 23°52′N, 110°08′W, *A. Campos V. et al. 4516* (CAS); Sierra de la Giganta, W slope of Cerro Gabilán, ca. 25°50′N, 111°24′W, *A. Carter 5112* (CAS); E side of Sierra de la Victoria, near "Tapon" (jct with La Chuparosa trail), Arroyo de San Francisquito, 23°29–31′N, 109°47–55′W, *A. Carter & R. Ferris 3370* (DS, SD, UC); Sierra de la Giganta, Cañón de Tiojo, S of La Victoria, ca. 25°51′N, 111°25′W, *A. Carter & R. Ferris 3940* (CAS); Cerro de la Giganta, ridge NW of main peak, 26°08′N, 111°36′W, *A. Carter et al. 2045* (DS); Llano de Magdalena, 11.5 km S of San Domingo, *A. Carter et al. 2146* (DS); San Francisco Mts, Rancho Los Corralitos, 2.8 mi W of Rancho San Francisco, *D. Charlton 88* (RSA, UCR); Llanos de Yres (Madgalena Plain) 11 mi N of Salada (Medano), *L. Constance 3157* (CAS, DS, SD, UC); Cape San Lucas, *T. Craig 743* (POM); along Hwy 1 between San Antonio and San Bartolo, ca. 4 km SE of San Antonio, ca. 23°48′N, 110°01′W, *T. Daniel & M. Butterwick 6868* (BR, CAS, HCIB, MEXU, MICH, SBBG, US); along Hwy 1, 4.4 mi NW of El Triunfo, *T. Daniel et al. 2489* (ASU, CAS); Rancho La Burrera, W slope of Sierra de la Laguna, ca. 22 km NE of Todos Santos, ca. 23°31′N, 110°02′W, *T. Daniel et al. 6865* (CAS, ENCB, HCIB, K, MO); Puerto Escondido, SW side of lagoon, *E. Dawson 6400* (RSA); Cerro El Picacho, 23°35′N, 110°02′W, *R. Domínguez C. 46R* (HCIB); Isla San José, lado O de la isla, 2 km de la playa, 25°00′N, 110°35′W, *G. Flores F. 438* (RSA); San Bartolo, *F. Gander 9650* (CAS, SD); Cerro de la Giganta, *H. Gentry 4285* (DS); S end of Vizcaíno Desert, ca. 15 mi N of San Ignacio, *B. Hammerly 93* (CAS); Sierra de la Laguna, base of El Picacho Peak, *B. Hammerly 328* (CAS); Cape Region, Boca de Tinaja, *D. Johansen 547* (DS); Laguna Mts, Cota Ranch, 14 mi E of Todos Santos, *M. Jones 24153* (SD), *24155* (DS, GH, POM), *24156* (DS); W side of the Lagunas, *M. Jones 27392* (POM, UC); Cañón de la Burrera, Ojo de Agua, 23°32′N, 110°04′W, *J. León de la Luz 937* (HCIB); tramo Las Palapas-Las Playitas, cerca de Todos Santos, *J. León de la Luz 1010* (HCIB); "El Comitán," 17 km NW de La Paz, 24°13′N, 110°20′W, *J. León de la Luz 2140* (HCIB, SD); Cape Region, 11 km N of Santa Anita, ca. 23°15′N, 109°42′W, *R. Moran 6926* (CAS, DS, RSA, SD); Cape Region, ca. 4.5 km W of La Palmilla, ca. 23°01′N, 109°45′W, *R. Moran 7067* (CAS, DS, SD); San José Island, Arroyo de Aguada, ca. 25°03′N, 110°39′W, *R. Moran 9408* (DS, SD); Cerralvo Island, Ruffo Ranch Canyon, ca. 24°11′N, 109°50′W, *R. Moran 9536* (DS, SD); Arroyo Tabor (E slopes of Sierra de la Giganta, W of Puerto Escondido), ca. 25°48′N, 111°21–23′W, *R. Moran 18209* (CAS, UC); Sierra San Francisco, Rancho La Laguna, 27°35′N, 113°02′W, *R. Moran 23819* (SD);

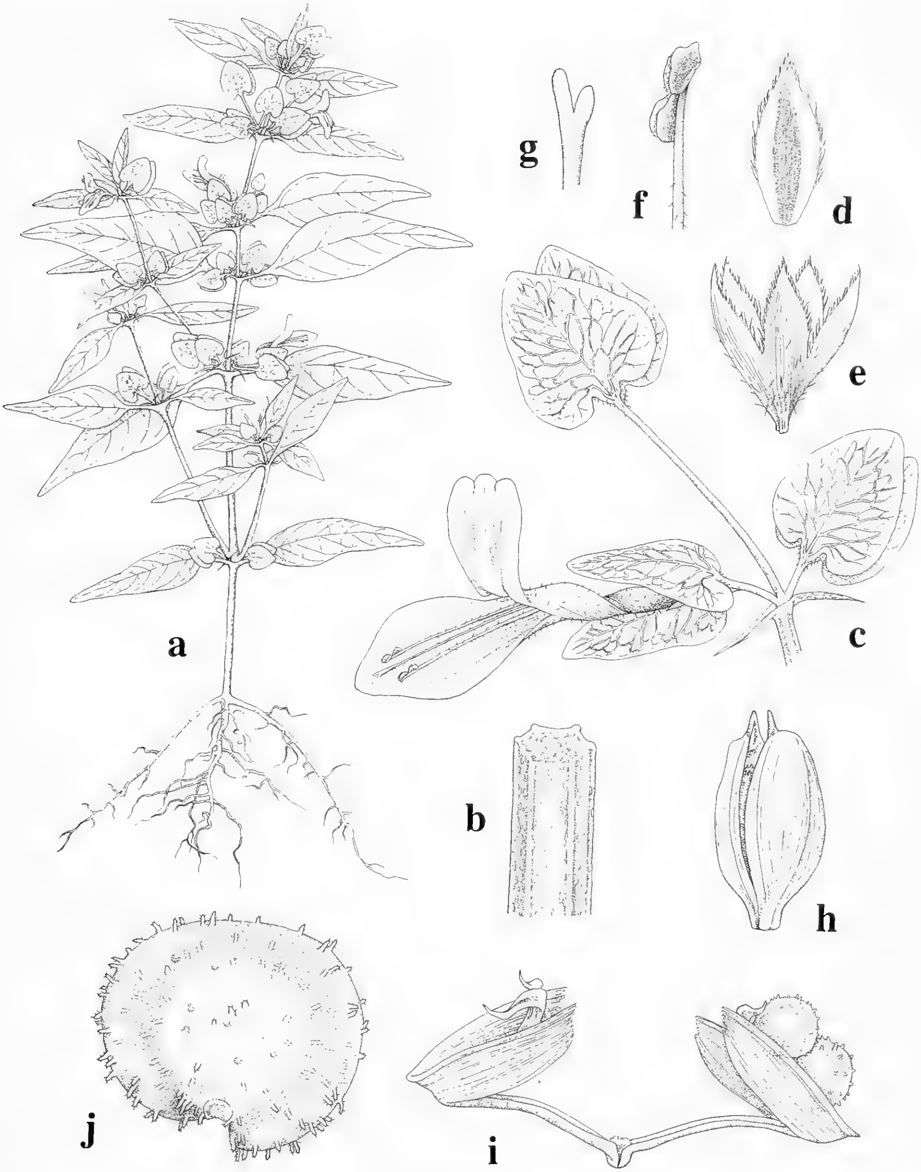


FIGURE 9. *Dicliptera resupinata*. a. habit (*Daniel & Butterwick 6868*), × 0.5; b. portion of sectioned stem (*Daniel et al. 2489*), × 7; c. cyme with three cymules and a flower (*Daniel & Butterwick 6868*), × 2.2; d. inner cymule bracteole (*Daniel & Butterwick 6868*), × 9; e. calyx (*Daniel & Butterwick 6868*), × 7; f. distal portion of stamen (*Daniel & Butterwick 6868*), × 10; g. distal portion of style with stigma (*Daniel & Butterwick 6868*), × 18; h. capsule (*Daniel et al. 2489*), × 4; i. fully opened capsule (*Daniel 5178*), × 5; j. seed (*Carter & Ferris 3940*), × 11.5. Drawn by Jenny Speckels.

La Paz, *E. Palmer 119* (GH); Santiago, 3 mi S of Caduano, *R. Peters 21* (UC); 4 mi SE of Agua Caliente on rd to Los Frailes, *D. Porter 296* (CAS, DS); San Pablo, *C. Purpus 84* (CAS, DS, UC); Sierra de la Laguna, Cañón de la Zorra, between "Las Pozas" and "La Punta del Ancón Grande," ca. 23°30′N, 109°53′W, *T. Ross et al. 2000* (RSA); Sierra de la Laguna, Cañón de la Zorra, vicinity of "La Punta del Ancón Grande," ca. 23°30′N, 109°54′W, *T. Ross et al. 2061* (RSA), *T. Ross et al. 2095* (RSA); 2 km SE of

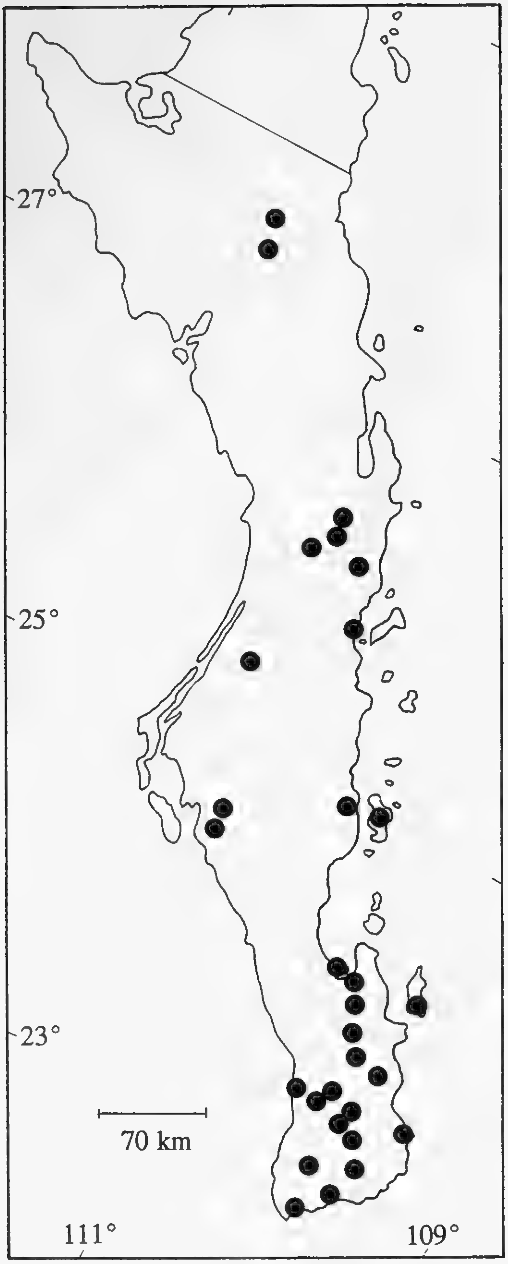


FIGURE 10. Distribution of *Dicliptera resupinata* in the peninsula of Baja California.

La Ribera, SW of Punta Arena, ca. 23°31′N, 109°29′W, *A. Sanders et al. 3355* (UCR); near Santiago de las Cosas, 23°30′N, *F. Shreve 7285* (DS); vicinity of San José del Cabo, *I. Wiggins 5686A* (DS, POM, UC); 6 mi W of Canipolé, *I. Wiggins 11450* (CAS, DS, RSA, UC); 4.8 mi E of La Paz-Todos Santos rd, along rd to El Triunfo, *I. Wiggins 14690* (CAS, DS, UC); ca. 15 mi S of La Paz, along rd to Todos Santos, ca. 24°01′N, 110°06′W, *I. Wiggins 15308* (CAS, DS); Sierra de la Giganta, Cañada de los Leones, between La Presa and Laguna Caquihui, 24°55′N, 110°53′W, *I. Wiggins 15540* (CAS, DS); ca. 10 mi S of Mission Dolores, 25°00′N, 110°47′S, *I. Wiggins et al. 313* (DS, UC).

The species as described by Vahl (1804) is based, at least in part, on Cavanilles' description and figure of *J. sexangularis* Cav. (1795). Vahl listed Cavanilles' name as a synonym and cited the figure. The epithet was presumably altered by Vahl owing to the prior existence of *J. sexangularis* L. Cavanilles' protologue was based on plants, which flowered in September at some time prior to 1795 at the Real Jardín Botánico. The provenance of the garden plants was listed as "Nova-Hispania" (i.e., Mexico). Subsequently, Cavanilles (1798:71) noted that Née had found this species at Acapulco (i.e., during the Malespina Expedition of 1789–1794). The description and accompanying figure (tab. 203) in the protologue concur with plants from western North America commonly treated as *D. resupinata* in most characteristics except for the outer cymule bracteoles which are described and figured as ovate. There are no specimens labeled as *J. sexangularis* nor any resembling *D. resupinata* in Cavanilles' herbarium at MA. There are several specimens in the general herbarium at MA labeled as *J. sexangularis* that were grown at the Real Jardín Botánico in the early nineteenth century (i.e., 1803–1819 and possibly earlier as several specimens lack the date of collection; none of these collections notes the month of collection). These comprise similar plants with relatively small outer cymule bracteoles (i.e., 5–9 mm long), but with slight differences in the shape of the outer cymule bracteoles. In some individuals, the bracteoles vary from elliptic to ovate to broadly ovate whereas in others they vary from ovate to deltate to subcordate. Plants with the subcordate bracteoles are indistinguishable from plants usually treated as *D. resupinata*. They resemble some of the individuals with smaller bracteoles encountered in Baja California Sur (e.g., *Moran 9408* at DS), on the Islas Marías (i.e., *Mason 1798*), and on the mainland of western Mexico (e.g., *Abrams 13283* from Sonora, *Breedlove 1546* from Sinaloa, *Daniel & Butterwick 3226* from Jalisco). Individuals with elliptic to broadly ovate bracteoles, which more closely resemble Cavanilles' tab. 203, likely exhibit an extreme expression of bracteolar shape in the species.

A specimen at MA with individuals of each bracteolar form noted above, and labeled as *J. sexangularis* Cav., is noted to have been collected by Née "ex nov. Hispania et Bonxia." Seeds from this material likely provided the source material for plants subsequently grown in Madrid. Seeds from this same source, or seeds obtained from plants grown at Madrid, likely also served as the source for plants of *D. resupinata* grown at the Botanical Garden of Copenhagen. Two specimens grown at that institution are extant in Vahl's herbarium at C. Microfiche images of these specimens agree with the specimens at MA (i.e., with outer cymule bracteoles varying from broadly ovate to deltate to subcordate). These specimens (or other plants cultivated at the garden in Copenhagen) undoubtedly were used by Vahl in drawing up his protologue of *J. resupinata*, which is more detailed than (and thus not derived solely from) that of Cavanilles. Indeed, the handwriting of the names on these specimens matches that of Vahl (Burdet 1979). Because he did not cite a type, a lectotype would need to be designated from among those materials used by Vahl in formulating his protologue (i.e., Cavanilles figure 203, the two specimens in the Vahl herbarium, and any other pertinent materials at C).

Gray (1885) noted two collections in his protologue of *D. pseudoverticillaris*. It is clear that Pringle's collection formed the greater part of Gray's concept of the species, and this collection at GH is here designated as the lectotype. In the protologue of *D. torreyi*, Gray (1885) cited unspecified collections from Arizona of Thurber, Wright, Schott, Rothrock, Lemmon, and Pringle. *Pringle s.n.* 15 May 1881 at GH conforms to the description and bears, in Gray's handwriting, "Dicliptera torreyi n.sp." Lectotypification is postponed until the other collections have been studied.

In the protologue of *Dianthera sexangularis*, a plate (number 22 of the Icones Florae Mexicanae) and a locality ("in Australis Oceani littore prope Coahuayanam," i.e., vicinity of Coahuayana, Michoacán) were cited. The plate represents *Dicliptera resupinata* which occurs in the region of Coahuayana. Specimens labeled as *Dianthera sexangularis* in the Sessé and Mociño herbarium at MA are referable to *Dicliptera peduncularis* Nees. Because the plate agrees with the description in the protologue, it is designated above as the lectotype of *Dianthera sexangularis*.

Plants previously recognized as *Dicliptera formosa* are here treated as conspecific with *D. resupinata* for the first time. A specimen in the Brandegee herbarium at UC bears the same number as the type (i.e., "455," see above), but was collected on a different date at a different locality. To the holotype at UC, a subsequent collection from Saucito (*Brandegee s.n.* 14 Oct. 1893) has been added. The three shoots of this subsequent collection resemble one another, but differ from the type, by their shorter outer cymule bracteoles (13–18 mm long vs. 18–23 mm long on type). All collections resembling the type of *D. formosa* (i.e., *Brandegee s.n.* 14 Oct. 1893, *Carter & Ferris 3370*, *Ross et al. 2000*, *2061*, *2095*) come from the eastern slope of the Sierra de la Laguna between lat. 23°25′ to 23°31′N and long. 109°47′ to 109°53′W. They differ from *D. resupinata* in Baja California Sur by the following combination of characters: longer corolla (28–30 vs. 12–26 mm long), longer corolla tube (14–17 vs. 6–11 mm long) with a wider (2–2.5 vs. 1.1–1.7 mm) diameter near midpoint, longer stamens (18–22 vs. 5.5–15 mm long) that are inserted in distal 1/2 (vs. near apex) of corolla tube, longer thecae (1.3–1.6 vs. 0.5–1.1 mm long), and longer style (26–32 vs. 10.5–22 mm long). Furthermore, they differ from most peninsular specimens of *D. resupinata* by their evenly and more or less densely pubescent (vs. nearly glabrous to sparsely pubescent) young stems, leaves, and outer cymule bracteoles; by their generally larger (13–24 vs. usually 5–18 mm long) outer cymule bracteoles; and by their longer (3.5–4.8 vs. 2–3 mm long) calyces. These distinctions are inadequate for discerning species when the total variation in *D. resupinata* from Baja California Sur and from other portions of its range is considered, however.

Most collections of *D. resupinata* from Baja California Sur have the young stems either nearly glabrous or very sparsely pubescent with flexuose to retrorse to retrorsely appressed eglandular trichomes restricted to the ridges, the leaves with trichomes restricted to the major veins, and the abaxial surface of the outer cymule bracteoles glabrous or with a few antrorse eglandular trichomes 0.1–0.2 mm long. Several collections from the southern portion of the Cape Region (i.e., *Brandegee 454*, *Brandegee s.n.* 21 Oct. 1890, *Brandegee s.n.* 9 Mar. 1892, *Moran 6926*, *Peters 21*, *Porter 296*, *Sanders et al. 3355*, *Shreve 7285*, and *Wiggins 5686A*) differ by having the young stems evenly and more or less densely pubescent with erect to flexuose to retrorse eglandular trichomes 0.3–0.7 mm long, the leaf surfaces evenly pubescent with eglandular trichomes, and the abaxial surface of the outer cymule bracteoles pubescent with erect to flexuose to antrorse eglandular trichomes to 0.6 mm long. (In *Wiggins 5686A* even some of the capsules are sparsely pubescent with erect to retrorse eglandular trichomes 0.1–0.2 mm long.) In vesture, these collections resemble those previously treated as *D. formosa*. *Porter 296* is somewhat intermediate in pubescence between the other collections noted above and more typical collections of *D. resupinata*. Like the more pubescent plants, *Porter 296* has a denser pubescence with longer trichomes, but like the more typical form, the trichomes are concentrated on, or restricted to, the ridges.

These pubescent collections are readily associated with the more common (and less pubescent) specimens of *D. resupinata* because they have the shorter bracteolar and floral characteristics usually encountered in that species. Other collections lack the prominent pubescence characteristic of plants previously treated as *D. formosa*, but resemble them in other ways. For example, *Brandegee s.n.* Nov. 1902 from the Sierra El Taste (UC 190888) has relatively large outer cymule bracteoles (15–21 mm long) and calyces (4.5 mm long). Mature corollas are not present on this specimen, but buds (ca. 20 mm long) present suggest that mature corollas would be relatively large. Another Brandegee collection (UC 102696) from this same locale, also collected in November 1902, resembles more typical *D. resupinata* (e.g., outer cymule bracteoles 10–15 mm long, and calyces to 3.5 mm long). Similarly, *Brandegee 455* from the "Sierra de la Laguna" (UC 102690), *Brandegee s.n.* without date (UC 185704) from the "Cape Region," and *Brandegee s.n.* 15 Sep 1893 (UC 139097) from "El Taste" lack the pubescence characteristic of *D. formosa* but have outer cymule bracteoles 14–20 mm long, calyces 4.5 mm long, and corollas to 30 mm long. These collections thus resemble *D. resupinata* in some features and *D. formosa* in others. Also, plants from at least two coastal regions on the mainland in Sonora (i.e., *Daniel 1947*, *Moran 4039* both from the vicinity of Guaymas) and Sinaloa (i.e., *Blakley B-1680*, *Gentry 14319*, *Hastings & Turner 64-121*, and *Moran 7585* all from the vicinity of Topolobampo) resemble the type of *D. formosa* in their outer cymule bracteoles (13–22 mm long), corollas (25–35 mm long), stamens (15–23 mm long) which are also inserted in the distal half of the corolla tube, thecae (1.2–2 mm long), and style (25–30 mm long). They differ from plants previously treated as *D. formosa* by their vesture which concurs with that of the common form of *D. resupinata* with shorter bracteoles and floral organs.

Thus the putative distinctions of *D. formosa* are combined in various ways among individuals of *D. resupinata* from Baja California Sur and the adjacent mainland. The lack of a suite of mutually exclusive characteristics between *D. formosa* and *D. resupinata*, combined with the general overlap in ranges of most character states that have been used to distinguish them, precludes recognition of two species at this time. Until *D. resupinata* and its relatives are better known, the pubescent, large-bracteoled, and long-flowered plants from the eastern slope of the Sierra de la Laguna (i.e., plants previously treated as *D. formosa*) are treated here as a localized expression of the species in a manner similar to the nearly glabrous, large-bracteoled, and long-flowered plants from coastal Sonora and Sinaloa.

Dicliptera resupinata var. *orbicularis* is also treated as a synonym of *D. resupinata* for the first time. In the protologue, Robinson and Seaton (1893) indicated that the type from Jalisco differed from the typical form by its larger, thinner, and more deeply cordate outer cymule bracteoles (as "involucral bracts"). The species exhibits considerable variation in these attributes throughout its range.

There is no recent taxonomic treatment of *Dicliptera*. *Dicliptera resupinata* shows similarities to *D. inutilis* Leonard in Mexico and Central America and to *D. sanctae-martae* Leonard in South America.

DYSCHORISTE

Dyschoriste Nees in Wall., Pl. asiat. rar. 3:75, 81. 1832. Lectotype (Britton & Brown, Ill. fl. n. U.S., ed. 2, 3:240. 1913). — *Dyschoriste depressa* Nees.

Calophanes D. Don in Sweet, Brit. fl. gard. ser. 2, 2:t. 181. 1833. Type. — *Calophanes oblongifolia* (Michx.) D. Don in Sweet (≡ *Ruellia oblongifolia* Michx.).

Linostylis Fenzl ex Sond., Linnaea 23:94. 1850. Type. — *Linostylis ovata* Sond.

Decumbent to erect perennial herbs with cystoliths. Leaves opposite, sessile or petiolate, margin entire to crenate. Inflorescence of dichasia in leaf axils throughout plant or restricted to axils of distal leaves or bracts and forming a spicate or capitate thyrse; dichasia alternate or opposite, 1–many-flowered, sessile to pedunculate. Bracts (if present) opposite, green, margin entire. Flowers homostylous, subtended by 2 homomorphic bracteoles, sessile to subsessile (in ours). Calyx 5-lobed, tube often as long as or longer than lobes during anthesis, regions between lobes usually subhyaline, often splitting nearly to base in fruit, lobes equal to subequal in length, usually somewhat setaceous. Corolla blue to blue-purple to white (in ours, elsewhere also pinkish purple, red, and yellow), tube gradually or abruptly expanded distally into a ± distinct throat, limb subactinomorphic to bilabiate, upper lip 2-lobed, lower lip 3-lobed, corolla lobes contorted in bud. Stamens 4, didynamous, filaments connate in pairs (i.e., a long and a short stamen connate) proximally, inserted at or near base of throat of corolla, exserted from mouth of corolla (at least longer pair and usually with at least a portion of anthers of shorter pair also), anthers 2-thecous, thecae equal in length, parallel to subsagittate, equally inserted, appendaged at base with awns or stout trichomes (in ours, elsewhere sometimes unappendaged at base), dehiscing toward lower lip (i.e., flower nototribal); pollen (Fig. 8c) subprolate to prolate, 3-colporate, mesocolpia multi-striate with 4–15 pseudocolpi of irregular lengths, colpi often very short (often shorter than pseudocolpi), exine minutely verrucate; staminodes 0. Style exserted from mouth of corolla, stigma unequally 2-lobed, 1 lobe greatly reduced, rudimentary, or sometimes not evident. Capsule substipitate, subellipsoid to ellipsoid, retinacula present, septae with attached retinacula remaining attached to inner wall of mature capsule. Seeds 2–4, homomorphic, lenticular, covered with appressed hygroscopic trichomes. ($x = 15$).

A genus of approximately 75 species occurring in tropical and warm-temperate regions of America, Africa, and Asia. The genus is best developed in the New World where it has a discontinuous distribution from the southern United States southward through Mexico and Central America to northern Argentina. Major concentrations of species are found in west-central and southern Mexico and southeastern Brazil. The actual number of Mexican species is likely fewer than the 22 presently recognized. Six species are reported as occurring in the United States. *Dyschoriste* is a complex genus whose species offer few characters for their recognition. Kobuski's (1928) treatment of the American species is now outdated and inadequate both for delimiting and identifying taxa.

Reference. — Kobuski, C. E. 1928. A monograph of the American species of the genus *Dyschoriste*. Ann. Missouri Bot. Gard. 15:9–91.

1. Dyschoriste decumbens (A. Gray) Kuntze, Revis. gen. pl. 2:486. 1891. *Calophanes decumbens* A. Gray, Syn. fl. N. Amer. 2(1):325. 1878. Type. — In the protologue, Gray mentioned unspecified collections of Wright from western Texas and Thurber, Wright, and Rothrock from southern Arizona. To my knowledge, a lectotype has not been designated from among the syntypes, which are presumably all at GH.

Decumbent to ascending perennial herbs to 1.3 dm tall. Young stems quadrate, evenly pubescent with retrorse eglandular trichomes 0.05–0.1 mm long. Leaves sessile to petiolate, petioles to 2 mm long, blades (linear to) narrowly elliptic to broadly elliptic to obovate, (3.5–) 8–28 mm long, 2–6 mm wide, 1.5–7 times longer than wide, rounded to acute at apex, acute to attenuate at base, surfaces pubescent with mostly erect eglandular trichomes 0.05–0.1 mm long (occasionally with flexuose eglandular trichomes to 0.5 mm long as well), margin entire, pubescent like surfaces except with trichomes mostly antrorse. Inflorescence of dichasia in leaf axils from near base of plant to apex; dichasia alternate, 1-flowered, sessile to subsessile (i.e., borne on peduncles to 1 mm long). Bracteoles subfoliose, usually petiolate, linear to narrowly elliptic, 5–9 mm long, 1–2 mm wide, abaxial surface and margin pubescent like leaves. Flowers sessile to subsessile (i.e., borne on pedicels to 1 mm long). Calyx 11–15.5 mm long, tube 3–5.5 mm long, lobes lance-subulate, 7–10 mm long, 1.3–2.7 times longer than tube, abaxially and marginally pubescent with flexuose eglandular trichomes 0.05–0.2 mm long. Corolla pale purple with darker purple markings in throat, 15–17 mm long, externally pubescent with erect to flexuose to retrorse eglandular trichomes 0.1–0.2 mm long, tube expanded distal to midpoint, 10–11 mm long, 1.5–2.5 mm in diameter near midpoint, limb subactinomorphic, 10–12 mm in diameter, upper lip 5.5–6.5 mm long, lobes 4.5 mm long, 2.5–3.3 mm wide, lower lip 6–6.5 mm long, lobes 4.5 mm long, 2.5–3.4 mm wide. Longer pair of stamens 7.5 mm long, shorter pair of stamens 6 mm long, thecae parallel, 1.5–1.7 mm long (including basal appendage), awned at base, awns pointed, 0.3–0.5 mm long. Style 8–10 mm long, pubescent with eglandular trichomes, stigma unequally 2-lobed, 1 lobe 1.8–2 mm long, other lobe 0.1–0.2 mm long. Capsule 9–10 mm long, glabrous, stipe 2.5 mm long, head ellipsoid. Seeds 4, 2.9–3 mm long, 1.8–2 mm wide. (*n* = 15, Grant 1955). Fig. 11.

PHENOLOGY. — Flowering and fruiting: March–May.

DISTRIBUTION AND HABITAT. — Southwestern United States (Arizona, New Mexico, Texas) and Mexico (Baja California Sur, Chihuahua, Coahuila, Durango, Hidalgo, Querétaro, San Luis Potosí, Sonora, Zacatecas); in our region the species is known only from the eastern escarpment of the Sierra de la Laguna in the nondesert portion of the Cape Region (Fig. 4) where plants occur in dry rock crevices at an elevation of about 1000 m. According to Moran's field notes, plants collected in the vicinity included: *Justicia austrocapensis*, *Nolina beldingii*, *Lepechinia hastata*, and *Erythea brandegeei*.

ADDITIONAL SPECIMENS EXAMINED. — MEXICO. **Baja California Sur**: Laguna Mountains, *M. Jones 24437* (POM); Cape Region, Protrero de Almenta near head of S fork of Cañón San Pedro, ca. 23°19′N, 109°56′W, *R. Moran 7392* (DS).

Marcus Jones collected this species in the Sierra de la Laguna on 2 March 1928. According to Lenz (1986), Jones departed from Miraflores by horseback for the Sierra de la Laguna to the west on 1 March 1885 and returned to Miraflores on 3 March. The ascent was presumably via the Cañón San Pedro (as "San Pedro y San Pablo canyon" in Lenz 1986) in which the specimen of *D. decumbens* was collected on 2 March. Moran recollected this species 31 years later in the same or a nearby locale.

The description above is derived solely from the Baja California collections. This species forms a major component of a taxonomically unresolved complex that also includes *D. linearis* (Torr. & A. Gray) Kuntze, *D. schiedeana* (Nees) Kuntze, *D. crenulata* Kobuski, *D. poliodes* Leonard & Gentry, *D. greenmanii* Kobuski, and others. The putative distinctions among taxa in this assemblage involve habit, vesture, leaf shape, and corolla size. *Dyschoriste decumbens* was considered to be distinctive in the genus on the basis of its cinereous pubescence consisting of strictly eglandular and very short trichomes, axillary inflorescences, and generally nonlinear leaves with entire margins (Kobuski 1928).

ELYTRARIA

Elytraria Michx., Fl. bor.-amer. 1:8. 1803, nom. cons. TYPE. — *Elytraria virgata* Michx., nom. illegit. (= *E. caroliniensis* (J. F. Gmel.) Pers.).

Tubiflora J. F. Gmel., Syst. nat. 2:27. 1791, nom. rej. TYPE. — *T. caroliniensis* J. F. Gmel.

Erect to ascending, acaulescent to caulescent perennial herbs lacking cystoliths. Leaves alternate, mostly in basal rosettes or crowded at apices of branches, sometimes ± diffuse along stems, subsessile to petiolate, margin entire to crenate (in ours, elsewhere also pinnatifid). Inflorescence of scapose or pedunculate densely bracteate axillary and terminal dichasiate spikes, spikes slender, cylindric, simple or sometimes branched, scapes or peduncles covered with imbricate, coriaceous, clasping scales; dichasia alternate (spirally arranged), 1-flowered, sessile in axil of a bract. Bracts alternate (spirally arranged), green or partially hyaline, coriaceous, sometimes apically toothed and/or winged. Brac-

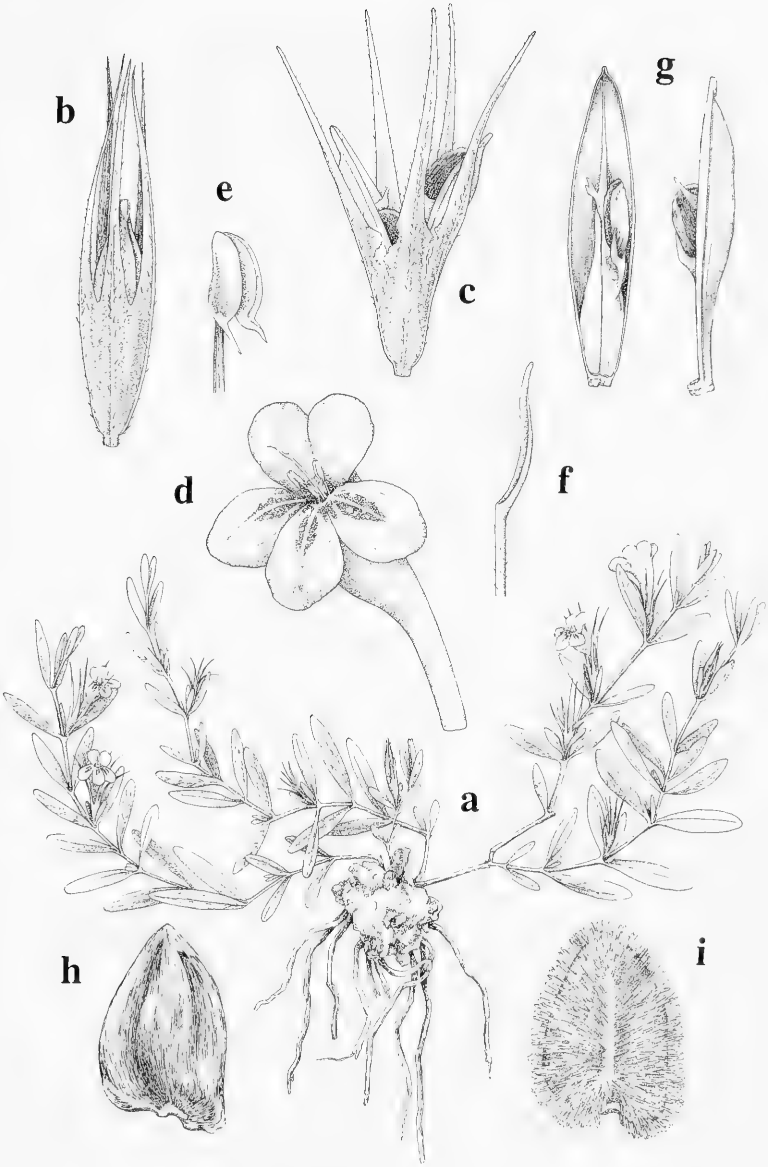


FIGURE 11. *Dyschoriste decumbens*. a. habit (*Moran 7392*), × 0.7; b. calyx with unopened capsule (*Jones s.n.*, 4 Sep 1903), × 3; c. calyx with opened capsule (*Parfitt & Christy 4593*), × 2.8; d. flower with calyx removed (*Moran 7392*), × 2.8; e. distal portion of stamen with anther (*Moran 7392*), × 12; f. distal portion of style with stigma (*Daniel 591*), × 12; g. capsule valves (*Jones 24437*), × 4.5; h. dry seed (*Jones 24437*), × 10; i. moistened seed (*Jones 24437*), × 10. Drawn by Jenny Speckels.

teoles often mostly hyaline. Flowers homostylous, subtended by 2 homomorphic bracteoles, sessile. Calyx deeply 4-lobed, mostly hyaline, lobes heteromorphic, anterior and posterior lobes external, anterior lobe 2-dentate to ± deeply 2-cleft. Corolla relatively small, pinkish or blue or white or yellow, often with colored markings near mouth, tube cylindric or slightly expanded near mouth, throat indistinct or evident only near mouth, limb bilabiate, upper lip 2-lobed, lower lip 3-lobed, corolla lobes often apically divided or 2-cleft, imbricate in bud. Stamens 2, inserted at or near apex of corolla tube, anthers partially exserted from mouth of corolla, 2-thecous, thecae (covered by stigma during anthesis) equal in size, parallel, equally inserted, lacking basal appendages (at least in ours), dehiscing toward lower lip (i.e., flower nototribal); pollen (Fig. 8d) prolate, 3-colpate, exine minutely verrucate to foveolate-reticulate; staminodes 0–2, minute. Style exserted from mouth of corolla, stigma unlobed, expanded, flat, subelliptic to subspatulate, folded over anthers during anthesis and straightening when touched (touch-sensitive) and gradually refolding. Capsule estipitate, subconic to ovoid, sometimes irregularly proximally constricted, retinacula absent, placentae minute, papilliform. Seeds numerous (up to 20 per capsule), irregularly shaped (often blocky or cube-like), lacking trichomes. ($x = 11$ or 12?).

A genus of about 15 species occurring in the tropics and subtropics of both Old and New Worlds. The majority of species are American; four are known from Mexico and three occur in the United States.

REFERENCE. — LEONARD, E. C. 1934. The American species of *Elytraria*. J. Wash. Acad. Sci. 24:443–447.

1. Elytraria imbricata (Vahl) Pers., Syn. pl. 1:23. 1805. *Justicia imbricata* Vahl, Eclog. amer. 1:1. 1796. TYPE. — Not located, based on material from "herbario Marcgravii." In his Enum. pl. of 1804, Vahl cited a Marcgrav collection from Brazil and a collection of von Rohr from Santa Marta, Colombia. The latter collection in the Vahl herbarium at C pertains to our species.

Verbena squamosa Jacq., Pl. hort. schoenbr. 1:3. 1797. *Tubiflora squamosa* (Jacq.) Kuntze, Revis. gen. pl. 2:500. 1891. *Elytraria squamosa* (Jacq.) Lindau, Anales Inst. Fís.-Geogr. Nac. Costa Rica 8:299. 1895. TYPE. — Unknown.

Elytraria tridentata Vahl, Enum. pl. 1:107. 1804, nom. illegit. (*Justicia imbricata* Vahl cited as synonym).

See Daniel (1995) for a complete listing of synonyms for this species.

Ascending to erect caulescent perennial herbs to 3.5 dm tall. Stems subterete to subquadrate, often irregularly fissured or angled, sparsely pubescent with flexuose to appressed eglandular trichomes to 0.5 mm long or glabrate. Leaves (sometimes absent or nearly so during anthesis) mostly clustered near stem apices, petiolate, petioles to 50 mm long (naked portion to 12 mm long), blades narrowly to broadly elliptic to oblanceolate to obovate, (9–) 13–120 mm long, (3–) 5–33 mm wide, 1.7–4.9 times longer than wide, acute to acuminate at apex, long-attenuate at base (often tapered along petiole nearly to node), adaxial surface pubescent with coarse flexuose eglandular trichomes to 1 mm long, abaxial surface with pubescence mostly restricted to major veins, margin entire. Peduncles to 130 (–260) mm long (sometimes nearly absent), often branching distally, scales conduplicate, lanceolate, 2–4.5 mm long, 0.7–1.2 mm wide, acuminate-mucronate at apex, abaxial surface glabrous or scabrous along midvein with retrorse eglandular trichomes to 0.05 mm long, margin ciliate with silky-crinkled eglandular trichomes to 1.5 mm long (villous). Spikes 3–7 mm in diameter near midpoint, rachis ridged, villous. Bracts usually ± conduplicate, ovate to subelliptic to rectangular, 5–6.5 mm long, 1.5–2.2 mm wide, margin proximally and distally hyaline, central portion of bract (including margin) green, apex 3-dentate, lateral teeth hyaline and winglike, central tooth awnlike, abaxial surface of bracts glabrous, margin ± villous-ciliate. Bracteoles lanceolate, 2.3–3 mm long, 0.5–0.6 mm wide, surface mostly hyaline except for green central portion (keel), abaxial surface glabrous except keel pubescent with antrorse eglandular trichomes. Calyx 3.5 mm long, anterior lobe constricted proximally, linear, 2.6–3 mm long, 0.5–0.6 mm wide, 2-lobed at apex, lobes 0.1–0.3 mm long, posterior and lateral lobes linear to lanceolate, 2.3–3 mm long, 0.5–0.9 mm wide, all lobes abaxially glabrous, margin ciliate distally with straight to flexuose eglandular trichomes to 1 mm long. Corolla blue with a yellow spot in a white region at the base of the lower lip, 4–9.5 mm long, externally glabrous, tube 2.3–4.5 mm long, upper lip 1–1.9 mm long, lobes 0.5–0.7 mm long, lower lip 1.7–5 mm long, lobes 1.2–3.2 mm long, central lobe largest, lobes of lower lip apically cleft. Stamens 1.2–1.5 mm long, thecae 0.5–0.6 mm long. Style 2.5–2.7 mm long, glabrous, stigma 0.7–0.9 mm long, 0.4 mm wide. Capsule 2.8–4.1 mm long, glabrous. Seeds 10, irregularly shaped, often ± blocky, 0.4–0.8 mm long, surfaces minutely papillose. (*n* = 12, Daniel et al. 1990; *n* = 11, Ward 1984). Fig. 12.

PHENOLOGY. — Flowering and fruiting: September–June.

DISTRIBUTION AND HABITAT. — Southwestern United States (Arizona, Texas), Mexico (Baja California Sur, Campeche, Chihuahua, Chiapas, Coahuila, Colima, Guerrero, Jalisco, México, Michoacán, Nayarit, Oaxaca, Sinaloa, Sonora, Veracruz, Yucatán, Zacatecas), Belize, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Venezuela, Ecuador, Peru, Bolivia, Brazil, Argentina, and West Indies; in our region the species is restricted to the Cape Region, the Sierra de la Giganta, and the Sonoran Desert (Central Gulf Coast and Magdalena subdivisions) of Baja California Sur (Fig. 13); plants occur in and along watercourses, in valley bottoms, on rocky slopes and plains, and on sandy beaches in desertscrub, thornscrub, tropical deciduous forest, and oak woodland from near sea level to 1400 m elevation.

LOCAL NAMES. — "Cordoncello" [*Palmer 6* from the vicinity of La Paz fide Vasey and Rose (1890)]; "cordoncillo" (numerous herbarium labels).

USE. — A hot tea made from the plant is used for stomach pains [*Palmer 6* fide Vasey and Rose (1890)].

ADDITIONAL SPECIMENS EXAMINED. — MEXICO. **Baja California Sur**: Purísima, *T. Brandegee 440* (DS); San José del Cabo, *T. Brandegee 440* (UC); Río del Salada along rd from Puerto Chale to Santa Rita, *D. Breedlove & D. Axelrod 43123* (CAS); 3 km E de San Pedro de la Soledad, entrando por la carr. Cabo San Lucas-Todos Santos, 23°15′N, 109°56′W, *A. Campos V. et al. 4514a* (CAS); 12 km NW of San Bartolo, 23°46′N, 109°50′W, *A. Carter 2655* (DS, UC); Cape Region, Sierra El Taste, arroyo NE of La Carrerita, ca. 23°11′N, 109°55′W, *A. Carter & F. Chisaki 3574a* (UC); between Rancho Palmilla and headwaters of arroyo NW of El Encinal, ca. 23°10′N, 109°58′W, *A. Carter & F. Chisaki 3597* (UC); Sierra de la Giganta, Cuesta de Chuenque, ca. 22 km S of Loreto on rd to Puerto Escondido, ca. 25°51′N, 111°20′W, *A. Carter & R. Ferris 4725* (CAS, UC); Sierra de la Giganta, Cañón del Cayuco, E base of Cerro de la Giganta, 26°05′N, 111°33′W, *A. Carter & L. Kellogg 3114* (DS, UC); Sierra de la Giganta, vic. of Portezuelo de Peloteado (SW of Notrí), ca. 25°49′N, 111°23′W, *A. Carter & F. Leal 4685* (UC); Sierra de la Giganta, vic. of Rancho Tasajera, ca. 3.5 km NE of San José de Agua Verde, ca. 25°30′N, 111°10′W, *A. Carter & H. Sharsmith 4930* (UC); W branch of Arroyo Hondo, N side of Cerro de la Giganta, 26°10′N, 111°36′W, *A. Carter et al. 2066* (DS, UC); Cape San Lucas, 1 mi from beach, *T. Craig 733* (POM), *751* (POM); Arroyo La Huerta near Hwy 286 between La Paz and San Juan de los Planes, 2.7 km SE of La Huerta, ca. 24°03′N, 110°09′W, *T. Daniel & M. Butterwick 6837* (CAS, ENCB, MICH, US); Rancho La Burrera, W slope of Sierra de la Laguna, ca. 22 km NE of Todos Santos, ca. 23°31′N, 110°02′W, *T. Daniel et al. 6854* (BR, CAS, HCIB, K, MEXU, MO, SBBG); Rancho La Burrera, cuesta "El Arado," 23°30′N, 110°04′W, *R. Domínguez C. 357* (HCIB); San Bartolo, *F. Gander 9675* (CAS, SD); Sierra Giganta, Arroyo Hondo, *H. Gentry 4113* (DS); Sierra de la Laguna, Las Animas, ranch at river-fork near base of El Picacho Peak, *B. Hammerly 271* (CAS, DS); Rancho La Huerta area, ca. 12 km SE of La Paz toward San Juan de los Planes, ca. 24°02′N, 110°09′W, *D. Harder & W. Appleby 1096* (RSA); Agua Verde Bay, *I. Johnston 3897* (CAS); San Antonio, *M. Jones 22522* (POM); Laguna Mts, Cota Ranch, *M. Jones 24050* (POM); Todos Santos, *M. Jones 24654* (POM); Loreto, Cayuca Ranch, *M. Jones 27353* (POM), *27444* (UC); abajo del Rancho San Pedro de la Soledad, *J. León de la Luz s.n.* (HCIB); El Comitán, 24°13′N, 110°20′W, *J. León de la Luz 2139* (HCIB); Rancho La Burrera, NE de Todos Santos, 23°30′N, 110°04′W, *J. León de la Luz 2344* (HCIB); Sierra de La Laguna, Cañón La Burrera, El Palmillar, 23°28′N, 109°55′W, *J. León de la Luz 2569* (HCIB); Cape Region, 11 km N of Santa Anita, ca. 23°15′N, 109°42′W, *R. Moran 6921* (DS, RSA, SD); Cape Region, 3 km N of Cabo San Lucas, ca. 22°55′N, 109°55′W, *R. Moran 7039* (CAS, DS, SD); Cape Region, S fork of Cañón San Pedro, ca. 23°19′N, 109°55′W, *R. Moran 7415* (CAS, DS, SD, UC); Sierra de Guadalupe, San Sebastián, 27°01′N, 112°24′W, *R. Moran 18781* (SD);Santiago, 3 mi S of Caduano, *R. Peters 22* (UC); 8.5 mi SE of La Ribera on rd to Los Frailes, *D. Porter 297* (CAS, DS); 4 mi S of Miraflores, *J. Whitehead 924* (DS); N of Comondú, *I. Wiggins 5481* (DS); between La Paz and San Pedro, *I. Wiggins 5594* (CAS, DS, UC); 15.5 mi S of La Paz, along rd to Todos Santos, ca. 24°01′N, 110°06′W, *I. Wiggins 15309* (CAS, DS, UC); 2.5 mi N of Rancho El Obispo, ca. 24°44′N, 111°10′W, *I. Wiggins 15469* (DS).

The closest relative of *Elytraria imbricata* appears to be *E. mexicana* Fryxell & S.D. Koch, a morphologically similar species from southwestern Mexico that differs by its bracts with merely a spinose tip and its cream to white corollas with the lobes of the upper lip dark purple.

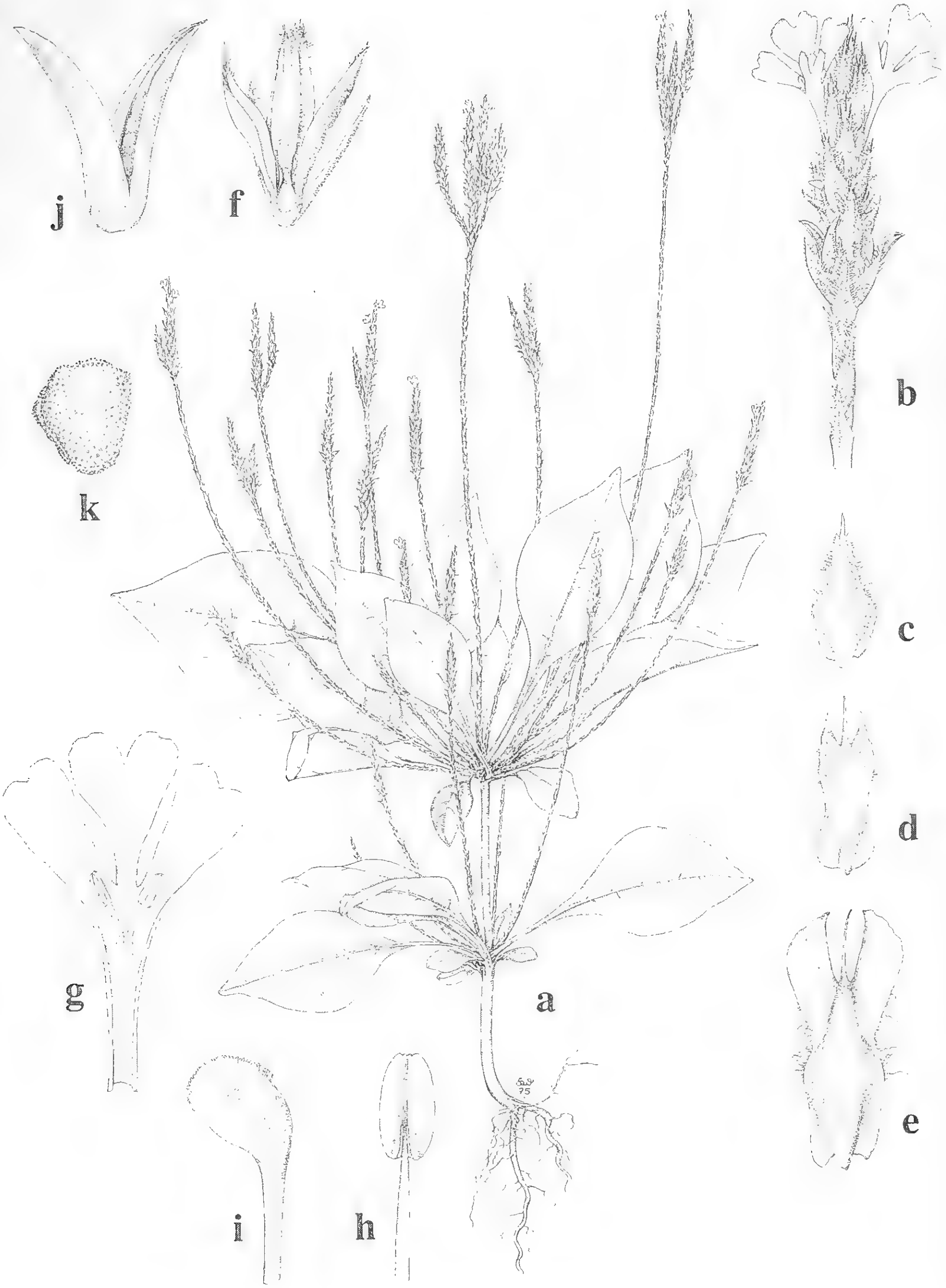


FIGURE 12. *Elytraria imbricata*. (a–d, f–k from *Feddema 2736*, e from *González 80-A*). a. habit, × 0.5; b. inflorescence, × 2.5; c. bract from proximal portion of inflorescence, × 5; d. bract from distal portion of inflorescence, × 5; e. bract with typical winglike lateral teeth, × 5; f. bracteoles and calyx, × 7.5; g. corolla with upper lip removed showing stamens, × 5; h. stamen, × 15; i. distal portion of style with stigma, × 15; j. capsule, × 10; k. seed, × 30. Drawn by Karin Douthit. Copyright reserved to University of Michigan Herbarium, used with permission.

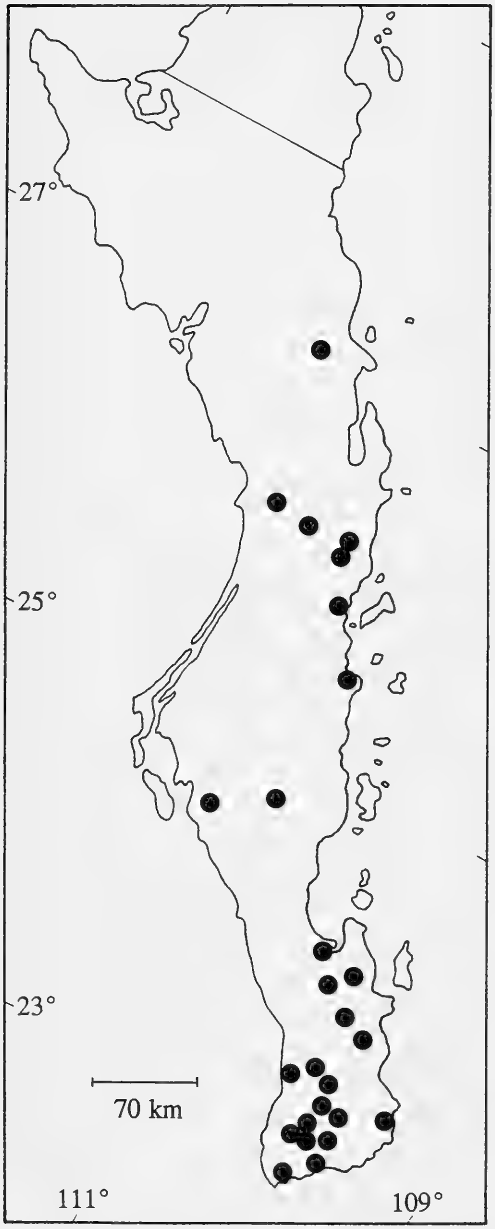


FIGURE 13. Distribution of *Elytraria imbricata* in the peninsula of Baja California.

HENRYA

Henrya Nees ex Benth., Bot. voy. *Sulphur*, t. 49. 1845. TYPE. — *H. insularis* Nees ex Benth.

Solenoruellia Baill., Hist. pl. 10:445. 1891. TYPE. — *S. galeottiana* Baill. (= *Henrya insularis* Nees ex Benth.).

Erect or ascending perennial herbs or shrubs with cystoliths. Older stems with epidermis exfoliating. Leaves opposite, subsessile to petiolate, petioles detaching at junction with stem, margin entire. Inflorescences of axillary and terminal stout to lax dichasiate spikes (to thyrses) collectively forming leafy terminal panicles; dichasia alternate or opposite, 1–3-flowered, sessile or short-pedunculate in axils of bracts. Bracts opposite, green, usually less conspicuous than bracteoles, margin entire. Bracteoles oblanceolate to obovate, concavoconvex, fused from base to near apex along side adjacent to rachis, rounded to acute at apex, mucronate with straight, apical or dorsal, erect or divergent pointed projection, secondary bracteoles, if present, much reduced. Flowers homostylous, sessile, subtended by 2 homomorphic bracteoles. Calyx deeply 5-lobed, lobes homomorphic or heteromorphic (i.e., posterior lobe reduced in size). Corolla white, cream, or yellow, with maroon, purple, yellow, and/or white markings on upper lip, externally glabrous, tube subcylindric to cylindric, shorter than limb, throat indistinct, limb pseudopapilionaceous, upper lip obovate to spatulate, bifid, lower lip 3-lobed, lateral lobes obovate, lower-central lobe obovate to broadly obovate and keeled, corolla lobes imbricate in bud. Stamens 2, inserted at or near mouth of corolla, anthers 2-thecous, thecae subequal, parallel, equally to subequally inserted, lacking basal appendages, dehiscing toward upper lip (i.e., flower stenotribal); pollen (Fig. 14a; from extralimital material) prolate, 3-colporate, colpi broad (i.e., far exceeding width of centrally positioned ora), 6-pseudocolpate, pseudocolpi 2 per mesocolpium, exine reticulate; staminodes 0. Style exserted from mouth of corolla, glabrous, stigma 2-lobed, lobes triangular, equal, often inconspicuous. Capsule stipitate, head subspheric to broadly ellipsoidal, retinacula present, septae with attached retinacula separating slightly from inner wall of mature capsule. Seeds 2, homomorphic, planoconvex, subcircular to subelliptic in outline, flat surface smooth to bumpy, convex surface and margin either pubescent with hygroscopic trichomes or covered with stout, branched or barbed tubercles. ($x = 18$).

Henrya comprises two species occurring in dry regions from the southwestern United States southward to Costa Rica. Both species occur in Mexico.

REFERENCE. — DANIEL, T. F. 1990. Systematics of *Henrya* (Acanthaceae). Contr. Univ. Michigan Herb. 17:99–131.

1. Henrya insularis Nees ex Benth., Bot. voy. *Sulphur*, t. 49. 1845. TYPE. — Plate 49 of Bentham's *The Botany of the Voyage of H. M. S. Sulphur*, see Daniel (Taxon 38:265–270. 1989.)

Henrya costata A. Gray, Proc. Amer. Acad. Arts 21:406. 1886. *Tetramerium costatum* (A. Gray) Millsp., Publ. Field Columbian Mus., Bot. Ser. 1:47. 1895. TYPE. — MEXICO. **Chihuahua**: near Batopilas, Aug–Nov 1885, *E. Palmer 211* (holotype: GH!; isotypes: K!, LE!, MEXU!, NY!, PH!, US!).

Henrya grandifolia Fernald, Bot. Gaz. (Crawfordsville) 20:537. 1895. TYPE. — MEXICO. **Sinaloa**: Esquinapa, Jan 1895, *F. Lamb 505* (holotype: GH!).

Henrya costata A. Gray var. *glandulosa* Brandegee, Zoe 5:171. 1903. TYPE. — MEXICO. **Baja California Sur**: Cape Region, Santa Anita, 1901, *C. Purpus 266* (lectotype, Contr. Univ. Michigan Herb. 17:117. 1990: UC!; isolectotypes: ARIZ!, MO!, US!).

Henrya brevifolia Happ, Ann. Missouri Bot. Gard. 24:547. 1937. TYPE. — MEXICO. **Sonora**: Las Durasnillas, 18 May 1892, *T. Brandegee s.n.* (holotype: UC!; isotypes: DS!, GH!, NY!, PH!, US!).

Henrya ortegana Happ, Ann. Missouri Bot. Gard. 24:552. 1937. TYPE. — MEXICO. **Sinaloa**: Sind. San Juan, San Ignacio, Mar 1931, *J. Ortega 6868* (holotype: MO!; isotypes: CAS!, F!, MIN!).

See Daniel (1995) for a complete listing of synonyms for this species.

Ascending to erect perennial herbs to 8 dm tall. Young stems subterete to terete, sometimes multistriate, densely and evenly pubescent with erect glandular trichomes 0.2–0.7 mm long (glandular pubescent). Leaves petiolate, petioles to 15 mm long, blades ovate to elliptic, 16–90 mm long, 9–55 mm wide, 1.4–2.8 times longer than wide, acute to subacuminate at apex, rounded to subacute at base, surfaces glandular pubescent when young, older leaves becoming mostly eglandular. Spikes to 150 mm long, rachises glandular pubescent; dichasia alternate or opposite at inflorescence nodes, sessile to subsessile (i.e., borne on peduncles to 1 mm long). Bracts near midspike obovate to linear-elliptic, 2.5–4 mm long, 0.8–1.3 mm wide, abaxial surface glandular pubescent, apically mucronate. Bracteoles obovate, 7–9 mm long, unfused for 2–3 mm along side adjacent to rachis, abaxially glandular pubescent, subacute and mucronate at apex, mucro erect, 0.1–0.4 mm long. Flowers sessile to subsessile (i.e., borne on pedicels to 0.3 mm long). Calyx 1.5–1.8 mm long, lobes homomorphic or heteromorphic, abaxial surface nearly glabrous or sparsely pubescent with glandular and eglandular trichomes 0.05–0.1 mm long, margins of lobes ciliate with longer trichomes. Corolla cream to pale yellow with a whitish spot outlined with purple on upper lip, 9–11 mm long, tube 3–4 mm long, upper lip 6–6.5 mm long, 1–2 mm wide, lower lip 5–7 mm long, lobes 5–6.2 mm long, 2–3 mm wide. Stamens 6–8.5 mm long, filaments pubescent proximally, thecae 1.5–2 mm long. Style 9–10 mm long, glabrous. Capsule 5–6 mm long, glabrous or sparsely pubescent proximally with glandular (and sometimes eglandular) trichomes. Seeds 1.7–2 mm long, 1.4–1.7 mm wide, flat surface smooth to bumpy, convex surface and margin covered with dense, appressed, flexuose, hygroscopic trichomes 0.3–0.7 mm long. ($n = 18$, Daniel 1990, Daniel and Chuang 1993, Daniel et al. 1984, 1990). Fig. 15.

PHENOLOGY. — Flowering and fruiting: February–May.

DISTRIBUTION AND HABITAT. — Southwestern United States (Arizona), Mexico (Aguascalientes, Baja California Sur, Chiapas, Chihuahua, Colima, Guanajuato, Guerrero, Jalisco, México, Michoacán, Nayarit, Oaxaca, San Luis Potosí, Sinaloa, Sonora, Tamaulipas, Veracruz, Yucatán), Guatemala, Honduras, El Salvador, Nicaragua, and Costa Rica; in our region the species is restricted to southern, nondesert portions of the Cape Region (Fig. 16); plants occur on rocky slopes and along trails in thornscrub, tropical deciduous forest, and oak woodland at 600–1140 m elevation.

ADDITIONAL SPECIMENS EXAMINED. — MEXICO. **Baja California Sur**: Sierra de Laguna, *T. Brandegee s.n.* (GH, PH, UC); Rancho Poza Larga, Arroyo de San

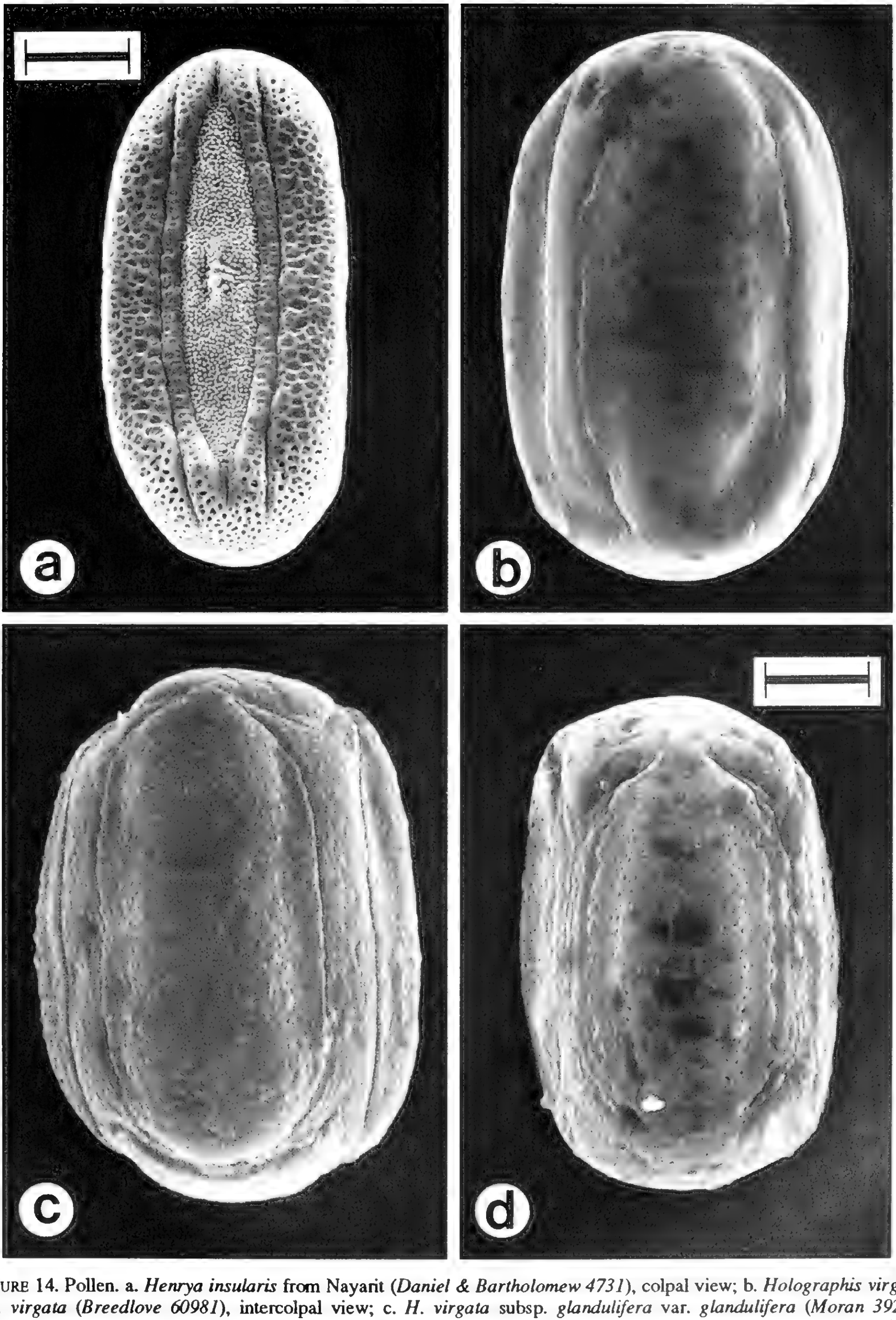


FIGURE 14. Pollen. a. *Henrya insularis* from Nayarit (*Daniel & Bartholomew 4731*), colpal view; b. *Holographis virgata* subsp. *virgata* (*Breedlove 60981*), intercolpal view; c. *H. virgata* subsp. *glandulifera* var. *glandulifera* (*Moran 3928*), intercolpal view; d. *H. virgata* subsp. *glandulifera* var. *palmeri* (*Carter & Ferris 3819*), intercolpal view. Scale for a and c = 11.5 µm; scale for b and d = 7.5 µm.

Francisquito, E side Sierra de la Victoria, 23°29–31′N, 109°47–55′W, *A. Carter & R. Ferris 3388* (DS, SD, UC); "La Parrita," Rancho La Burrera, NE de Todos Santos, 23°35′N, 110°00′W, *M. Domínguez L. 251* (HCIB); cerca del Rcho. San Pedro de la Soledad, SE de Todos Santos, 23°15′N, 109°58′W, *J. León de la Luz 1052* (CAS, HCIB); Sierra de la Laguna, Vereda, fondo del Cañón La Burrera, 23°29′N, 110°01′W, *J. León de la Luz 2496* (HCIB); Cape Region, trail above La Burrera, ca. 23°32′N, 110°02′W, *R. Moran 7454* (ARIZ, CAS, DS, ENCB, GH, MEXU, RSA, SD, UC, US); W slope of Sierra de la Victoria between La Burrera and La Laguna, *J. Thomas 7931* (ARIZ, CAS, DS, GH, MEXU, MICH, SD, UC, US).

As here treated, this is an extremely variable species with a broad distribution. A detailed discussion of the various forms of the species and their distributions was provided by Daniel (1990). Based on the few collections from the peninsula of Baja California, it appears that plants there are rather homogeneous in morphological attributes. The description above pertains only to specimens from Baja California Sur. During the dry season (e.g., March–May) this species can form a dominant element of the herbaceous understory in regions of tropical dry forest whereas at other times of the year (e.g., December) traces of it are difficult to locate. Information on reproductive biology and pollination ecology were provided by Daniel (1990).

The closest relative of this species, and the only other species in the genus, is *H. tuberculosperma* T. F. Daniel. It occurs in western Mexico and differs by its longer calyx, reddish or dark brown mature stems, and seeds that lack trichomes but have the convex surface and margin covered with conical tubercles bearing barbs.

HOLOGRAPHIS

Holographis Nees in A. DC., Prodr. 11:728. 1847. TYPE. — *Holographis ehrenbergiana* Nees.

Berginia Harv. ex Benth. & Hook. f., Gen. pl. 2:1096. 1876. TYPE. — *Berginia virgata* Harv. ex Benth & Hook. f. (≡ *Holographis virgata* (Harv. ex Benth. & Hook. f.) T. F. Daniel).

Pringleophytum A. Gray, Proc. Amer. Acad. Arts 20:292. 1885. TYPE. — *Pringleophytum lanceolatum* A. Gray. (= *Holographis virgata* (Harv. ex Benth. & Hook. f.) T. F. Daniel).

Lundellia Leonard, Wrightia 2:1. 1959. TYPE. — *Lundellia argyrea* Leonard (≡ *Holographis argyrea* (Leonard) T. F. Daniel).

Erect to ascending perennial herbs or shrubs lacking cystoliths. Leaves opposite (rarely subopposite) or quaternate, sessile to petiolate, sometimes anisophyllous, margin entire (in ours, elsewhere also subsinuate and spinose-dentate). Inflorescence of axillary or terminal dichasiate spikes (in ours, elsewhere also reduced to 2 flowers); dichasia opposite (in ours, elsewhere also alternate), 1-flowered, sessile in axil of a bract. Bracts opposite (in ours, elsewhere also alternate), green or somewhat reddish, margin entire (in ours, elsewhere also spinose-dentate). Flowers homostylous, sessile, subtended by 2 homomorphic bracteoles. Calyx deeply 5-lobed, lobes homomorphic. Corolla greenish white to white or pinkish or purplish or yellow, often with colored nectar guides, long axis horizontally to vertically oriented, tube subcylindric to ± abruptly expanded distally into a throat, limb bilabiate, upper lip 2-lobed, lower lip 3-lobed, corolla lobes imbricate in bud. Stamens 4, inserted in distal 2/3 of corolla tube, equally inserted to ± didynamous, anthers slightly exserted from mouth of corolla, anthers 1-thecous, often connivent, pubescent, lacking basal appendages, dehiscing toward lower lip (i.e., flower nototribal); pollen (Fig. 14b-d) prolate, 3-colpate, colpi often bifurcate near poles, exine foveolate to fossulate to fossulate-reticulate; staminode 1, borne between posterior pair of stamens, short. Style slightly exserted from mouth of corolla, stigma subfunnelform or 2-lobed, lobes equal or unequal. Capsule substipitate, ellipsoid to obovoid, retinacula present, septae with attached retinacula remaining attached to inner wall of mature capsule. Seeds 4 (or fewer by abortion), homomorphic, lenticular. ($x = 13$).

A genus of 15 species restricted to, but occurring nearly throughout, the dry regions of Mexico.

REFERENCES. — DANIEL, T. F. 1983. Systematics of *Holographis* (Acanthaceae). J. Arnold Arbor. 64:129–160. DANIEL, T. F. 1988. Three new species of *Holographis* (Acan-

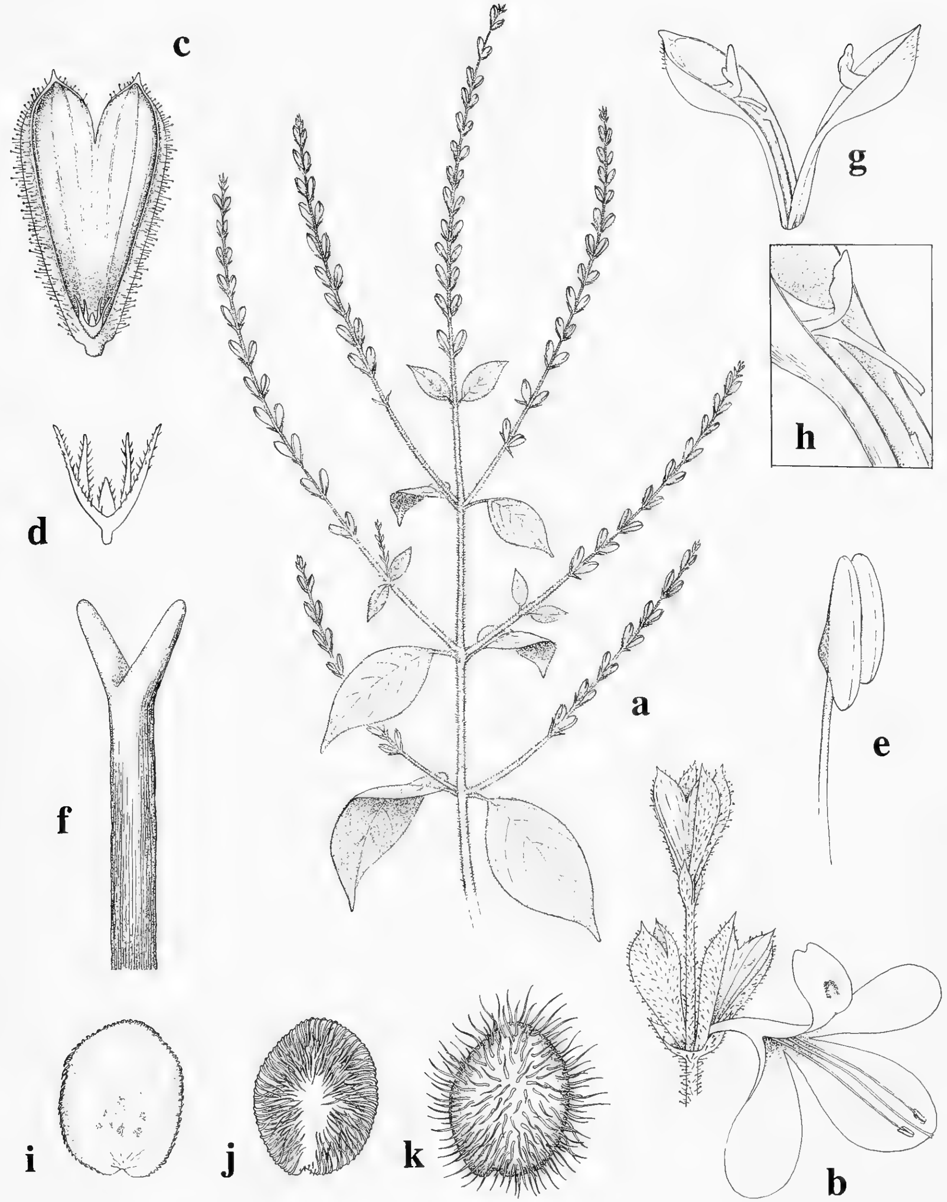


FIGURE 15. *Henrya insularis*. a. habit (*Breedlove 31276*), × 0.5; b. inflorescence nodes (*Moran 7454* and *Daniel 4072*), × 2.5; c. bracteoles opened to show calyx (*Moran 7454*), × 4.7; d. calyx (*Ton 3897*), × 11; e. distal portion of stamen with anther (*Daniel & Bartholomew 5027gh*), × 14; f. distal portion of style with stigma (*Gallagher 294*), × 62; g. capsule (*Breedlove 50470*), × 5; h. septum and retinaculum in one capsule valve (*Breedlove 50470*), × 8.5; i. dry seed, flat surface (*Breedlove 50470*), × 8.5; j. dry seed, convex surface (*Breedlove 50470*), × 8.5; k. moistened seed, convex surface (*Breedlove 50470*), × 8.5). Drawn by Ellen del Valle and Jenny Speckels.

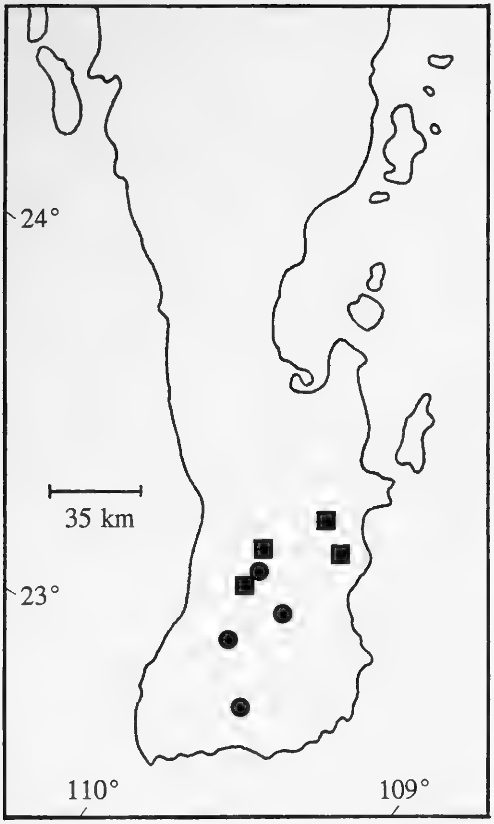


FIGURE 16. Distribution of *Henrya insularis* (circles) and *Ruellia intermedia* (squares) in the peninsula of Baja California.

thaceae) from Mexico. Proc. Calif. Acad. Sci., ser. 4, 46:73–81.

1. **Holographis virgata** (Harv. ex Benth. & Hook. f.) T. F. Daniel, J. Arnold Arbor. 64:139. 1983. *Berginia virgata* Harv. ex Benth. & Hook. f., Gen. pl. 2:1097. 1876. TYPE. — "California incola," without date, *T. Coulter 603* (holotype: K!; isotypes: GH!, K!).

Shrubs to 2 m tall. Young stems subquadrate to quadrate, evenly pubescent with erect, flexuose, or retrorse eglandular trichomes 0.05–0.7 (–1) mm long. Leaves opposite (or subopposite), sessile to petiolate, petioles to 5 mm long, blades linear-lanceolate to obovate, (4–) 6–50 mm long, 2–26 mm wide, 1.1–9.2 (–17) times longer than wide, acute to rounded (rarely emarginate) at apex, acute to attenuate at base, surfaces pubescent, margin entire, flat to revolute, ciliate. Inflorescences terminal, loosely or densely bracteate dichasiate spikes to 15 cm long, rachises pubescent with eglandular trichomes or with a mixture of eglandular and glandular trichomes; dichasia opposite (to subopposite) at nodes. Proximal bracts (up to 6 series) often sterile, triangular to circular, distal bracts fertile, somewhat foliaceous, lance-ovate to ovate to elliptic to circular, 3–8 mm long, 1.5–5 mm wide, usually pubescent like rachis. Bracteoles lance-subulate to linear to lanceolate, ± equal to or shorter than subtending bract, 2–6 mm long, 0.5–1.5 mm wide, pubescent with eglandular or a mixture of eglandular and glandular trichomes. Calyx 5–8 mm long, lobes lanceolate or oblanceolate, pubescent like bracteoles. Corolla reddish pink with white markings, 9–14.5 mm long, externally pubescent with eglandular trichomes (rarely with glandular trichomes as well in subsp. *glandulifera* var. *glandulifera*), tube 5–8 mm long, expanded distally, upper lip (2.5–) 3–5 mm long, lobes 1.5–4 mm long, lower lip 4–8 mm long, lobes spatulate, 2.5–6 mm long, 1.5–3.5 mm wide. Stamens 2.8–5 mm long, filaments pubescent or nearly glabrous, thecae 1.6–2.5 mm long; staminode 0.5–0.8 mm long. Style 5–7 mm long, glabrous or pubescent, stigma subequally 2-lobed, 0.3–0.5 mm long. Capsules 7–12 mm long, 3–5 mm in diameter, pubescent or essentially glabrous, trichomes eglandular, 0.05–0.3 mm long, often restricted to apex. Seeds obliquely cordate to widely elliptic, 2–3.5 mm long, 2–3 mm wide, pubescent with dendritic trichomes to 0.3 mm long. (*n* = 26, 39, Daniel et al. 1984). Fig. 17.

PHENOLOGY. — Flowering: October–June; fruiting: February–June.

DISTRIBUTION. — Northwestern Mexico (Baja California, Baja California Sur, and Sonora); in our region (Figs. 18, 19) the species occurs in the Cape Region, the Sierra de la Giganta, and parts of the Sonoran Desert (Central Gulf Coast and Vizcaíno subdivisions).

This species was treated from throughout its range by Daniel (1983b) who also presented a rationale for the infraspecific classification that is utilized here. Subspecies are recognized on the basis of a geographic discontinuity between eglandular populations in Baja California and Sonora and glandular populations in Baja California Sur. Two varieties within the southern subspecies are recognized on the basis of minor differences in pubescence that are largely correlated with elevation.

Relationships within *Holographis* remain to be fully resolved. Morphologically, *H. virgata* appears most similar to *H. tamaulipica* T. F. Daniel from Tamaulipas and *H. tolantongensis* T. F. Daniel from Hidalgo; however, neither of these species should be regarded as a particularly close relative at the present time.

Key to Infraspecific Taxa of *Holographis virgata*

1. Inflorescence rachises, bracts, bracteoles, and calyx eglandular (rarely with inconspicuous glands on bracteoles and calyx); bracteoles 0.5–1 mm wide; north of lat. 28°N . . . . 1a. subsp. *virgata*.
1. Inflorescence rachises, bracts, bracteoles, and calyx conspicuously glandular; bracteoles 1–1.5 mm wide; mostly south of lat. 28°N.
    2. Leaves and young stems scaberulous, trichomes retrorse, 0.05–0.1 mm long; usually below 600 m elev . . . . 1b′. subsp. *glandulifera* var. *glandulifera*.
    2. Leaves and young stems hirtellous, trichomes straight to flexuose, 0.1–1 mm long; usually above 600 m elev . . . . 1b″. subsp. *glandulifera* var. *palmeri*.

1a. Holographis virgata subsp. virgata

Pringleophytum lanceolatum A. Gray, Proc. Amer. Acad. Arts 20:293. 1885. Type. — MEXICO. Sonora: 50 mi below Altar and 30 mi from Gulf of California, 13 Mar 1884, *C. Pringle s.n.* (holotype: GH!; isotypes: A!, F!, MA!, NY!, US!).

Trichomes of younger stems erect to retrorse, 0.05–0.1 mm long. Leaves sessile to subsessile, blades linear-lanceolate to lanceolate to elliptic (to obovate), (4–) 7–43 mm long, 2–9 (–14) mm wide, (1.6–) 3–17 times longer than wide. Inflorescence rachises pubescent with eglandular trichomes 0.05–0.2 (–0.5) mm long. Bracts 1.5–3 mm wide, pubescent like rachis. Bracteoles 0.5–1 mm wide, pubescent like rachis (rarely also with scattered glandular trichomes to 0.2 mm long). Calyx pubescent like bracteoles. Lower lip of corolla 5–8 mm long, lobes 4–6 mm long, 2.5–3.5 mm wide. Capsule essentially glabrous to pubescent, trichomes (if present) often restricted to apex. (*n* = 26, Daniel et al. 1984). Fig. 17d, f.

Distribution and Habitat. — Western and central Sonora and southern Baja California; in our region the subspecies is known only to the north of latitude 28°N in the Vizcaíno and Central Gulf Coast subdivisions of the Sonoran Desert (Fig. 18); plants occur on slopes and along watercourses in desertscrub at 15–1300 m elevation.

Additional Specimens Examined. — MEXICO. **Baja California**: S base of Mesa El Portezuelo, 63 mi S of Bahía de Los Angeles toward San Francisquito, ca. 28°23′N, 113°06′W, *S. Boyd & T. Ross 5694* (RSA); 5 km NE of San Borja on rd to Bahía de Los Angeles, *D. Breedlove 60981* (CAS, RSA); Mina Desengaña, ca. 16 mi N of Punta Prieta, *H. Gentry & Cech 8887* (MEXU, MICH, RSA, US); ca. 22 mi from Bahía Los Angeles toward San Borja, *H. Gentry & L. McGill 23313* (ASU, DES, MICH); 7 mi W of San Francisquito Bay, *C. Harbison 41665* (RSA, SD); Las Animas Bay, *I. Johnston 3509* (CAS, GH, NY, UC); 6.4 mi S of Rancho de Mesquital, 5.3 mi S of site of Manuela, ca. 28°11′N, 113°48′W, *D. Michener et al. 4255* (CAS, RSA); Mesa de Mesquital, ca. 1.3 mi S of Rancho de Mesquital, ca. 28°15′N, 113°49′W, *D. Michener et al. 4260* (RSA); Paredones, *Montufar 42* (ENCB); near Agua de Higuera, ca. 28°57′N, 113°51′W, *R. Moran 7956* (ARIZ, DS, MICH, RSA, SD, UC); Sierra San Borja, San Juan Mine, ca. 28°43′N, 113°38′W, *R. Moran 8060* (DS, SD, UC); Sierra San Borja, canyon above El Terminal, 28°45′N, 113°35′W, *R. Moran 8511* (SD); Viscaíno Region, Llano Berrendo, 6.4 mi S of Rancho de Mesquital, ca. 28°11′N, 113°46′W, *B. Prigge et al. 4676* (LA, SD, UCR); Calmallí, *C. Purpus 56* (DS, F, NY, UC pro parte, US); 8 mi N of Mission San Borja, *R. Thorne & J. Henrickson 32677* (MICH, RSA); near El Infierno, *J. Whitehead 708* (LA); 3 mi S of Agua Higuera, along rd to Misión San Borjas, *I. Wiggins & D. Wiggins 14830* (CAS, DS, MEXU, MICH).

This is the most widely distributed subspecies of *H. virgata*. It occurs primarily to the north and east of the range of *H. virgata* subsp. *glandulifera*, but the ranges of the two subspecies overlap slightly in southern Baja California between about lat. 28°00′N and lat. 28°30′N. Intermediates (e.g., *Purpus 56 pro parte* at UC; *Boyd & Ross 5694*, cited above), with sparsely glandular inflorescence rachises, have been collected in

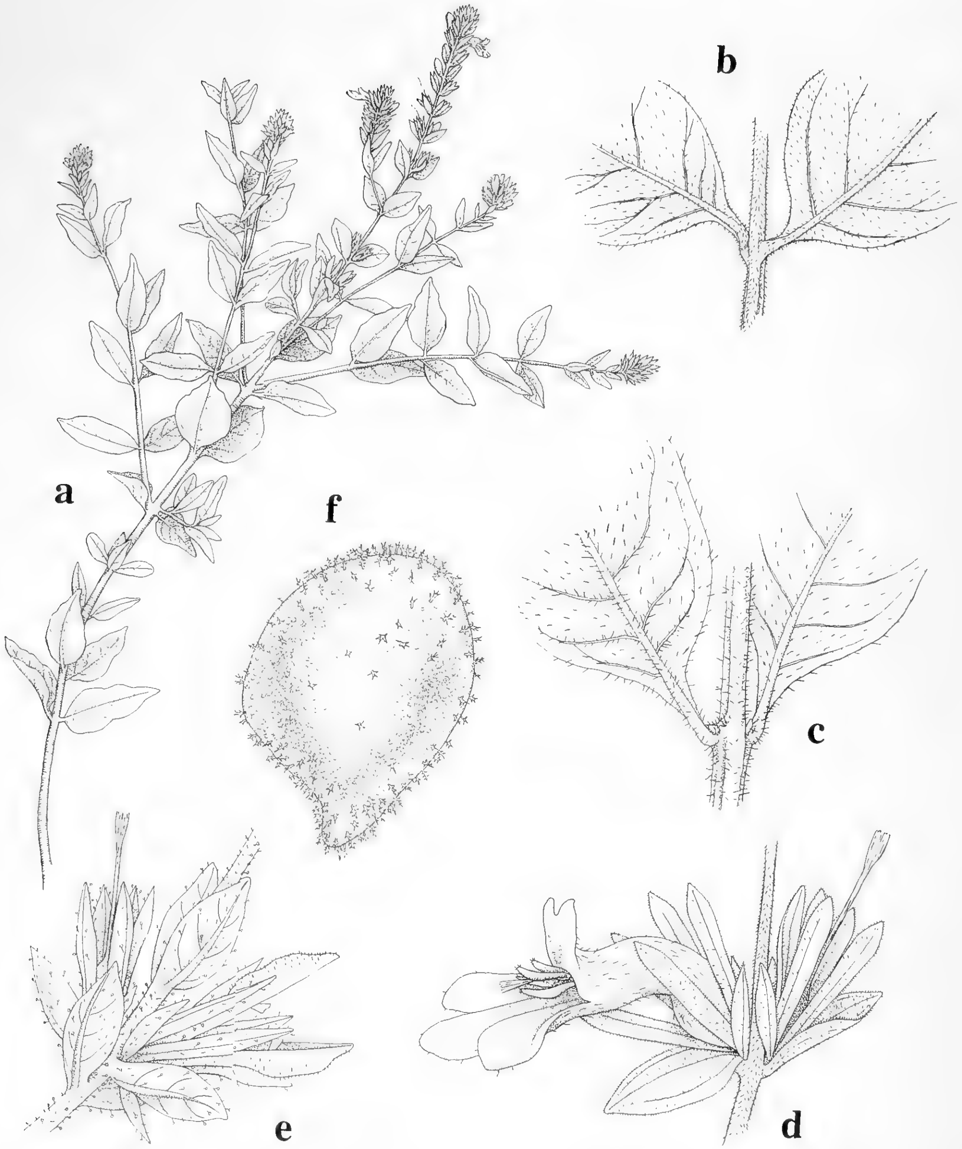


FIGURE 17. *Holographis virgata*. (a, b, e from subsp. *glandulifera* var. *glandulifera*, c from subsp. *glandulifera* var. *palmeri*, d, f from subsp. *virgata*). a. habit (*Gentry 7872*), × 0.5; b. vegetative node (*Carter 5420*), × 2.5; c. vegetative node (*Carter & Reese 4574*), × 2.5; d. inflorescence node with flower (*Moran 7956*), × 3.3; e. inflorescence node with capsule (*Johnston 3820*), × 2.5; f. seed (*Lott & Atkinson 2518*), × 11.5. Drawn by Jenny Speckels.

this zone of overlap. Daniel (1993b) provided additional information on this subspecies and intermediates with subsp. *glandulifera*.

1b. Holographis virgata subsp. **glandulifera** (Leonard & C.V. Morton) T. F. Daniel, J. Arnold Arbor. 64:143. 1983. *Berginia virgata* var. *glandulifera* Leonard & C.V. Morton, Contr. Dudley Herb. 4:24. 1950. TYPE. — MEXICO. **Baja California Sur**: 32 mi S of Mulegé, 15 Mar 1935, *F. Shreve 7101* (holotype: US!; isotypes: ARIZ!, DS!, F!, MICH!).

Trichomes of younger stems retrorse to flexuose to erect, 0.05–0.7 (–1) mm long. Leaves sessile to petiolate, petioles (if present) to 5 mm long, blades lance-ovate to oblanceolate to obovate, 6–50 mm long, 3–26 mm wide, 1.1–3.8 times longer than wide. Inflorescence rachises pubescent with glandular and eglandular trichomes 0.05–1 mm long. Bracts (2–) 2.5–5 mm wide, pubescent like rachis or proximal ones pubescent like leaves. Bracteoles 1–1.5 mm wide, pubescent like rachis or with glands more numerous. Calyx pubescent like bracteoles. Lower lip of corolla 4–7 mm long, lobes 2.5–5 mm long, 1.5–3 mm wide. Capsules pubescent. (*n* = 26, 39, Daniel et al. 1984).

DISTRIBUTION.— Endemic to southern Baja California and Baja California Sur (Figs. 18, 19); the subspecies occurs mostly to the south of lat. 28°N in the Cape Region, the Sierra de la Giganta, and the Sonoran Desert (Central Gulf Coast and Vizcaíno subdivisions).

1b′. Holographis virgata subsp. glandulifera var. glandulifera.

Trichomes of younger stems retrorse, 0.05–0.1 mm long. Leaves subsessile, petioles to 3 mm long, blades lance-ovate to oblanceolate, 6–50 mm long, 3–22 mm wide, 1.3–3.8 times longer than wide. Inflorescence rachises pubescent with glandular trichomes 0.1–0.3 mm long and erect to flexuose eglandular trichomes 0.05–0.3 mm long. Proximal bracts pubescent like leaves, distal bracts pubescent like rachis. (*n* = 26, 39, Daniel et al. 1984). Fig. 17a, b, e.

DISTRIBUTION AND HABITAT.— Southern Baja California and eastern and central Baja California Sur (Fig. 19); the variety is known from desert areas of the Cape Region, the Sierra de la Giganta, and the Sonoran Desert (Central Gulf Coast and Vizcaíno subdivisions); plants occur on rocky slopes and along watercourses in desertscrub and thornscrub at 15– 600 m elevation.

ADDITIONAL SPECIMENS EXAMINED.— MEXICO. **Baja California:** 20 mi W of Bahía San Francisquito, *Humphrey 6830a* (ARIZ); Calmallí, *C. Purpus 56* (UC pro parte). **Baja California Sur:** Arroyo San Bruno, SE of Santa Rosalía, 4.8 mi W of Hwy 1 toward San José de Magdalena, ca. 27°04′N, 112°12′W, *S. Boyd & T. Ross 5837* (RSA, UCR); N Sierra La Giganta, S of Mulegé, 11.2 mi W of Hwy 1 on rd from Rosarito to San Isidro, ca. 26°21′N, 111°45′W, *S. Boyd & T. Ross 5958* (CAS, RSA); Comondú, *T. Brandegee s.n.* (F, GH); Purísima to Comondú, *T. Brandegee s.n.* (UC); 12.4 km SE of La Paz on rd to Los Planes, *A. Carter 2625* (DS, MEXU, MICH, SD, UC, US); Sierra de la Giganta, ridge S of Tinaja de Naucajoa, Cerros de Naucajoa (W of Llanos de San Juan), ca. 26°15′N, 111°38′W, *A. Carter 4502* (UC); Sierra de la Giganta, between Rancho San Mártir and summit of grade, rd from Loreto to San Javier, ca. 25°56′N, 111°32′W, *A. Carter & F. Chisaki 1315* (UC); near Rancho Los Burros, E of Llanos de San Pedro, NE of Comondú, 26°05′N, 111°40′W, *A. Carter & R. Ferris 3430* (DS, MEXU, SD, UC); Arroyo Carrizal, E of Rancho El Horno (NE of San Xavier), ca. 25°53′N, 111°31′W, *A. Carter & R. Ferris 3829a* (CAS, UC); Isla Carmen, Puerto Balandra, ca. 26°05′N, 111°10′W, *A. Carter & J. Reese 4548* (UC); arroyo upstream (E) from Rancho Agua Escondido, ca. 25°06′N, 111°00′W, *A. Carter et al. 5724* (CAS, UC); 11.9-14.5 mi W of Hwy 1 in Rosarito, *T. Daniel 1929* (ASU, CAS), *1940* (ASU, CAS); along Hwy 286 between La Paz and San Juan de los Planes, near Paraje Los Chinos (8.3 km NW of La Huerta), ca. 24°06′N, 110°15′W, *T. Daniel & M. Butterwick 6833* (CAS); along Hwy 1 in S end of Sierra de la Giganta, 38.3 mi NW of jct Hwy 11 in La Paz, *T. Daniel et al. 2453* (ASU, CAS, MICH, NY); Puerto Escondido, *E. Dawson 1098* (F, MICH, RSA), *6399* (RSA); 1–2 mi inland from Agua Verde Bay, *E. Dawson 6259* (RSA), *6272* (RSA); Las Cuevitas, below Comondú, *H. Gentry 4235* (DES, DS, MICH, MO); between San Ignacio and Los Martiles, *H. Gentry 7872* (DS, RSA, UC); San Nicholas Bay, *I. Johnston 3729* (CAS); Carmen Island, Puerto Balandra, *I. Johnston 3820* (CAS, GH, NY, UC, US); Carmen Island, Balandra Bay, 26°00′N, 111°10′W, *R. Moran 3928* (DS, SD, UC, US); NE side of San Marcos Island, Arroyo de los Chivos, 27°15′N, 112°06′W, *R. Moran 8999* (SD); Danzante Island, 25°48′N, 111°15′W, *R. Moran 9249* (SD); Sierra de la Giganta, summit of Cerro Mechudo, ca. 24°48′N, 110°43′W, *R. Moran 18945* (SD, UC); island in Conception Bay, *P. Rempel 197* (ARIZ, RSA), *208* (ARIZ, RSA); 14 mi S of Mulegé, *F. Shreve 7086* (ARIZ, F, GH, LA, MICH, MO); Isla del Carmen, Puerto Balandra, ca. 26°01′N, 111°11′W, *M. Sousa P. 142* (RSA); 13 mi S of Mulegé, *J. Whitehead 745* (DS); ca. 2 mi S of Punta Escondido along Hwy 1, *D. Zippin 49* (SD).

1b″. Holographis virgata subsp. **glandulifera** var. **palmeri** (Rose) T. F. Daniel, J. Arnold Arbor. 64:144. 1983. *Berginia palmeri* Rose, Contr. U. S. Natl. Herb. 1:86. 1890. TYPE.— MEXICO. **Baja California Sur:** Santa Rosalía, 15 Mar 1890, *E. Palmer 272* (holotype: US!;

isotypes: A!, C!, DS!, F!, G!, GH!, MEXU!, NY!).

Trichomes of the younger stems erect to flexuose, 0.1–0.7 (–1) mm long. Leaves sessile to petiolate, petioles to 5 mm long, blades lance-ovate to obovate, (6–) 11–46 mm long, (4–) 7–26 mm wide, 1.1–3.3 times longer than wide. Inflorescence rachises pubescent with glandular trichomes 0.2–1 mm long and erect to subflexuose eglandular trichomes 0.2–0.5 mm long. Bracts pubescent like rachis. (Chromosome number unknown.) Fig. 17c.

DISTRIBUTION AND HABITAT. — Endemic to eastern Baja California Sur (Fig. 18); the species occurs in nondesert portions of the Cape Region, the Sierra de la Giganta, and the Sonoran Desert (Central Gulf Coast subdivision); plants occur on rocky slopes and along watercourses in desertscrub and thornscrub primarily at elevations above 600 m (i.e., 550–1100 m except in the Cape Region where known from ca. 30 m, see Daniel 1983b).

LOCAL NAME. — "Rama blanca" (*Peters 206*).

ADDITIONAL SPECIMENS EXAMINED. — MEXICO. **Baja California Sur:** Sierra de Laguna, *T. Brandegee 443* (UC); Sierra de la Giganta, La Esperanza, ca. 25°48′N, 111°24′W, *A. Carter 4403* (UC); Sierra de la Giganta, vic. of Portezuelo W of summit of Cerro Gabilán, ca. 25°50′N, 111°25′W, *A. Carter 5106* (UC); Sierra de la Giganta, Mesa de San Gerónimo, N from Rancho Viejo, (on rd from Loreto to San Javier), ca. 25°58′–26°N, 111°32–34′W, *A. Carter 5131* (CAS, GH, MICH, SD, UC, US); Aguaje de San Antonio, Arroyo el Coyote (SE of La Soledad, N of Cerro Mechudo), ca. 24°49′N, 110°46′W, *A. Carter 5420* (CAS, UC); Sierra de la Giganta, Arroyo Carrizal, E of Rancho El Horno(NE of San Xavier), ca. 25°53′N, 111°31′W, *A. Carter & R. Ferris 3819* (CAS, MEXU, UC, US); S side of Valle de los Encinos, S side of Cerro Giganta, ca. 26°03′N, 111°34′W, *A. Carter & R. Ferris 4001* (CAS, UC); Sierra de la Giganta, S of La Puerta, W end of Valle de los Encinos, S side of Cerro Giganta, ca. 26°04′N, 111°36′W, *A. Carter & J. Reese 4574* (CAS, MEXU, UC, US); Sierra de la Giganta, N slope of Pilón de las Parras, W of Loreto, ca. 25°58′N, 111°30′W, *A. Carter & H. Sharsmith 4215* (CAS, F, MO, NY, UC, US); 5 mi S of San Bartolo, *M. Gallagher 139* (ASU); Sierra Giganta above Pto. Escondido, *H. Gentry 3762* (A, ARIZ, DES, MICH, MO, UC); 21.2 mi NE of summit of Volcán Tres Vírgenes, 27°30′N, 112°33′W, *J. Henrickson 9010* (SD); N base of Volcán las Tres Vírgenes, 27°29′N, 112°36′W, *R. Moran 20459* (POM, SD); La Ciénega Arroyo, Distr. Buena Vista, *R. Peters 206* (UC); 8 mi E of pass of Tres Vírgenes Peak, *F. Shreve 7051a* (ARIZ); El Purgatorio grade W of Santa Rosalía, along rd to San Ignacio, *I. Wiggins & D. Wiggins 18206* (CAS, DS, MEXU).

Daniel (1983b) further discussed the distribution of and morphological variation in this variety.

JUSTICIA

Justicia L., Sp. pl. 1:15. 1753, nom. cons. prop. LECTOTYPE (Hitchcock and Green, International Botanical Congress, Cambridge (England), 1930: Nomenclature Proposals by British Botanists. 116. 1929). — *Justicia hyssopifolia* L.

Dianthera L., Sp. pl. 1:27. 1753. TYPE. — *Dianthera americana* L. (≡ *Justicia americana* (L.) Vahl).

Beloperone Nees in Wall., Pl. asiat. rar. 3:76. 1832. LECTOTYPE (Kew Bull. 43:609. 1988). — *Beloperone amherstiae* Nees (≡ *Justicia brasiliana* Roth).

Sericographis Nees in Mart., Fl. bras. 9:107. 1847. LECTOTYPE (Contr. U. S. Natl. Herb. 31:650. 1958). — *Sericographis rigida* Nees (≡ *Justicia sericographis* V. A. W. Graham).

Jacobinia Nees in Moric., Pl. nouv. Amér. 156. 1847. TYPE. — *Jacobinia lepida* Nees (≡ *Justicia lepida* (Nees) Wassh.).

Siphonoglossa Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1854:159. 1855.

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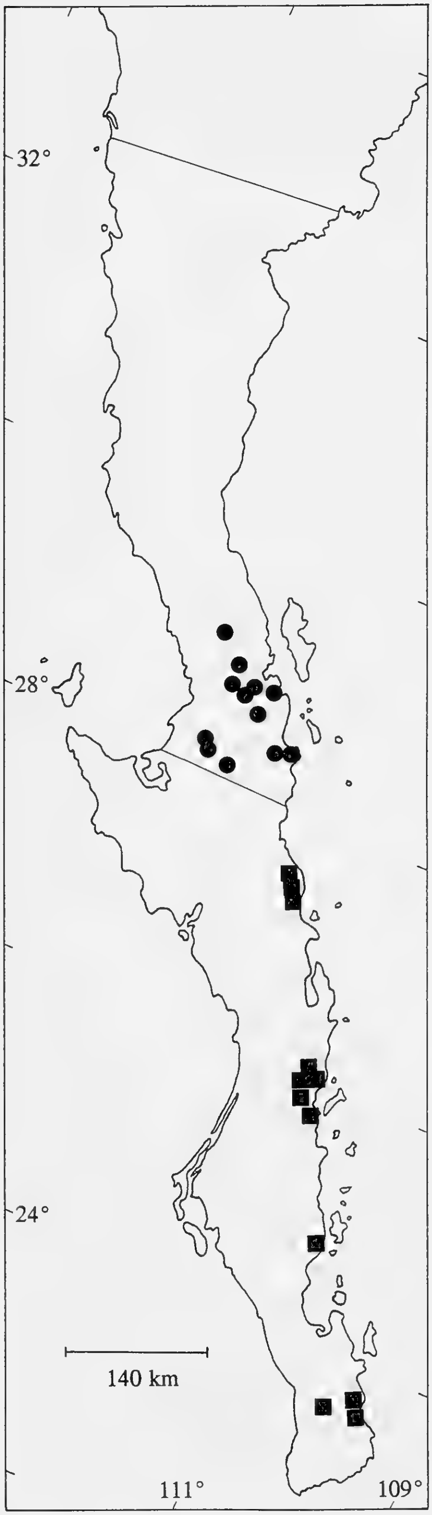
FIGURE 18. Distribution of *Holographis virgata* subsp. *virgata* (circles) in the peninsula of Baja California and *H. virgata* subsp. *glandulifera* var. *palmeri* (squares).



TYPE. — *Siphonoglossa ramosa* Oerst. (≡ *Justicia ramosa* (Oerst.) V. A. W. Graham).

Decumbent to erect perennial herbs, shrubs, or small trees with cystoliths. Leaves opposite, sessile to petiolate, margin entire to sinuate to crenate. Inflorescence of dichasia in leaf axils (or in axil of 2 partially fused bracts forming a cupulate involucre) or of axillary or terminal dichasiate spikes, racemes, thyrses, or panicles; dichasia alternate or opposite, 1 (–3)-flowered, subtended by a leaf or a bract, sessile or pedunculate. Bracts homomorphic (in ours) or heteromorphic, alternate or opposite, green or brightly colored, prominent or inconspicuous, margin entire (in ours). Flowers homostylous, subtended by 2 homomorphic bracteoles, sessile or pedicellate. Calyx deeply 4–5-lobed, lobes equal or unequal in size, posterior lobe sometimes greatly reduced in flowers with 5 calyx lobes. Corolla greenish, white, yellow, orange, pinkish, red, or purplish, usually with white or colored markings (often restricted to lower lip), tube cylindric to expanded distally, usually lacking a distinct throat, limb strongly zygomorphic, bilabiate, upper lip internally rugulate (i.e., with a stylar furrow), entire to 2-lobed, lower lip 3-lobed, corolla lobes imbricate in bud. Stamens 2, inserted at various positions within corolla tube, exserted from mouth of corolla, anthers 2-thecous (1 theca rarely sterile), thecae equal or unequal in length, equally inserted, unequally inserted (but overlapping for some portion of their length), or superposed (i.e., not overlapping), parallel to perpendicular, 1 or both with a basal appendage or appendages absent, dehiscing toward lower lip (i.e., flower nototribal); pollen subprolate to perprolate, 2–4-aperturate (varying from porate to colporate with distinctness of colpi sometimes questionable), apertures flanked on each side by 1-several rows of ± circular insulae and/or peninsulae (in ours) or by both a solid band of exine and a pseudocolpus, exine usually reticulate; staminodes 0 (although pubescent thickenings near attachment of filaments rarely present). Style exserted from mouth of corolla, stigma lobes indistinct to distinct, when distinct equal to unequal in length (1 lobe sometimes vestigial). Capsule stipitate, retinacula present, septa with attached retinacula remaining attached to inner wall of mature capsule. Seeds 2–4, homomorphic, lenticular to globose. ($x = 11, 14$).

Justicia is the largest genus of Acanthaceae with estimates of up to 600 species worldwide. It is also the largest genus of the family in Mexico with about 80 species there. About 14 species of *Justicia* are native to the United States. Morphological diversity in the genus is extensive and the above generic description is derived from North and Central American species only. The synonymy given above only includes genera in which species from our region have been previously treated. Daniel (1995) provided a more complete listing of generic synonyms in which American species have been treated. Graham (1988) presented a comprehensive generic account of *Justicia* that includes generic synonyms on a world-wide basis.

REFERENCE. — GRAHAM, V. A. W. 1988. Delimitation and infra-generic classification of *Justicia* (Acanthaceae). Kew Bull. 43:551–624.

Key to Species of *Justicia*

1. Calyx 4-lobed; corolla pinkish, 15–27 mm long, tube subsaccate or cylindric.
    2. Inflorescence of 1-flowered dichasia in leaf axils; pubescence of bracteoles, calyx, and capsules comprising eglandular trichomes only; corolla 22–27 mm long, tube cylindric, 1.3–1.4 mm in diameter near midpoint; thecae lacking basal appendages; seeds lacking trichomes .... *J. austrocapensis*
    2. Inflorescence of dichasiate spikes or panicles of spikes, dichasia 1-flowered and borne in axils of bracts; pubescence of bracteoles, calyx, and capsules including glandular trichomes; corolla 15–22 mm long, tube subsaccate on anterior side, 4.5–6 mm in diameter near midpoint; lower theca of a pair with a prominent basal appendage; seeds covered with retrorsely barbed trichomes ... *J. insolita*
1. Calyx 5-lobed; corolla orange to red (rarely yellow), (21–) 27–55 mm long, tube expanded distally (i.e., funnelform).
    3. Inflorescence of dichasiate thyrses; dichasia 1-flowered, usually opposite at inflorescence nodes, pedunculate, peduncles (1–) 1.5–21 mm long; thecae dorsally pubescent; capsules 15–24 mm long; seeds subglobose to subcompressed, 1.8–2.4 mm thick.
        4. Bracts caducous, ovate to lance-elliptic to elliptic to obovate, 2.5–10 mm long, 1–4 mm wide; calyx 3–13 mm long; southwestern United States and northwestern Mexico .... *J. californica*
        4. Bracts persistent, cordate to broadly ovate, 10–43 mm long, 8.5–33 mm wide; calyx 9–23 mm long; Cape Region of Baja California Sur only............................ *J. purpusii*
    3. Inflorescence of dichasiate spikes or panicles of spikes or of dichasia in leaf axils; dichasia 1-flowered, alternate at inflorescence nodes, sessile to subsessile (i.e., peduncles to 1.5 mm long); thecae dorsally glabrous; capsules 11–17 mm long; seeds compressed, 0.8–1.3 mm thick.
        5. Stems multi-grooved (i.e., grooves > 8), pubescence of young stems resulting in a pallid aspect, the epidermis not (or only barely) visible; bracteoles petiolate, spatulate to oblanceolate to obovate to elliptic, 1–4.5 mm wide; lower theca of a pair with a conspicuous basal appendage to 0.3 mm long .... *J. palmeri*
        5. Stems with 4–8 grooves (if grooves evident at all), pubescence of young stems not resulting in a pallid aspect, the epidermis usually clearly visible; bracteoles sessile, triangular to subulate to lanceolate to linear to ovate, 0.6–1 mm wide; thecae lacking basal appendages or with inconspicuous appendages to 0.1 mm long.
            6. Bracteoles 8–10 mm long; pubescence of external surface of corolla comprising eglandular trichomes

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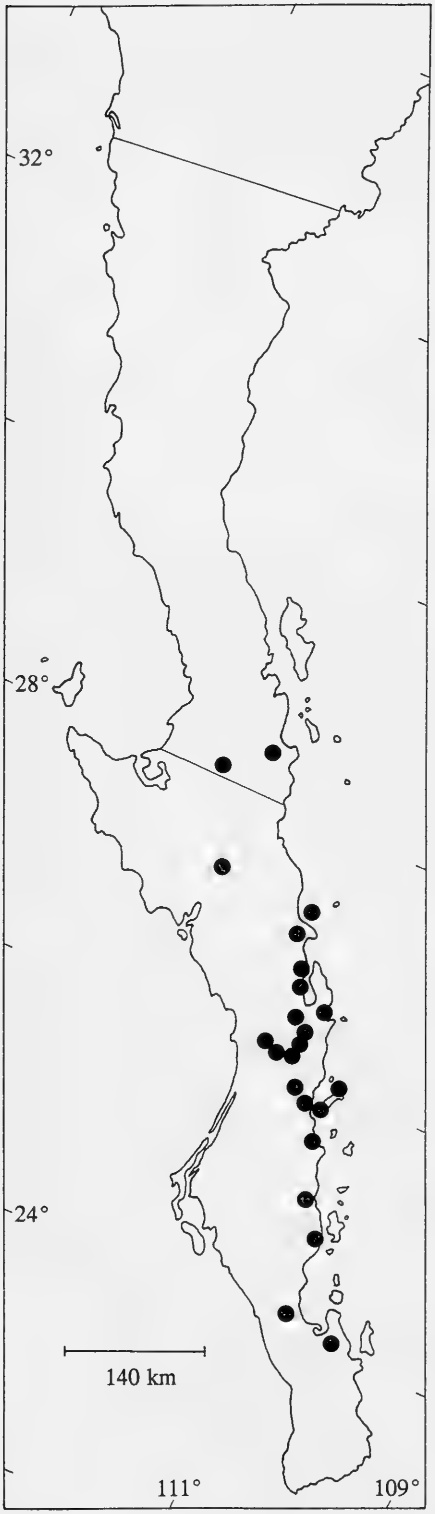
FIGURE 19. Distribution of *Holographis virgata* subsp. *glandulifera* var. *glandulifera*.



only; seeds reddish, surfaces smooth to irregularly bumpy . . . *J. candicans*

6. Bracteoles 2–3.6 mm long; external surface of corolla pubescent with eglandular and glandular trichomes or external surface glabrous distally and inconspicuously pubescent proximally with glandular trichomes only; seeds dark brown, surfaces bubbly tuberculate to papillate with subconic papillae.
   7. Young stems suboctagonal, pubescent with trichomes 0.05–0.1 (–0.2) mm long; pubescence of inflorescence rachis including glandular trichomes; bracts 2.2–2.8 mm long, pubescence of the abaxial surface comprising glandular and eglandular trichomes; corolla 25–31 mm long, externally pubescent with glandular and eglandular trichomes, the lower lip spreading with lobes 5–7.5 mm long; capsule pubescent with glandular and eglandular trichomes; seeds bubbly tuberculate; native . . . . *J. hians*
   7. Young stems subterete to quadrate, pubescent with trichomes 0.5–1.2 mm long; pubescence of inflorescence rachis comprising eglandular trichomes only; bracts 1–2 mm long, abaxial surface glabrous; corolla 33–55 mm long, externally glabrous distally and pubescent with inconspicuous glands only proximally, lower lip recoiled with lobes 0.8–2.5 mm long; capsule glabrous; seeds covered with subconic papillae; introduced . . . . *J. spicigera*

1. Justicia austrocapensis T. F. Daniel, nom. nov. *Dianthera incerta* Brandegee, Proc. Calif. Acad. Sci., ser. 2, 3:226. 1892, non *Justicia incerta* C.B. Clarke (1912). *Siphonoglossa incerta* (Brandegee) Hilsenb., Brittonia 31:378. 1979. TYPE. — MEXICO. **Baja California Sur**: San Bartolomé [San Bartolo], 24 Oct 1890, *T. Brandegee 456* (lectotype, designated here: UC!; isolectotype: UC!).

Erect to ascending perennial herbs to 1 m tall. Young stems quadrate to quadrate-sulcate, pubescent with flexuose to retrorse eglandular trichomes 0.3–1 mm long, trichomes either ± evenly disposed or concentrated in and soon restricted to 2 lines, epidermis visible. Leaves subsessile to petiolate, petioles to 6 mm long (petiolar stubs to 2 mm long remaining at nodes after leaves have fallen), blades lance-ovate to ovate to broadly ovate, (9–) 16–55 mm long, 3.5–44 mm wide, 1.1–2.3 (–4) times longer than wide, (rounded to) acute to acuminate at apex, acute to truncate to cordate at base, surfaces pubescent with flexuose to antrorse eglandular trichomes and sometimes ± glandular punctate as well, margin entire to subsinuate. Inflorescence of dichasia in leaf axils (or distal leaves sometimes reduced and bractlike); dichasia alternate to opposite, 1-flowered, 1 (–3) per axil, sessile to subsessile (i.e., peduncles to 1 mm long). Bracteoles sessile, lance-subulate, 2.2–5.5 mm long, 0.6–0.9 mm wide, abaxial surface pubescent with cauline type trichomes. Flowers sessile. Calyx 4-lobed, 3–7 mm long, lobes lance-subulate, 2.5–5.5 mm long, subequal in length, 0.6–0.7 mm wide, abaxially pubescent like bracteoles. Corolla rose-pink with a white and darker rose-pink crow's-foot pattern on lower lip (just distal to mouth of corolla), (18–) 21–30 mm long, externally pubescent with erect to flexuose eglandular and glandular trichomes 0.1–0.4 mm long, tube cylindric (i.e., not expanded distally), (11–) 14–17 mm long, (1–) 1.3–1.4 mm in diameter near midpoint, upper lip usually ± recurved, 5–10.5 mm long, entire at apex, lower lip spreading, 5–14 mm long, lobes 4–9 mm long, 2.3–5.5 mm wide. Stamens inserted near apex of corolla tube, 4–5 mm long, filaments glabrous, thecae 1–1.7 mm long, subequal to ± unequal, subparallel to subperpendicular, unequally inserted (overlapping by 0.7–1.3 mm), dorsally glabrous, lacking basal appendages; pollen (Fig. 20a, b) 2-aperturate, apertures flanked on each side by 2 rows of insulae (to peninsulae), exine reticulate. Style 14–18 mm long, proximally pubescent with eglandular trichomes, stigma lobes 0.3–0.6 mm long, unequal or indistinct from one another. Capsule 9–13.5 mm long, pubescent with flexuose to retrorse eglandular trichomes 0.2–0.3 mm long, stipe 2.5–4.5 mm long, head subellipsoid, 6–9 mm long. Seeds 4, white (immature) to brown (mature), compressed, 2–3 mm long, 1.8–2.6 mm wide, 0.8–1.1 mm thick, surfaces and margin bubbly tuberculate. ($n = 11$, Hilsenbeck 1983a).

PHENOLOGY. — Flowering and fruiting: September–December and April–May.

DISTRIBUTION AND HABITAT. — Endemic to nondesert portions of the southern Cape Region of Baja California Sur (Fig. 21); plants occur on slopes and along watercourses in tropical deciduous forest, oak woodland, and pine-oak woodland at 460–1230 m elevation.

ADDITIONAL SPECIMENS EXAMINED. — MEXICO. **Baja California Sur:** Saucito, *T. Brandegee s.n.* (GH); San José del Cabo, *T. Brandegee s.n.* (GH); Cape Region, *T. Brandegee s.n.* (UC); El Taste, *T. Brandegee s.n.* (POM, UC); Cape Region, Rancho San Bernardo, E side of Sierra de la Victoria, ca. 23°25′N, 109°57′W, *A. Carter 2681* (UC); Sierra El Taste, N of portezuelo between Rancho El Venado and El Encinal, 23°10′N, 109°56′W, *A. Carter & F. Chisaki 3585* (CAS, UC); E side of Sierra de la Victoria, near "Tapon" (jct with La Chuparosa trail), Arroyo de San Francisquito, 23°29–31′N, 109°47–55′W, *A. Carter & R. Ferris 3372* (DS, SD, UC); along rd from Hwy 1 across Cape Region mts to Hwy 19, 16-20 km W of Hwy 1, ca. 23°14′N, 109°55′W, *T. Daniel & M. Butterwick 6926* (BR, CAS, ENCB, MO, SBBG, US); 6929 (CAS, HCIB, MEXU, MICH); Rancho La Burrera, W slope of Sierra de la Laguna, ca. 22 km NE of Todos Santos, ca. 23°31′N, 110°02′W, *T. Daniel et al. 6862* (CAS); Ojo de Agua, Cañón de La Burrera, 23°30′N, 110°02′W, *M. Dominguez L. 362* (HCIB); San Bartolo, *F. Gander 9676* (CAS); Sierra de la Laguna, Las Animas, ranch at river-fork near base of El Picacho Peak, *B. Hammerly 279* (CAS); El Jacinto, Cañón de La Burrera, 23°02′N, 109°57′W, *J. León de la Luz 4926* (HCIB); Cape Region, potrero de Almenta near head of S fork of Cañón San Pedro, ca 23°19′N, 109°56′W, *R. Moran 7373* (CAS, DS, SD).

Brandegee (1892) did not designate a type or cite a particular specimen in his protologue of *Dianthera incerta*. He merely stated, "San Bartolomé and slopes of the mountains above Agua Caliente." According to information provided by Brandegee (1891, 1892), material on which his species was based was collected in 1890 at "San Bartolomé." Indeed, the collection from San Bartolo noted above is the only one of this species in the Brandegee herbarium at UC that was collected in 1890. Other collections of *J. austrocapensis* in Brandegee's herbarium (i.e., from "El Taste" and the "Cape Region") and Brandegee

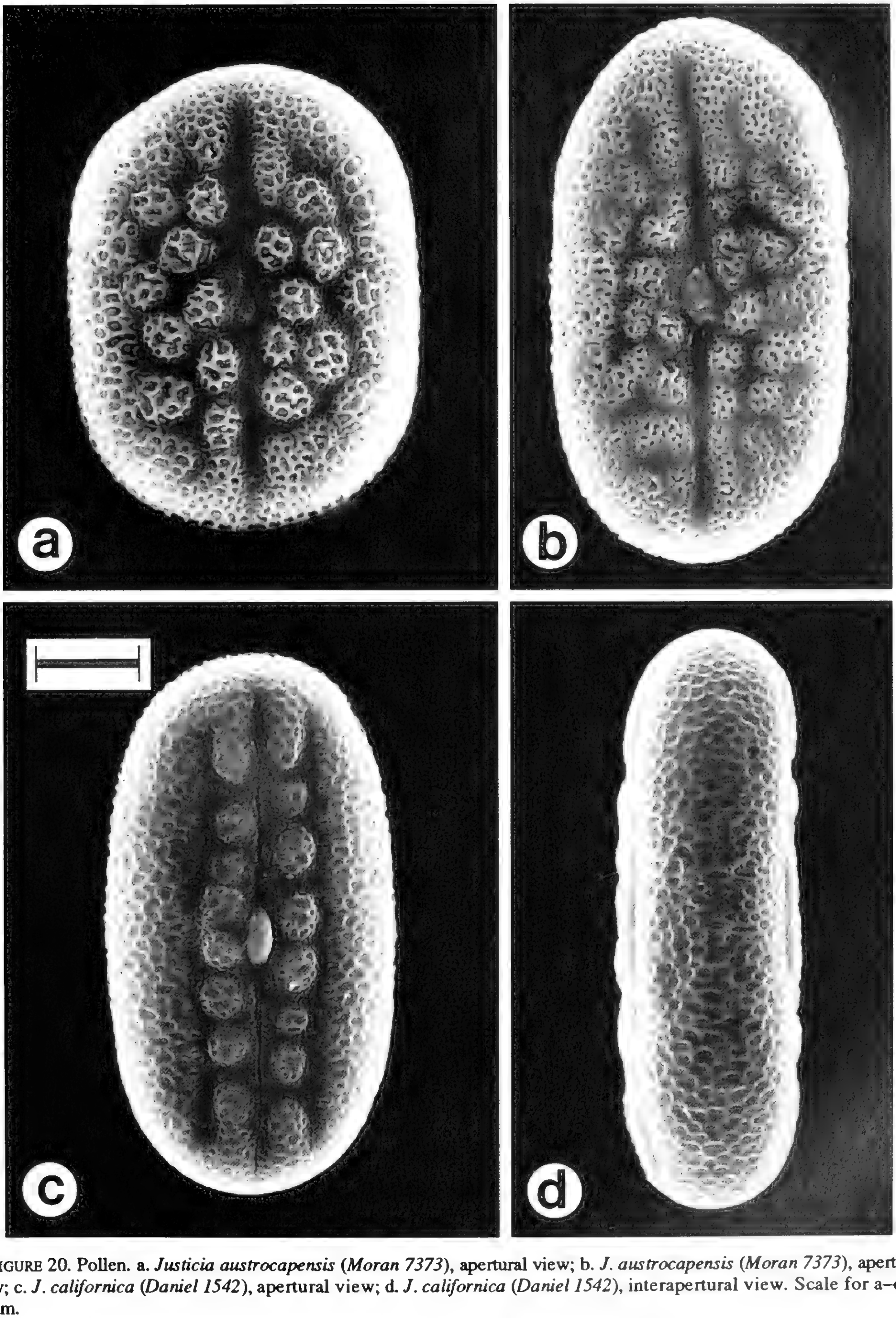


FIGURE 20. Pollen. a. *Justicia austrocapensis* (*Moran 7373*), apertural view; b. *J. austrocapensis* (*Moran 7373*), apertural view; c. *J. californica* (*Daniel 1542*), apertural view; d. *J. californica* (*Daniel 1542*), interapertural view. Scale for a–d = 10 µm.

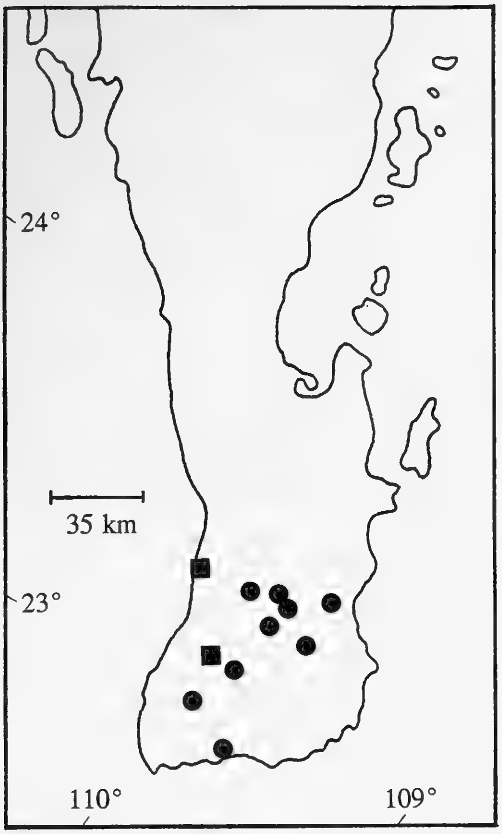


FIGURE 21. Distribution of *Justicia austrocapensis* (circles) and of *Ruellia inundata* (squares) in the peninsula of Baja California.

collections in other herbaria (e.g., from "Saucito" and "San José del Cabo," both at GH) were collected in subsequent years. There are two specimens of *Brandegee 456* in the Brandegee Herbarium. One of these was annotated by Hilsenbeck as the lectotype of *D. incerta* and the other as an isolectotype, but these designations were not published. The specimen designated as an isolectotype by Hilsenbeck contains the annotation "Dianthera incerta" in Brandegee's handwriting whereas the specimen designated by Hilsenbeck as the lectotype does not. Both specimens contain flowers and fruit and agree with the protologue. I chose to follow Recommendation 9A.3 of the International Code of Botanical Nomenclature (Greuter et al. 1994) and designate the specimen annotated by Brandegee as the lectotype. This specimen is mounted on a sheet with another of Brandegee's collections of *J. austrocapensis* (i.e., "El Taste" collected on 12 Sep 1893).

This species has been variously reported from the peninsula of Baja California as *Dianthera sp.* (Brandegee 1891), *Dianthera incerta* (Brandegee 1892), *Siphonoglossa ramosa* Oerst. (Johnson 1958), *S. longiflora* (Torr.) A. Gray (Wiggins 1980), and *S. incerta* (Brandegee) Hilsenb. (Henrickson and Hilsenbeck 1979, Hilsenbeck 1990). *Siphonoglossa* was included in *Justicia* by Graham (1988). Daniel (1995) agreed with this inclusion and discussed the putative distinctions between the genera.

The closest relative of *J. austrocapensis* is undoubtedly to be found among those species of *Justicia* sometimes treated as comprising *Siphonoglossa*. Hilsenbeck (1983b) indicated that it was most similar to *J. sessilis* Jacq. (as *S. sessilis* (Jacq.) D. N. Gibson), a species occurring in the West Indies and northern South America.

2. Justicia californica (Benth.) D.N. Gibson, Fieldiana, Bot. 34:67. 1972. *Beloperone californica* Benth., Bot. voy. *Sulphur*, 38. 1844. *Jacobinia californica* (Benth.) Nees in A. DC., Prodr. 11:729. 1847. *Sericographis californica* (Benth.) A. Gray in Torr. in Emory, Rep. U. S. Mex. bound. 2(1):125. 1858. TYPE. — MEXICO. **Baja California Sur**: Cape St. Lucas, *R. Hinds s.n.*, 1841 (holotype: K!).

Shrubs to 3 m tall, sometimes clambering through other growth. Young stems multigrooved and terete to quadrate, densely and evenly pubescent with erect to antrorse to retrorse to appressed eglandular trichomes 0.05–0.2 mm long, these giving the stems a pallid aspect, sometimes with an overstory of flexuose glandular trichomes (or rarely erect eglandular trichomes only) to 1 mm long as well, epidermis not visible. Leaves (plants often leafless at anthesis) petiolate, petioles to 20 mm long (petiolar stubs to 2 mm long remaining at nodes after leaves have fallen), blades (elliptic to) ovate to deltate to subcircular to cordate, 7–70 mm long, 4–48 mm wide, 1–2.9 times longer than wide, rounded to acute at apex, cordate to truncate to acute at base, surfaces pubescent with erect to flexuose eglandular trichomes to 0.6 mm long, margin entire to subsinuate. Inflorescence of (axillary and) terminal dichasiate thyrses to 135 (–180) mm long, these often terminating axillary branches and collectively appearing as or forming an open terminal panicle of thyrses, rachises pubescent like young stems or with an understory of erect eglandular trichomes to 0.2 mm long and an overstory (sometimes absent) of flexuose mostly glandular trichomes to 1 (–2.5) mm long; dichasia (alternate to) opposite, 1-flowered, 1 (–2) per axil, pedunculate in axils of distal leaves or bracts, peduncles (1–) 1.5–14 mm long, pubescent like rachis. Bracts caducous, (alternate to) opposite, sessile to subsessile, ovate to lance-elliptic to elliptic to obovate, 2.5–10 mm long, 1–4 mm wide, abaxial surface pubescent like rachis, bracts at proximalmost 1–2 nodes often petiolate and larger. Bracteoles sessile, subulate to linear, 1.5–6 mm long, 0.5–1 mm wide, abaxial surface pubescent like rachis. Flowers sessile to pedicellate, pedicels to 3 mm long. Calyx 5-lobed, 3–13 mm long, lobes linear-elliptic to lanceolate to lance-subulate, 2.5–11.5 mm long, equal to subequal in length, 0.8–1.8 mm wide, abaxially pubescent like rachis. Corolla dark red or orange-red with yellowish coloration proximally on internal surface of lips (rarely corolla entirely yellow), 21–41 mm long, externally pubescent with erect to flexuose eglandular (and occasionally a few glandular) trichomes 0.1–0.5 mm long, tube expanded distally, 11–20 mm long, 2.5–4 mm in diameter near midpoint, upper lip 9–21 mm long, 2-lobed at apex, lobes 0.1–0.4 mm long, lower lip spreading, 9–20 mm long, lobes 1–5.5 mm long, 1–3 mm wide. Stamens inserted near apex of corolla tube, 15–19 mm long, filaments pubescent with eglandular trichomes, thecae 2–3.3 mm long (including basal appendage), equal to subequal, subparallel to subsagittate to subperpendicular, unequally inserted (overlapping by 0.9–2 mm), dorsally pubescent with eglandular trichomes (upper theca densely so, lower theca sparsely so to nearly glabrous), lower (and sometimes upper) theca with a ± bulbous basal appendage to 0.6 mm long; pollen (Fig. 20c, d) 2-aperturate, apertures flanked on each side by 1 row of insulae, exine reticulate. Style 24–37 mm long, proximally pubescent with eglandular trichomes, stigma 2-lobed, lobes 0.1–0.2 mm long, equal to unequal. Capsule (13–) 15–24 mm long, pubescent with an understory of erect to flexuose eglandular (and sometimes glandular) trichomes 0.2–0.4 mm long and an overstory (sometimes absent) of flexuose glandular trichomes to 2.5 mm long, stipe (6–) 8–12 mm long, head broadly subellipsoid to obovoid with a medial constriction and a vertical constriction outlining seeds, 6–12 mm long. Seeds 4, brown (often mottled with darker brown), subglobose to subcompressed, 2.5–3.5 mm long, 3–4.5 mm wide, 1.8–2.3 mm thick, smooth and lacking trichomes. (*n* = 14, Grant 1955, Daniel et al. 1984).

PHENOLOGY. — Flowering and fruiting: throughout the year.

DISTRIBUTION AND HABITAT. — Southwestern United States (Arizona and California) and northwestern Mexico (Baja California, Baja California Sur, Sinaloa, and Sonora); the species is known from virtually all portions of our region (Fig. 22), but is very rare in the California Floristic Province (see above); plants occur mostly in or along rocky or sandy watercourses and on slopes in desertscrub and thornscrub from near sea level to 920 m elevation. The species is often cultivated for ornament in gardens of southern California. Collections of cultivated plants are not listed among the specimens cited below.

LOCAL NAME. — "Chuparosa" (numerous herbarium labels); "candalilla" (*Wiggins 4397*); "rama blanca" (*Peters 117*).

ADDITIONAL SPECIMENS EXAMINED. — UNITED STATES: **California**: Imperial Co: 17–20 mi S of Palo Verde, *R. Alava et al. 1822* (JEPS, UC); Coyote Wells, *N. Cooper 3078* (RSA); 4.6 mi NE jct. U. S. 80 on county rd S2, *T. Crovello 275* (UC); 2.5 mi E of Mt Springs on the El Centro Rd, *R. Ferris 7087* (DS, POM); In-Ko-Pah Gorge, *F. Gander 4657* (SD); Myers Creek bridge, foot of Mt Springs grade, *W. Jepson 11783* (JEPS); base of Mt Springs Grade, 3 mi E of San Diego Co. line, *D. Keck 3908* (DS); Coyote Wells, *E. McGregor 827* (DS); Shiphands Bridge W of Coyote Wells, *E. McGregor 1053* (DS); foot of Mt Springs Grade, *P. Munz 7815a* (POM); SE end of Chocolate Mts, Paymaster Mine, *A. Sanders 9519* (RSA), *9519.1* (UCR); 17 mi S of Palo Verde, *Sears 1171* (UCR); jct of State Hwys. 80 and 98, *I. Wiggins 14073* (DS); Pinto Wash, 32°38′N, 116°00′W, *H. Witham 686* (SD); 5 mi W of Coyote Wells on rd to Mt Springs, *C. Wolf 1889* (DS, RSA), *2279* (CAS, DS, RSA). Riverside Co: Palm Springs to Palm Canyon, *L. Abrams 11063* (DS); ca. 1 mi from JT Mon Rd and pipeline jct, *N. Aitkenhead 2105* (CAS); Indio, *J. Augsburg s.n.* (CAS); Box Canyon, Mecca, Coachella Valley, *M. Beal 862* (JEPS); San Jacinto Mts, beginning of Hemet

Rd, *L. Benson 4183* (RSA); 2 mi W of Shaver Summit E of Indio on Hwy 66, *L. Benson & R. Benson 14857* (POM); Tahquitz Canyon, *E. Blondin s.n.* (CAS); Cat Creek, 3 mi SW of Palm Desert, *D. Breedlove 1879* (DS); 2.2 mi N of entrance from Hwy 10 to Joshua Tree Natl. Monument, *S. Carlquist 15672* (RSA); Deep Canyon, *M. Clary 9a* (JEPS); 2 mi W of Coral Reef Ranch, Coachella Valley, *M. Clary 1732* (JEPS); Carrizo Canyon, 18 mi W of Indio, *M. Clary s.n.* (JEPS); Mecca, *J. Clemens s.n.* (CAS); Cottonwood Spring Wash, *J. Cole 455* (UC); near Palm Springs, *H. DeForest s.n.* (SD); Orocopia Mts, Box Canyon, *R. Dressler 413* (RSA); S of Palm Desert, *D. Dreyer s.n.* (CAS); Tahquitz Canyon, *W.R. Dudley s.n.* (DS); Palm Springs, *A. Eastwood 3025* (CAS), *3025a* (CAS); Cottonwood Springs, *B. Evermann s.n.* (CAS); 5 mi E of Desert Center, *J. Ewan 4145* (UC); 1 mi below Cottonwood Springs, *R. Ferris & R. Rossbach* 9557 (DS); Palm Springs, *G. Grant 101* (UC); Joshua Tree Natl. Monument, ca. 4 mi from jct of rd leading through park and Hwy 70, *R. Gustafson 839* (RSA); 7 mi W of Coachella, *H. Hall 5776* (DS); Mecca Canyon, *G. Hanna & M. Hanna s.n.* (CAS); 3 mi below Cottonwood Springs, *C. Hitchcock 5965* (DS, RSA, UC); Dead Indian Canyon, *R.F. Hoover 10163* (CAS, UC); 2 mi E of Shaver's Well, *J. Howell 3306* (CAS, JEPS); Mecca, Box Canyon, *J. Janish 1026* (DS); Painted Canyon, Mecca Hills, *W. Jepson 11674* (JEPS); near Palm Springs, *I. Johnston 1079* (DS, UC); Shaver's Well, *M. Jones s.n.* (DS); W of Blythe, *M. Jones s.n.* (CAS); Indio, *M. Jones s.n.* (POM); Palm Springs, *H. Mason 4251* (UC); Palm Canyon, *H. Mason 14212* (SD, UC); 6 mi up Painted Canyon, *E. McGregor 731* (DS, POM); Santa Rosa Mts, Deep Canyon along Coyote Wash, *D. Michener 3451b* (RSA); Eagle Mts, Cottonwood Pass, *R. Moran 855* (CAS, DS, RSA); Deep Canyon, Coachella Valley, *P. Munz 11971* (POM, UC); Eagle Mts, 3 mi S of Cottonwood Springs, *P. Munz 15692* (CAS, DS, POM, UC); vicinity of Corn Springs, Chuckwalla Mts, *P. Munz & D. Keck 4902* (POM, UC); Palm Canyon, *P. Munz et al. 2383* (DS); Palm Springs, *A. Nelson & R. Nelson 3219* (DS, UC); Palm Springs, *S. Parish 4136* (JEPS), *19193* (UC); Cottonwood Springs, *S. Parish 10840* (DS); Palms to Pines Hwy, mouth of Santa Rosa Canyon, *H. Parks & S. Parks 24166* (UC); 20 mi E of Desert Center, *R. Perkins & H. de Forest s.n.* (RSA); W side of Chuckwalla Mts ca. 2 mi S of I-10, ca. 33°40'N, 115°31'W, *B. Pitzer 640* (RSA, SD, UCR); Coachella Valley, *E. Rixford s.n.* (CAS); Chuckwalla Mts, above Corn Spring, *J. Roos 4233* (UCR); Tahquitz Canyon Wash, Palm Springs, *L. Rose 46304* (CAS, DS, POM, UC); base of Orocopia Mts, Box Canyon, *J. Shevock 5811* (CAS); Eagle Mts, E end of Box Canyon, *B. Stark 3753* (DS, RSA, UC); S part of Palm Springs, *J. Thomas 59* (DS); Lower Cottonwood Springs Wash, N of I-10, *B. Trowbridge 6099* (CAS); 5 mi W of Shaver's Well, *I. Wiggins 8757* (DS, UC); 9 mi W of Desert Center, *I. Wiggins 9689* (DS, RSA, UC); 15 mi NE of Mecca, T4S, R9E, Thermal Quad, *H. Yates 6445* (UC); N slope of Santa Rosa Mts, jeep rd to Coyote Canyon from Deep Canyon Research Center, *W. Zabriskie 103* (CAS, UCR). San Diego Co: Borrego Park on Rte. 78, 35 mi W of jct U. S. Hwy 99 and Rte 78, *L. Abrams 13898* (DS), *13899* (DS); S of Borrego Valley, *R. Bacigalupi 3571* (JEPS); San Diego River, Lakeside, 32°52'N, 116°53'W, *R. Beauchamp & B. Mackintosh 2986 (SD); Tubbs Canyon,* W edge of Borrego Valley, *D. Breedlove 58570* (CAS); Vallecitos Station, *C. Brown s.n.* (SD); Mine Wash, T12S, R6E, Whale Peak Quad, near old mine site, *D. Clemons & E. Jonsson 1974* (SD); Borrego Desert below Julian, *N. Cooper 2320* (RSA), *2321* (RSA); between Jacumba and Mt Springs, *A. Eastwood 10* (CAS); Yaqui Wells, *A. Eastwood 2724* (CAS); Hell Hole Canyon, near Borrego, *C. Epling & W. Robison s.n.* (DS, CAS, RSA, UC); along Coyote Creek ca. 3 mi SE of Lone Palm, N end of Borrego Valley, *F. Gander 134.51* (SD); Vallecitos Station, *F. Gander 176.27* (SD); Round Granite Hill near The Narrows, *F. Gander 295.6* (SD); S end of Pinyon Mountain, *F. Gander 357* (SD); Borrego Palm Cañón, *F. Gander 1253* (SD); Fish Creek, across from gypsum mine, *F. Gander 4696* (SD); Mt Palm Springs, *F. Gander 4856* (SD); Crane Break Cañón, *F. Gander 4874* (SD); Lakeside, near Van der Veer Ranch, *F. Gander 7018* (SD); near Palm Canyon, Borrego Valley, *H. Gentry s.n.* (DS); Borrego, *S. Harter s.n.* (SD); between Ocotillo Well and Agua Caliente Hot Springs, 1 mi E of Anza-Borrego State Park, *C. Hitchcock 24266* (UC); N Borrego Valley, *J. Howell 3220* (CAS, UC); Lakeside, *F. Hubby 14* (DS); Vallecito, *W. Jepson 8567* (JEPS, SD); Wagon Wash near Sentenac Canyon, *W. Jepson 8773* (JEPS); Yaqui Well, *M. Jones s.n.* (DS); San Felipe Hill, *M. Jones s.n.* (DS); Jacumba, *M. Jones s.n.* (POM); along Hwy S-2, Carrizo Valley, T15S, R7E, Sweeney Pass Quad, *E. Jonsson & D. Clemons 1227* (SD); ca. 2 mi N of summit of Yaqui Pass, *D. Kyhos 62-8* (DS); Carrizo Gorge, *M. Leeper s.n.* (SD); Borrego Desert State Park, Palm

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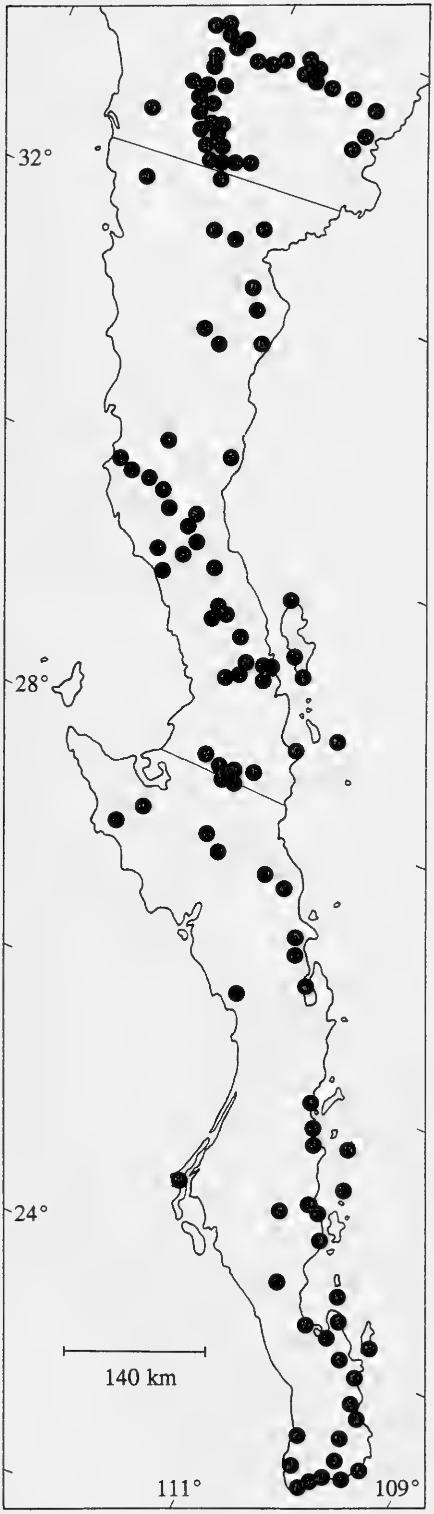
FIGURE 22. Distribution of *Justicia californica* in California, Baja California, and Baja California Sur.



Canyon, 1.8 mi W of headquarters, *R. Malloory 403* (RSA); 1 mi N Tamarisk Grove, *J. Massey & J. Henrickson 1057* (RSA); 15 km W of Borrego Springs, *A. Mayers s.n.* (UCR); Mt Spring, *E. Mearns 3104* (DS); San Felipe Wash near Borrego Valley, *C. Meyer 41 (JEPS, UC); near head of Borrego Valley, P. Munz 12885* (RSA); NW end of Borrego Valley, *P. Munz 15589* (CAS, POM); below Cranebrake Canyon, near Vallecitos, *P. Munz 15842* (POM); Borrego Springs, *G. Muth 548* (DS); mts back of Agua Caliente, *S. Parish & W. Parish 12* (DS, UC); San Felipe Creek near base of Sentenac Canyon, *F. Peirson 7736* (DS, RSA); Lakeside, *N. Pettibone & F. Hubby s.n.* (CAS); Borrego Valley, *E. Purer 4912* (SD); Vallecito Stage Station, *E. Purer 6412* (SD); Mt Palm Springs, *P. Raven 11542* (CAS, JEPS); 3 mi E of Sentenac Canyon on Hwy 79, *E. Rush 137* (POM); foot of Palm Canyon, Borrego Valley, *P. Silva 15* (RSA); Borrego Desert, *S. Stone 30* (SD); Yaqui Springs in Anza Desert State Park, near Hwy 78, *J. Thomas 365* (DS); Mason Valley, *F. Tose s.n.* (CAS); Vallecito Stage Station, Vallecito Creek, *G. True 8129* (CAS); San Felipe Canyon, T12S, R6E, Seventeen Palms Quad, *H. Yates 5463* (UC).

MEXICO: **Baja California:** sierra E of La Ramona on rd from Guayaquil to Puerto Santa Catarina, NW of Cataviña, *S. Boyd & T. Ross 5395* (RSA); Sierra La Asamblea, 13.5 mi N of jct with rd to Bahía de Los Angeles, ca. 29°16′N, 114°06′W, *S. Boyd & T. Ross 5560* (RSA); 34 km S of El Rosario, *D. Breedlove 60744* (CAS); 20-30 mi S of Punta Canoas along tract to Punta Cono, *D. Breedlove 62503* (CAS); 38 km N of jct to Bahía de Los Angeles along rd to Cataviña, *D. Breedlove & C. Burns 72796* (CAS); 15 km inland from Punta Canoas on rd to Cataviña, *D. Breedlove & C. Burns 72842* (CAS); Cataviña, *F. Cronemiller 3060* (DS, POM); Cañón Carrizo, E side of Sierra Juarez, *T. Dallman & M. Guzy 27* (UCR); along Hwy 3 in San Matias Pass, 6.2 mi SE of San Matias, *T. Daniel 1336* (ASU, CAS); along Hwy 5, 5.9 mi S of La Ventana, *T. Daniel 1542* (ASU, CAS); Puerto Refugio, *E. Dawson 1029* (RSA); 3.1 km WSW of Rancho El Arenoso, ca. 3.4 km WSW of Hwy 1 and ca. 75 km NW of Cataviña, 30°02′N, 115°20′W, *J. Dice 697* (SD, RSA); ca. 12 mi WNW of Bahía de Los Angeles, *M. Dillon et al. 1887* (RSA, UCR); 2 mi S of Calmallí, *C. Epling & W. Robison s.n.* (DS, UC); KM 40 de San Felipe a Puertecitos, *E. Ezcurra et al. s.n.* (RSA); 12 mi E of Rosario on San Augustine rd, *R. Ferris 8534* (DS); 3.5 mi S of Laguna Seca Chapala on rd to Punta Prieta, *R. Ferris 8579* (DS, RSA); Bahía de Los Angeles, S shore, W of La Mona, *P. Fritsch et al. 1298* (RSA, UCR); E slope of Sierra Juarez, N of Gaskill's Tanks, *F. Gander 2964* (SD); 5 mi W of Calmallí, *A. Haines & W. Stewart s.n.* (DS); Calmallí, *C. Harbison 41682* (RSA), *s.n.* (SD); Miraflores Rancho (El Arco), *C. Harbison s.n.* (SD); Yubay Mesa area, ca. 29°10′N, 113°55′W, *D. Harder & W. Appleby 1012* (RSA); Rosario Arroyo, *D. Harvey s.n.* (UC); San Francisquito wash, 18.7 mi SW of Bahía San Luis Gonzaga, *J. Hastings & R. Turner 63-160* (DS, SD); 5 mi S of Rancho Arenoso, ca. 36 mi E of El Rosario, *J. Henrickson 2305* (DUKE); 6.5 mi E of El Rosario, *J. Howell 30994* (CAS, SD); Rancho Ramona, 29°53′N, 115°06′W, *E. Huey s.n.* (SD); San Fernando, 29°58′N, 115°15′W, *E. Huey s.n.* (SD); Hwy 1, 51 km N of parador near Punta Prieta, S of San Martín, *D. Johansen 128* (CAS); San Esteban Island, *I. Johnston 3188* (CAS); Valley of the Palms, *M. Jones 3724* (CAS, DS, POM, UC); Sierra de San Pedro Mártir, ca. 50 mi NW of San Felipe, from SW fork of Valle Trinidad Rd, Borrego Wash, San Felipe Desert, *S. Kaune 693* (CAS); 30 mi S of El Rosario, *K. Kirtland et al. 13183-20* (UCR); 6.6 km NW of Bahía de Los Angeles at Arroyo Columpia, ca. 28°59′N, 113°36′W, *G. Levin 2146* (UCR); San Esteban Island, SE side, *G. Lindsay s.n.* (DS); ca. 64 mi S of Rancho de Mesquital, ca. 5.3 mi N of site of Manuela, ca. 28°11′N, 113°48′W, *D. Michener et al. 4254* (RSA); Sierra San Pedro Martir, E side of San Matias Pass along Mex. 3, ca. 31°17′N, 115°26′W, *D. Michener et al. 4284* (RSA); San Borja, 28°47′N, 113°57′W, *R. Moran 1990* (DS, UC); Isla Angel de la Guarda, second large canyon W of Punta Diablo, 29°14′N, 113°19′W, *R. Moran 7206* (SD); 10 mi N of San Borja, 28°53′N, 113°50′W, *R. Moran 7967* (SD); Arroyo Cataviña at Rancho San Luis, 29°43′N, 114°43′W, *R. Moran 11466* (SD); E base of Sierra Juarez, ca. 1 mi S of U. S. border, 32°37′N, 115°59′W, *R. Moran 14807* (SD, RSA); Arroyo Matomí, ca. 18 mi above (W of) mouth, ca. 31°29′N, 114°57′W, *R. Moran 21505* (SD, UC); Arroyo las Palmas, 1 km SE of Rancho los Gavilanes, ca. 32°20′N, 116°36′W, *R. Moran 25161* (RSA); 4.8 mi N of Cataviña, *E. Naranjo-Garcia s.n.* (UCR); Sierra Pinta, 60-65 mi S of Mexicali toward San Felipe, *J. Olmsted 1123* (RSA); Palm Valley, *C. Orcutt s.n.* (SD); Rosario, *C. Orcutt s.n.* (UC); 2.2 mi N of Cataviña on Hwy 1, Arroyo ElPalmarito, ca. 29°45′N, 114°45′W, *B. Pitzer 737* (RSA); Sierra Las Pintas, 0.2 mi W of Hwy 5 and 3.1 mi S of rd to Ejido J. Soldana, ca. 31°49′N, 115°09′W, *B. Prigge & D. Verity 7904* (UC, UCR); between Tijuana and Ensenada, *C. Pringle s.n.* (CAS); Arroyo Calmallí, *C. Purpus 87* (DS, UC); near KM 112 S of Mexicali on rd to San Felipe, *P. Raven 14804* (UC, RSA); 16 km SE of El Rosario, 30°00′N, 115°37′W, *P. Raven et al. 12483* (UC); Isla Angel de la Guarda, Puerto Refugio, *P. Rempel 275* (RSA); La Virgen, 7 mi N of Santa Ines, *R. Schmid 1976-32* (DAV); 13 mi E of El Arco, *L. Smith 19* (UCR); S end of Laguna Salada, *S. Smith 347* (UC); Isla Ventana, *L. Spear 49* (DAV); 15 mi S of Mexicali, *S. Stephenson 67-75* (DUKE, SD); Isla Angel de la Guarda, Puerto Refugio, *P. Tenorio L. 10838* (RSA); Bahía de los Angeles, *P. Tenorio L. 10985* (RSA); Mpio Ensenada, Isla Angel de la Guarda, Puerto Refugio, 29°33′N, 113°34′W, *P. Tenorio L. & C. Romero de T. 10838* (RSA); Mpio. Ensenada, Isla Angel de la Guarda SE, 29°04′N, 113°10′W, *P. Tenorio L. & C. Romero de T. 10956* (RSA); Mpio. Ensenada, La Junta, 35 km NE de El Arco, brecha a San Francisquito, 28°12′N, 113°11′W, *P. Tenorio L. & C. Romero de T. 13030* (CAS); Mpio. Ensenada, San Borja, 28°46′N, 113°55′W, *P. Tenorio L. & C. Romero de T. 13099* (CAS); Mpio. Ensenada, 23 km al NW de Guayaquil, carr. a Rosario, 30°03′N, 115°17′W, *P. Tenorio L. & C. Romero de T. 13135* (CAS); pass ca. 11 mi W of El Rosarito, W of S end of Sierra San Pedro Mártir, ca. 30°28′N, 115°25′W, *R. Thorne 32089* (DUKE, RSA); San Matias Pass, ca. 31°18′N, 115°25′W, *R. Thorne & D. Charlton 60186* (RSA); near Aguajito Ranch, ca. 18 mi from El Rosario, *R. Thorne & J. Henrickson 32549* (RSA); 2 mi up Arroyo Cataviña from Santa Inés, *R. Thorne & J. Henrickson 32619* (RSA); San Matias Pass, ca. 31°18′N, 115°30′W, *R. Thorne & W. Wisura 57610* (RSA); Cañón de Guadalupe, E face of Sierra Juarez, ca. 32°09′N, 115°47′W, *R. Thorne et al. 57764* (CAS, RSA, UCR); S of Valle de las Palmas, just E of Hwy 3, *R. Thorne et al. 62158* (POM); ca. 15.5 mi NW of Bahía de los Angeles, 29°00′N, 113°45′W, *G. Webster 21573* (DAV); ca. 4 mi NW of Cataviña, ca. 29°53′N, 114°50′W, *G. Webster 21724* (DAV); 8 mi from Rosario on rd to El Mármol, *I. Wiggins 4336* (CAS, DS, POM, UC); vicinity of El Mármol, *I. Wiggins 4367* (DS), *4378* (POM); 5–10 mi N of Cataviña, *I. Wiggins 4397* (CAS, DS, POM, UC); 8 mi SE of Rosario, *I. Wiggins 5264* (CAS, DS, POM, UC); 9 mi E of Pozo Alemán, *I. Wiggins 7788* (DS, UC); near S end of Isla San Esteban, *I. Wiggins 17199* (DS); ca. 18 mi toward Cerro Blanco from main rd between San Agustín and Laguna Chapala, 29°35′N, 114°47′W, *I. Wiggins & J. Thomas 149* (DS, SD); 3 mi S of Agua Higuera, along rd to Misión San Borjas, *I. Wiggins & D. Wiggins 14829* (CAS, DS); near KM 107 S of Mexicali along hwy to San Felipe, *I. Wiggins & D. Wiggins 15758* (DS); 10 mi W of Bahía de los Angeles, *I. Wiggins & D. Wiggins 16008* (DS); San Matias Pass, 31 mi W of San Felipe hwy, *I. Wiggins & D. Wiggins 16047* (DS); 15 mi NNE of Punta Catarina, *D. Zippin 42* (SD). **Baja California Sur**: NE base of Sierra El Placer, 18.5 mi E of Rancho San José del Castro on rd to Bahía Tortugas, *S. Boyd et al. 3339* (RSA); Arroyo San Bruno, SE of Santa Rosalía, 4.8 mi W of Hwy 1 toward San José de Magdalena, ca. 27°04′N, 112°12′W, *S. Boyd & T. Ross 5843* (RSA); San José del Cabo, *T. Brandegee 444* (DS, UC); Magdalena Island, *T. Brandegee s.n.* (DS, UC); Las Palmas, *T. Brandegee s.n.* (UC); E base of Sierra de Placeros, 40 km SE of San

José de Castro, *D. Breedlove 60892* (CAS, RSA); 24 km N of San Ignacio, *D. Breedlove & C. Burns 72733* (CAS); Sierra de la Giganta, Cañón de Matancita, near foot of Cuesta de Alta Gracia, ca. 25°41′N, 111°19′W, *A. Carter 4899* (CAS, UC); Sierra de la Giganta, Aguaje de San Antonio, Arroyo el Coyote, SE of La Soledad & N of Cerro Mechudo, ca. 24°49′N, 110°46′W, *A. Carter 5425* (CAS, UC); Sierra de la Giganta, Arroyo del Cajón de Tecomajá, SW of Puerto Escondido, 25°43′N, 111°20′W, *A. Carter & L. Kellogg 2893* (DS, SD, UC); 19.2 km SW of San José del Cabo, *A. Carter et al. 2236* (CAS, DS, POM, SD, UC); Carizal, between San Juanico Bay and Cadejé, 63 km NW of La Purísima, *A. Carter et al. 2495* (DS, UC); upstream (E) from Rancho Agua Escondido, ca. 25°06′N, 111°00′W, *A. Carter et al. 5727* (CAS, UC); Sierra de la Giganta, Ojo de Agua, Arroyo Bachomo, NW base of Mesa de Humí, ca. 25°03′N, 110°58′W, *A. Carter et al. 5792* (CAS, UC); 35 mi S of Todos Santos, *K. Chambers 874* (DS, UC); Bahía de las Palmas, 1 mi SE of Buena Vista, *L. Constance 3169* (DS, SD, UC); Muertos Bay, *T. Craig 711* (POM); between Santiago and Agua Caliente, 2.7-5 km SW of Santiago, ca. 23°27′N, 109°45′W, *T. Daniel & M. Butterwick 6877* (CAS, ENCB, HCIB, MEXU, MO, SBBG, US); along Hwy 19, ca. 16 km NW of Cabo San Lucas, ca. 23°00′N, 110°02′W, *T. Daniel & M. Butterwick 6961* (CAS, HCIB); near Hwy 1, SE of San Bartolo, 28.2 mi SE of El Triunfo, *T. Daniel et al. 2493* (ASU, BR, CAS, ENCB, MEXU, MICH, MO); Punta Frailes, *E. Dawson 1141* (RSA), *6192* (RSA); San José del Cabo, *E. Dawson 1217* (RSA); 1–2 mi inland from Agua Verde Bay, *E. Dawson 6228* (RSA); Bargo Island, Concepción Bay, *E. Dawson 6382* (RSA); El Tule, near Cape San Lucas, *F. Gander 9710* (SD); La Paz, *F. Gander 9784* (CAS); Sierra Giganta, Arroyo Hondo, *H. Gentry 4154* (DS); Sierra de la Giganta, Los Encinos, *H. Gentry 4261* (DS, UC); Cerro Tordillo and vicinity, systema de la Sierra Viscaíno, *H. Gentry 7440* (DS, RSA, UC); El Tule, *C. Harbison s.n.* (SD); Isla Espiritu Santo, 24°30′N, 110°24′W, *J. Hastings 71-177* (SD); Rancho Mezquital, S of Volcán Las Tres Vírgenes, 27°26′N, 112°39′W, *D. Howe 3733* (SD); San José del Cabo, *D. Johansen 519* (DS); Cabo San Lucas, *D. Johansen 531* (DS); Espiritu Santo Island, Cadeleros Bay, *I. Johnston 4079* (CAS); San José del Cabo, *M. Jones 24425* (POM); San Luis Gonzaga, *R. Kniffen s.n.* (UCR); 20 km N de San José del Cabo, carr. a Los Frailes, *J. León de la Luz 1079* (SD); Cape San Lucas, *H. Mason 1871* (CAS); middle of S coast, Cerralvo Island, 24°09′N, 109°54′W, *R. Moran 3577* (DS); W side of Santa Cruz Island, 25°17′N, 110°44′W, *R. Moran 3842* (DS); Cape Region, 11 km N of Santa Anita, ca. 23°15′N, 109°42′W, *R. Moran 6927* (CAS, DS, RSA, SD); near middle of W side of Catalina Island, ca. 25°39′N, 110°48′W, *R. Moran 9332* (CAS, SD); Cerralvo Island, Ruffo Ranch Canyon, 24°11′N, 109°51′W, *R. Moran 9522* (SD); Arroyo Calvario, NE of San Andrés, 27°21′N, 114°20′W, *R. Moran 20019* (SD); NE base of lower N slope of Volcán las Tres Vírgenes, ca. 27°29′N, 112°36′W, *R. Moran & J. Reveal 20213* (CAS, SD); Mulegé, *E. Palmer 16* (UC); Santa Agueda, *E. Palmer 255* (UC); La Paz, Coyote Bay, *R. Peters 12* (UC); arroyo into Muertos Bay, Los Planes, *R. Peters 117* (UC); 15.5 mi S of Todos Santos, *D. Porter 358* (CAS, DS); 25 mi N of Santa Rosalía, *F. Reed 6234* (POM); Cabeza Ballena, *P. Rempel 65* (RSA); Puerto Escondido, *P. Rempel 165* (RSA); Isla Cerralvo, 24°11′N, 109°52′W, *M. Sousa P. 200* (RSA); lado SW de Isla Santa Catalina, 25°37′N, 110°47′W, *M. Sousa P. 226* (CAS, RSA); 1.5 mi N of El Represso (near La Paz), *W. Taylor 6243* (RSA); Cape Region, between San Lucas and San José del Cabo, *J. Thomas 8501* (CAS, DS); Cabo San Lucas, 22°52′N, 109°53′W, *G. Webster 19555* (SD); 7.3 mi W of Los Planes, *I. Wiggins 14464* (CAS, DS, UC); 0.5 mi inland from El Coyote, E of La Paz, *I. Wiggins 14586* (CAS, DS); 1.5 mi W of El Coyote, E of La Paz, *I. Wiggins 14588* (DS); 2.5 mi from paved hwy along rd to San Hilario, ca. 24°21′N, 110°59′W, *I. Wiggins 15418* (DS, UC); 4 mi N of Rancho El Tablón, *I. Wiggins 16279* (DS); E side of Isla Catalina, 25°40′N, 110°45′W, *I. Wiggins 17636* (DS).

Most plants have overstory glands in the inflorescence and usually on the capsules as well (e.g., Imperial Co., Riverside Co., San Diego Co., B.C., and B.C.S.). Other plants lack the overstory glands altogether (e.g., Imperial Co., Riverside Co., San Diego Co., and B.C.). There is a greater tendency for plants from Baja California and Baja California Sur to have the overstory glandular pubescence. Indeed, the type from the southern Cape Region has an overstory of glandular trichomes in the inflorescence. There are many fewer collections of strictly eglandular plants from the peninsula and apparently none in the southern state. The southernmost known locales for eglandular plants in Baja California are at about lat. 29°30′N (i.e., *Hastings & Turner 63-160* and *Tenorio L. 10838*). Plants of *J. californica* from outside of our region comprise both glandular and eglandular plants (Sonora) or glandular plants only (Arizona, Sinaloa). The distinctions between the glandular and eglandular forms is not complete. Varying densities (i.e., very sparse to dense) of glands in the overstory are evident. For example, in *Moran 6927* and *Ganders 9784* the overstory pubescence in the inflorescence appears to consist mostly of erect to flexuose eglandular trichomes to 2 mm long and only a few scattered glands. In *Moran & Reveal 20213* and *Johansen 531* from Baja California Sur, and in *Breedlove 1879* and *Thomas 59* from California, the glandular pubescence is particularly dense. *Wiggins & Wiggins 15758* lacks overstory glands in the inflorescence but has sparse overstory glands on the capsules.

Yellow-flowered individuals represent a rare form of the species that is known from southern California (e.g., *Blondin s.n., Clemons & Jonsson 1974, Cooper 2321, Massey & Henrickson 1057, Zabriskie 103*) and Baja California Sur (e.g., *Moran & Reveal 20213, Sousa P. 226*). The yellow-flowered individuals occur intermixed among red-flowered individuals and are sometimes cultivated in gardens of southern California.

Grant and Grant (1966) noted visitation to (and, in some instances, pollination of) flowers of *J. californica* (as *Beloperone californica*) by black-chinned (*Archilochus alexandri*), Costa's (*Calypte costae*), and rufous (*Selasphorus rufus*) hummingbirds. The pollination biology of this species in southern California and Arizona was subsequently studied by Michener (1979). He found that *J. californica* exhibits floral features typically associated with pollination by hummingbirds but that pollinators apparently include an array of insect and avian visitors. Hummingbird visitors at his study sites in these states comprised the three species previously noted by Grant and Grant.

Hummingbird visitation to flowers of *J. californica* is noted on several collections (e.g., *Olmsted 1123, Gentry 4261, Harder & Appleby 1012*). During my studies, flowers of *Daniel & Butterwick 6877* from Baja California Sur were observed being visited by Xantus' hummingbird (*Hylocharis xantusii*). Also, the sugar composition of floral nectar from *Daniel 3976*, which was collected in Sonora, was analyzed by C.E. Freeman at the University of Texas at El Paso. The nectar shows a sucrose/hexose ratio of 1.8 (16.6% fructose, 19.5% glucose, 63.9% sucrose). Dr. Freeman indicated (in litt.) that this result is almost identical with those obtained from other samples of *J. californica* that he had analyzed. This ratio, which indicates a sucrose-dominant nectar, is typical of flowers in various plant families, including Acanthaceae, that are commonly visited (and sometimes known to be pollinated) by hummingbirds (Baker and Baker 1983).

The closest relative of *J. californica* appears to be *J. purpusii*. Graham (1988) noted this close relationship and indicated that their various adaptations for growing in arid environments (i.e., dense indumentum, caducous leaves and bracts, and smooth seeds with large food reserves) and for pollination by hummingbirds (i.e., large red flowers borne on well-developed pedicels) obscured their relationships to other species of the genus.

3. Justicia candicans (Nees) L. D. Benson in L. D. Benson and R. A. Darrow, Tr. & sh. southw. des., ed. 3, 218. 1981. *Adhatoda candicans* Nees in A. DC., Prodr. 11:396. 1847. *Dianthera candicans* (Nees) Hemsl., Biol. cent.-amer., Bot. 2:517. 1882. *Jacobinia candicans* (Nees) B. D. Jacks., Index kew. 1:1246. 1893. TYPE. — MEXICO. **Oaxaca**: Cordillerae Mexicanae, 5000 ft., Nov–Apr, *Galeotti 911* (K ex hb. Hooker, photo at CAS!; isotype.G, photo at US!).

Jacobinia ovata A. Gray, Proc. Amer. Acad. Arts 21:405. 1886. TYPE. — MEXICO. **Chihuahua**: near Batopilas, Aug–Nov 1885, *E. Palmer 220* (holotype: GH, photo at DS!; isotypes: NY, US!).

Jacobinia ovata var. *subglabra* S. Watson, Proc. Amer. Acad. Arts 24:67. 1889. *Jacobinia candicans* var. *subglabra* (S. Watson) L. D. Benson in L. D. Benson and R. A. Darrow, Tr. & sh. southw. des., ed. 2, 413. 1954. *Justicia candicans* var. *subglabra* (S. Watson) L. D. Benson in L. D. Benson and R. A. Darrow, Tr. & sh. southw. des., ed. 3, 218. 1981. TYPE. — MEXICO. **Sonora**: near Guaymas, Oct 1887, *E. Palmer 264* (GH, photo at DS!; isotypes: DS!, US).

Justicia mexicana Rose, Contr. U. S. Natl. Herb. 1:348. 1895. TYPE. — MEXICO. **Sonora**: Agiabampo, 3–15 Oct 1890, *E. Palmer 788* (holotype: US!; isotype: US!).

Shrubs to 1.8 m tall. Young stems quadrate to quadrate-sulcate, ± evenly pubescent with an understory of erect to flexuose eglandular trichomes 0.05–0.1 mm long (sometimes inconspicuous) and an overstory of flexuose to antrorse eglandular trichomes 0.3–1.2 mm long, the latter trichomes sometimes concentrated in 2 lines, epidermis clearly visible. Leaves petiolate, petioles to 13 mm long (petiolar stubs to 2 mm long remaining at nodes after leaves have fallen), blades ovate, 15–71 mm long, 7–37 mm wide, 1.9–2.5 times longer than wide, acuminate at apex, acute to rounded to truncate at base, surfaces pubescent with flexuose to antrorse eglandular trichomes, margin entire to subsinuate. Inflorescence of dichasia in leaf axils or in axils of subfoliose bracts along axillary sessile to short-pedunculate dichasiate spikes to 18 mm long (these sometimes appearing as a dense cluster of dichasia at nodes), spikes (if present) opposite, rachis (if present) pubescent like young stems; dichasia opposite to subopposite, 1-flowered, 1 per axil, sessile to subsessile (i.e., borne on peduncles to 1 mm long). Bracts (if present) subfoliose, opposite, sessile to petiolate, elliptic to narrowly elliptic to oblanceolate, 9–15 mm long, 1.5–3 mm wide, abaxial surface pubescent like leaves. Bracteoles sessile, linear to lance-subulate, 8–12 mm long, 0.6–1 mm wide, abaxial surface pubescent like leaves. Flowers sessile to subsessile (i.e., borne on pedicels to 0.5 mm long). Calyx 5-lobed, 6–8 mm long, lobes lance-subulate, 5–7 mm long, equal in length, 0.8–1 mm wide, abaxially pubescent with flexuose to antrorse eglandular trichomes 0.05–0.4 mm long. Corolla red with white markings on lower lip, 32–35 mm long, externally pubescent with flexuose eglandular trichomes 0.2–0.5 mm long, tube gradually expanded distally, 18–20 mm long, 4.5–5 mm in diameter near midpoint, upper lip 11–15 mm long, minutely 2-lobed at apex, lobes 0.2–0.5 mm long, lower lip spreading, 13–15 mm long, lobes 7–9.5 mm long, 3–4.8 mm wide. Stamens inserted near apex of corolla tube, 12–15 mm long, filaments proximally pubescent with eglandular trichomes, thecae 1.9–2.3 mm long, equal, parallel, unequally inserted (overlapping by 1.2–1.6 mm), dorsally glabrous, lower theca with an inconspicuous basal appendage to 0.1 mm long; pollen (Fig. 23a) 2-aperturate, apertures flanked on each side by 2 rows of insulae, exine reticulate. Style 31–35 mm long, proximally pubescent with eglandular trichomes, stigma lobes 0.2–0.3 mm long, equal. Capsule 11–15 mm long, glabrous, stipe 5–8 mm long, head subellipsoid with a slight medial constriction, 6–8 mm long. Seeds 4, reddish, compressed, 3–3.7 mm long, 2–3 mm wide, 1–1.3 mm thick, surfaces and margin smooth to somewhat irregularly bumpy. ($n = 14$, Daniel and Chuang 1993, Daniel et al. 1984).

PHENOLOGY. — Flowering: April, October; fruiting: April.

DISTRIBUTION AND HABITAT. — United States (Arizona) and Mexico (Baja California Sur, Colima, Durango, Jalisco, Michoacán, Oaxaca, Sinaloa, Sonora); in our region the species is known only from two collections from the Central Gulf Coast subdivision of the Sonoran Desert in northeastern Baja California Sur (Fig. 7); plants occur on moist slopes and along arroyos at 575–1060 m elevation. Gentry's collection was made in a region of oak-*Nolina* grassland. According to Moran's field notes, species growing in the vicinity of his collection included: *Tetramerium nervosum*, *Elytraria imbricata*, *Sapium biloculare*, *Esenbeckia flava*, *Ambrosia carduacea*, *Cassia goldmanii*, *Salvia peninsularis*, *Janusia californica*, and *Acalypha comonduana*.

ADDITIONAL SPECIMENS EXAMINED. — MEXICO. **Baja California Sur**: Sierra de las Palmas, La Champagna, S of Santa Rosalia, *H. Gentry & W. Fox 11804* (MICH); Sierra de Guadalupe, San Sebastián, 27°01'N, 112°24'W, *R. Moran 18787* (RSA, SD, UC).

In recent years the name *Justicia candicans* has been applied to plants resembling ours. The protologue and photographs of *Galeotti 911* (from Oaxaca) suggest that the name may apply to another, though similar, species with bracteoles shorter than the calyx. Collections with bracteoles shorter than the calyx, but otherwise similar to our plants, are also known from Sinaloa and Jalisco and have been treated with the name *Jacobinia mexicana* Seem. Additional studies will be necessary in order to determine whether our plants represent a taxon other than that represented by the type of *Justicia candicans*.

This is the first report of *J. candicans* in the peninsula of Baja California from where it is known only from the two collections noted above. The precise locality of *Gentry & Fox 11804* has not been located. Phil Jenkins examined Gentry's field notes at ARIZ and indicated (in litt.) that the collection was made on 29 April 1952 in a rocky arroyo at "La Champaña." Immediately prior to collecting at this locale, Gentry and Fox collected at Rancho San Sebastián (also in the "Sierra de las Palmas"), the locality

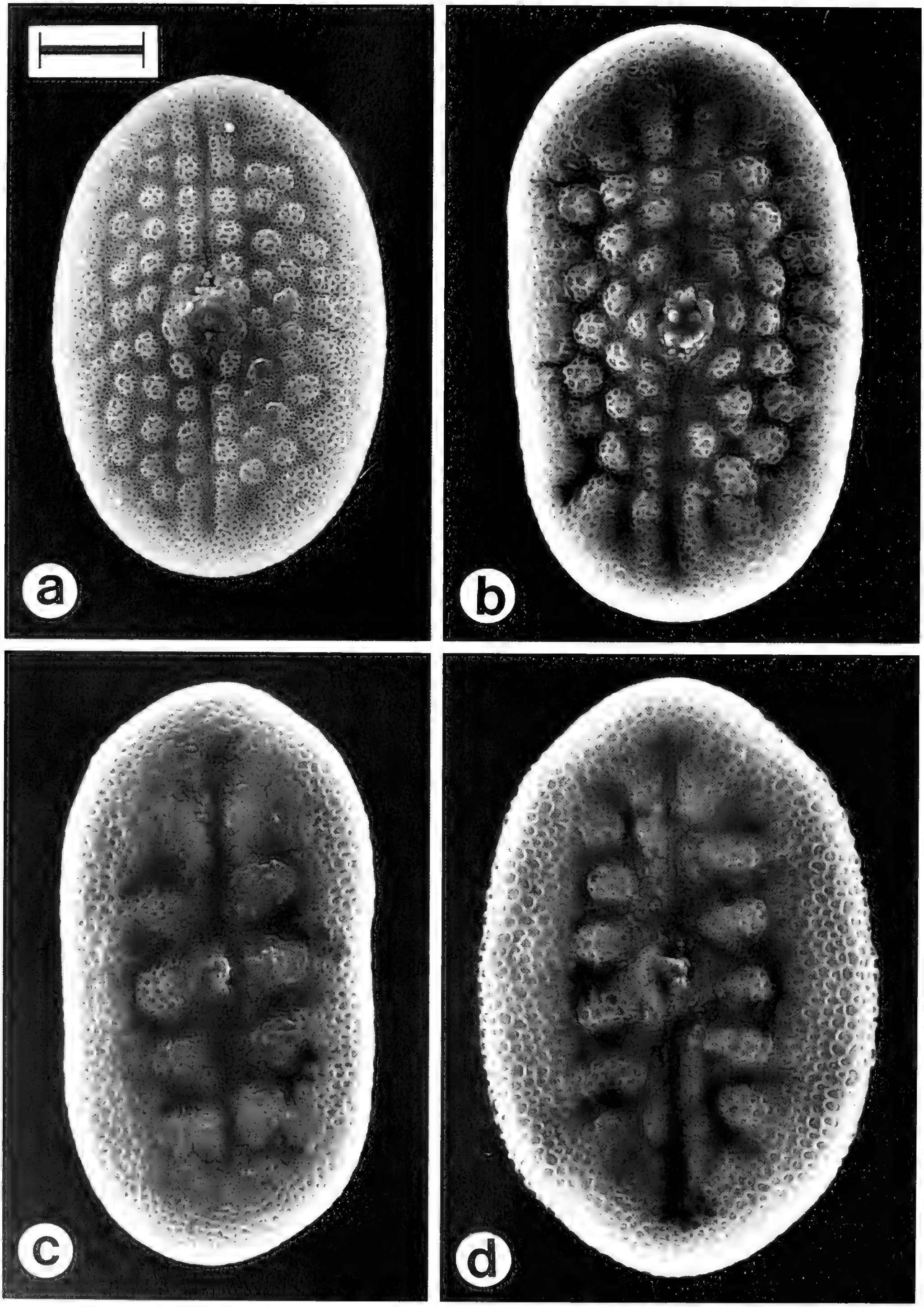


FIGURE 23. Pollen. a. *Justicia candicans* (*Moran 18787*), apertural view; b. *J. hians* (*Carter et al. 4164*), apertural view; c. *J. insolita* subsp. *insolita* (*Carter 5711*), apertural view; d. *J. insolita* subsp. *tastensis* (*León de la Luz 2334*), apertural view. Scale for a–d = 10 µm.

where Moran collected this species nearly 20 years later. No elevation is cited in Gentry's notes (vs. "4500 to 5000 feet" on the printed specimen label); however, Gentry's numbers 11803 and 11805 were collected at an elevation of about 3500 feet. This latter elevation is utilized here.

The species shows considerable variation throughout its broad range in pubescence and bracteole length. For example, young stems vary from having a dense pubescence to being nearly glabrous. Nearly glabrous plants have been treated as *J. candicans* var. *subglabra*. Plants on the Mexican mainland with exceptionally long and curved bracts and bracteoles, but otherwise greatly resembling ours, have been treated as *Jacobinia roseana* Leonard.

Graham (1988) treated *J. candicans* as a species peripheral to *Justicia* section *Plagiacanthus* (Nees) V. A. W. Graham. Morphologically similar species in Mexico include *Jacobinia roseana*, which occurs in southwestern Mexico (e.g., Jalisco, Colima, and Michoacán), and *J. palmeri* of Baja California Sur.

Because of these taxonomic uncertainties, the above description is based solely on the two collections from Baja California Sur.

4. **Justicia hians** (Brandegee) Brandegee, Univ. Calif. Publ. Bot. 6:194. 1915. *Beloperone hians* Brandegee, Proc. Calif. Acad. Sci., ser. 2, 2:194. 1889. TYPE. — MEXICO. **Baja California Sur**: cliffs of Comondú, 21 Mar 1889, *T. Brandegee s.n.* (holotype: UC!; isotype: US)

Justicia wigginsii Leonard, J. Wash. Acad. Sci. 32:342. 1942. TYPE. — MEXICO. **Baja California Sur**: 27.7 mi S of Pozo Alemán, 4 Mar 1935, *I. Wiggins 7874* (holotype: DS!; isotypes: UC!, US).

Erect perennial herbs (to shrubs) to 4 (–10) dm tall. Young stems suboctagonal, evenly and ± densely pubescent with retrorse to retrorsely appressed eglandular trichomes 0.05–0.1 (–0.2) mm long, epidermis occasionally not or barely visible. Leaves subsessile to petiolate, petioles to 4 mm long (petiolar stubs to 1.5 mm long persisting at nodes after leaves have fallen), blades lance-ovate to ovate to elliptic, 8–29 mm long, 3.7–15 mm wide, 1.4–2.6 times longer than wide, rounded to acute at apex, rounded to acute at base, surfaces pubescent (often sparsely so) with cauline type trichomes and sometimes glandular punctate as well, margin entire. Inflorescence of axillary (and terminal) pedunculate dichasiate spikes (or sometimes branched at base and becoming a panicle) to 85 mm long (including peduncle and excluding flowers), rachis pubescent with erect glandular trichomes 0.05–0.2 mm long and erect to retrorse eglandular trichomes 0.05–0.2 mm long; dichasia alternate, 1-flowered, 1 per axil, sessile in axils of bracts. Bracts opposite, sessile, linear-lanceolate to triangular-lanceolate, 2–2.8 mm long, 0.7–0.9 mm wide, abaxial surface pubescent like rachis. Bracteoles sessile, lanceolate to lance-subulate, 2–3.6 mm long, 0.6–0.8 mm wide, abaxial surface pubescent like rachis. Flowers sessile to subsessile (i.e., pedicels to 0.5 mm long). Calyx 5-lobed, 4–5.5 (–7) mm long, lobes lanceolate to lance-subulate, 2.4–4.5 (–5.5) mm long, subequal to unequal in length (i.e., posterior lobe ± shorter than others), 0.4–1.2 mm wide, abaxially pubescent like rachis. Corolla orange-red, 25–31.5 mm long, externally pubescent with erect eglandular and glandular trichomes 0.05–0.1 mm long, tube expanded distally, 12–16 mm long, 3–3.5 mm in diameter near midpoint, upper lip 12.5–16.5 mm long, 2-lobed at apex, lobes 0.2–0.7 mm long, lower lip spreading, 13–16 mm long, lobes 4–8 mm long, 1.8–3.5 mm wide. Stamens inserted near apex of corolla tube, 16–19 mm long, filaments glabrous, thecae 1.6–2.5 mm long, equal to subequal, subparallel to subperpendicular, equally to subequally inserted, glabrous, lacking basal appendages; pollen (Fig. 23b) 2-aperturate, apertures flanked on each side by 2–3 rows of insulae (third row sometimes of peninsulae), exine reticulate. Style 25–33.5 mm long, proximally pubescent with eglandular trichomes, stigma 0.3 mm long, lobes indistinct. Capsule 12–14.5 mm long, pubescent with erect to retrorse glandular and eglandular trichomes 0.05–0.1 mm long, stipe 4.5–5 mm long, head subellipsoid with a medial constriction, 7–9.5 mm long. Seeds 4, dark brown, compressed, 2.8–3.3 mm long, 2.3–2.7 mm wide, 0.9–1 mm thick, surfaces and margin bubbly tuberculate. (chromosome number unknown).

PHENOLOGY. — Flowering: October–March; fruiting: February–March.

DISTRIBUTION AND HABITAT. — Endemic to Baja California Sur (Fig. 7) where the species is known from the Cape Region, the Sierra de la Giganta, and the Sonoran Desert (Central Gulf Coast and Vizcaíno subdivisions); plants occur along watercourses and on slopes in thornscrub and desertscrub from 150–625 m elevation.

ADDITIONAL SPECIMENS EXAMINED. — MEXICO. **Baja California Sur**: without locality [vic. of San José del Cabo], *T. Brandegee s.n.* (UC); Sierra de la Giganta, Tanque de la Vuelta del Diablo, Mesa de San Alejo, W of San Javier, ca. 25°50′N, 111°34′W, *A. Carter & H. Sharsmith 4164* (CAS, SD, UC); SE edge of Viscaíno Desert, 27 km NW of San Ignacio, *A. Carter et al. 1964* (DS, CAS, UC); 19.2 km SW of San José del Cabo, *A. Carter et al. 2236* (CAS pro parte); Sierra de San Francisco, 50 km ENE of San Ignacio, W of Tres Vírgenes, Cañón Salsipuedes, *D. Charlton s.n.* (UCR); Cape Region, *C. Grabendorffer s.n.* (UC); 3 mi N of San José Comondú, ca. 26°05′N, 111°48′W, *R. Moran & J. Reveal 20054* (SD); ca. 18 mi NW from San Ignacio on rd to El Arco, *J. Thomas 8323* (CAS, DS, UC).

Brandegee (1915) included *Justicia palmeri* Rose within his *J. hians*. Leonard (1942) noted that *Brandegee s.n.* 21 Mar 1889 from cliffs at Comondú (i.e., the type of *J. hians*) represents the same taxon as his *J. wigginsii*. Leonard further noted that *J. wigginsii* is unusual in having the inflorescence of *J. hians* and the corolla of *J. mexicana* Rose, but that it differed from both by its irregular calyx. Subsequently, Leonard (1964) treated *J. wigginsii* as a synonym of *J. hians*.

As currently known, this species occurs over a broad area of Baja California Sur. Label information on Brandegee's collection from the Cape Region does not specify a locality but provides a date, 4 Sep 1893. According to Moran (1952), on this date, Brandegee was in the vicinity of San José del Cabo. *Carter 2236* at CAS from the southern Cape Region contains both *J. californica* and a shoot of *J. hians*. Because *J. hians* is known from a nearby locality her collection is assumed to represent a mixed gathering rather than subsequent confusion in arranging specimens.

Graham (1988) treated *J. hians* as a species peripheral to *Justicia* section *Sarotheca* (Nees) Benth. Gentry (1949) concluded that this species was a postinsular endemic of the Cape District. A likely sister species or close relatives remain to be determined.

5. **Justicia insolita** Brandegee, Proc. Calif. Acad. Sci., ser. 2, 2:195. 1889. TYPE. — MEXICO. **Baja California Sur**: San Gregorio, 6 Feb 1889, *T. Brandegee s.n.* (holotype: UC!; isotype: US).

Ascending to erect perennial herbs to shrubs to 1 m tall. Young stems subterete to subquadrate, evenly (and variously) pubescent (see below). Leaves subsessile to petiolate, petioles to 7 mm long (petiolar stubs to 0.5 mm long remaining at nodes after leaves fall), blades ovate to lance-elliptic to elliptic, 7–45 mm long, 5–22 mm wide, 0.9–4.7 times longer than wide, rounded to acute to acuminate at apex, rounded to acute to attenuate at base, surfaces pustulate and pubescent with erect to flexuose to antrorse to antrorsely appressed eglandular trichomes to 1.2 mm long and sometimes with inconspicuous stipitate glandular trichomes 0.05–0.1 mm long as well on distal leaves, margin entire to subsinuate. Inflorescence of (axillary and) terminal dichasiate spikes to 120 mm long, these sometimes branched at base and becoming a panicle of spikes to 160 mm long, rachis evenly pubescent with glandular trichomes 0.05–0.3 mm long (and sometimes with some eglandular trichomes like those of young stems intermixed with glands near base of spike); dichasia alternate, 1-flowered, 1 per axil, sessile in axils of bracts. Bracts opposite, sessile to subsessile, ovate-elliptic to elliptic to linear to obovate, 1.8–4 mm long, 0.7–1.7 mm wide, abaxial surface pubescent like rachis (and sometimes with some antrorsely appressed eglandular trichomes to 0.2 mm long as well). Bracteoles sessile to subsessile, lance-ovate to lanceolate to linear-elliptic to elliptic to obovate-elliptic, 2.7–4.7 mm long, 0.6–1.2 mm wide, abaxial surface pubescent like rachis. Flowers sessile to subsessile (i.e., pedicels to 1 mm long). Calyx 4-lobed, 4.5–9.4 mm long, lobes linear to lanceolate, 3.5–8 mm long, subequal in length, 1–1.5 mm wide, abaxially pubescent like rachis. Corolla white to pinkish and reddish pink (i.e., upper lip white to light pink and lower lip dark reddish pink with white markings on lower-central lobe), 15–22 mm long, externally pubescent with erect to flexuose glandular and eglandular trichomes 0.05–0.5 (–1) mm long, tube subsaccate on anterior side, not expanded distally, 4–8.5 mm long, 4.5–6 mm in diameter near midpoint, upper lip 10–16 mm long, 2-lobed at apex, lobes

0.5–2 mm long, lower lip spreading, 11–16 mm long, lobes 4–9 mm long, 3.5–9 mm wide. Stamens inserted near apex of corolla tube, 10–16 mm long, filaments glabrous or glandular proximally, thecae 1.5–3 mm long (including basal appendage), equal to unequal, subparallel to subperpendicular, unequally inserted (overlapping by 0.5–1.3 mm), dorsally pubescent with glandular and eglandular trichomes, lower theca with a ± bulbous basal appendage to 0.6 mm long, connective sometimes extended beyond upper theca as a broad deltate projection; pollen (Fig. 23c, d) 2-aperturate, apertures flanked on each side by 1 row of insulae (to peninsulae), exine reticulate. Style 13–18 mm long, pubescent with eglandular (and sometimes glandular proximally) trichomes, stigma lobes 0.1–0.2 mm long, unequal, or lobes indistinct. Capsule 13–21 mm long, pubescent with erect to retrorse glandular and eglandular trichomes 0.05–0.6 mm long, stipe 4.5–9.5 mm long, head subellipsoid with medial constriction, 8–13 mm long. Seeds 4, light brown, compressed, 2.5–3.5 mm long, 2–3.7 mm wide, 0.8–1.2 mm thick, surfaces and margin covered with retrorsely barbed (especially near apex) trichomes 0.2–0.3 mm long. (*n* = 12, Daniel et al. 1984). Fig. 24.

PHENOLOGY. — Flowering and fruiting: October–May.

DISTRIBUTION. — Endemic to Baja California Sur (Fig. 25) where the species is known from the Cape Region (mostly in nondesert portions), the Sierra de la Giganta, and the Sonoran Desert (Central Gulf Coast and Magdalena subdivisions).

Graham (1988) did not include this species in her classification of *Justicia*. In many features of the inflorescence, flower, pollen, and fruit *J. insolita* resembles *J. salviiflora* Kunth, a widespread Mexican species that might be expected to occur in the Cape Region of Baja California Sur.

Two varieties of *J. insolita* have been recognized based on features of the branches and pubescence. The distinctions between these taxa, noted in the key below, were found to be consistent among all specimens examined. I choose to elevate the varieties to the rank of subspecies based on these minor differences which are correlated with their allopatric distributions. Such treatment is consistent with that utilized here for the subspecies of *Holographis virgata* and *Ruellia californica*.

Key to the Subspecies of *Justicia insolita*

1. Branches ± divaricate and becoming spinescent at tips; epidermis of young stems not visible, covered by kinky-appressed trichomes 0.1–0.5 mm long giving the stems a conspicuously pallid aspect; corolla externally pubescent with trichomes 0.05–0.2 mm long; plants occurring from La Paz northward (i.e., north of lat. 24°05′N) . . . . subsp. *insolita*.
1. Branches neither divaricate nor spinescent; epidermis of young stems clearly visible, cauline trichomes erect to flexuose, (0.2–) 0.4–1.2 mm long, stems not appearing pallid; corolla externally pubescent with trichomes 0.1–0.5 (–1) mm long; plants occurring to the south of La Paz (i.e., south of lat. 24°05′N) . . . . subsp. *tastensis*.

5a. Justicia insolita subsp. insolita

Branches ± divaricate, becoming spinescent at tips; young stems densely pubescent with kinky-appressed eglandular (to glandular) trichomes 0.1–0.5 mm long giving the stems a conspicuous pallid aspect, epidermis not visible. Corolla externally pubescent with trichomes 0.05–0.2 mm long. (*n* = 12, Daniel et al. 1984). Fig. 24a, b, e, and f.

DISTRIBUTION AND HABITAT. — The subspecies is known from regions of the Sierra de la Giganta and the Sonoran Desert (Central Gulf Coast and Magdalena subdivisions) to the north of lat. 24°05′N (Fig. 25); plants occur along rocky and sandy watercourses in desertscrub and thornscrub from 25–600 m elevation.

ADDITIONAL SPECIMENS EXAMINED. — MEXICO. **Baja California Sur**: N Sierra de la Giganta, 11.2 mi W of Hwy 1 on rd from Rosarito to San Isidro, ca. 26°21′N, 111°45′W, *S. Boyd & T. Ross 5949* (RSA); Cape Region, *T. Brandegee s.n.* (UC); ridge W of summit of Cuesta de Las Parras, 20 km W of Loreto on rd to San Javier, ca. 25°57′N, 111°30′W, *A. Carter 5711* (CAS, UC); Arroyo Carrizal, E of Rancho El Horno, NE of San Xavier, ca. 25°53′N, 111°31′W, *A. Carter & R. Ferris 3827* (CAS, SD, UC); Sierra de la Giganta, between La Victoria and portezuelo to the E, ca. 25°52′N, 111°25′W, *A. Carter & R. Ferris 3916*

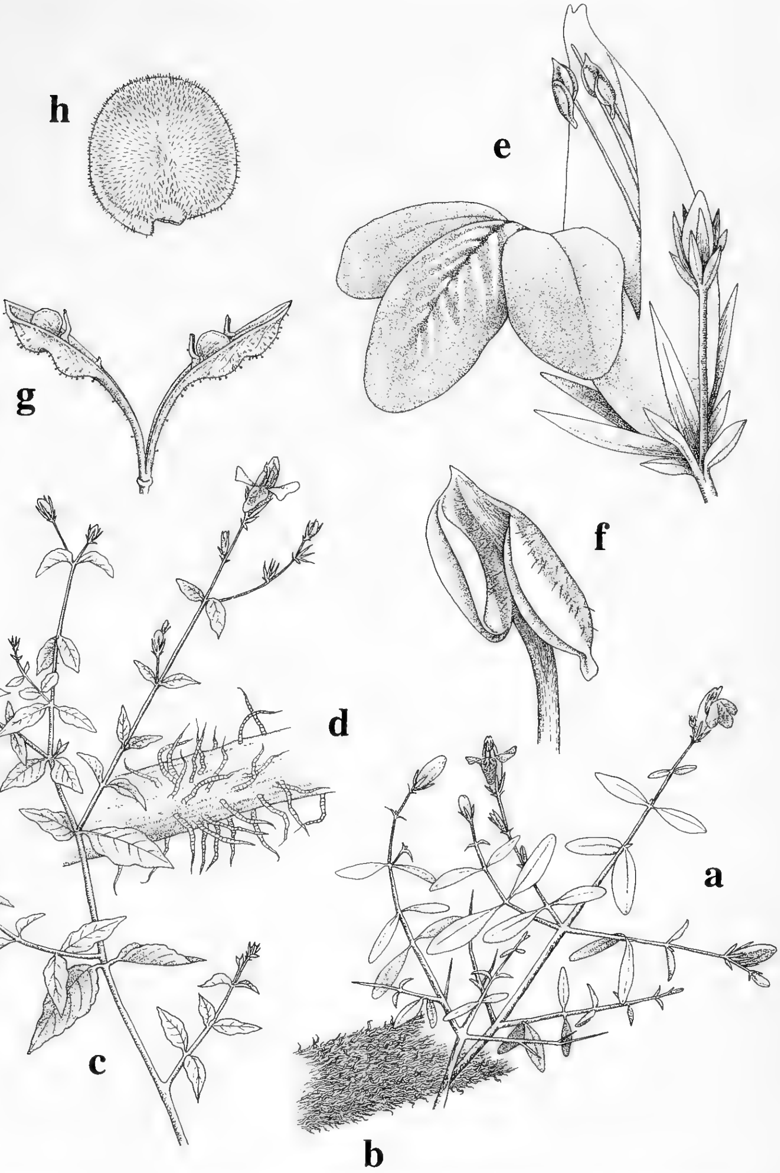


FIGURE 24. *Justicia insolita*. (a, b, e, f from subsp. *insolita*, c, d, g, h from subsp. *tastensis*). a. habit (*Johnston 3702*, *Wiggins 15207*, and *Wiggins 17444*), × 0.5; b. young stem (*Wiggins 17444*), × 10; c. habit (*Moran 7132*), × 0.5; d. young stem (*Moran 7107*), × 10; e. inflorescence node with flower (*Daniel et al. 2451*), × 3; f. anther (*Daniel et al. 2451*), × 9; g. capsule (*Thomas 7871*), × 1.5; h. seed (*Thomas 7871*), × 5. Drawn by Jenny Speckels.

(UC); 11.9-14.5 mi W of Hwy 1 in Rosarito, *T. Daniel 1929.5* (CAS); along Hwy 1 in S end of Sierra de la Giganta, 38.3 mi NW of jct Hwy 11 in La Paz, *T. Daniel et al. 2451* (ASU, BR, CAS, MEXU); "Puente Viejo," 15 km S de La Purísima, 26°09′N, 112°06′W, *R. Domínguez C. 1082* (HCIB); 10 mi W of Comondú, *H. Gentry 4081* (DS, UC); Santa Margarita Island, *D. Johansen 619* (DS); San Nicholas Bay, *I. Johnston 3702* (CAS); La Paz, *M. Jones 24418* (GH, POM); Pulpito Bay, ca. 26°30′N, 111°28′W, *R. Moran 9082* (RSA, SD); near KM 40 on hwy between La Paz and Santo Domingo, *J. Thomas 8460* (CAS, DS); 8 mi S

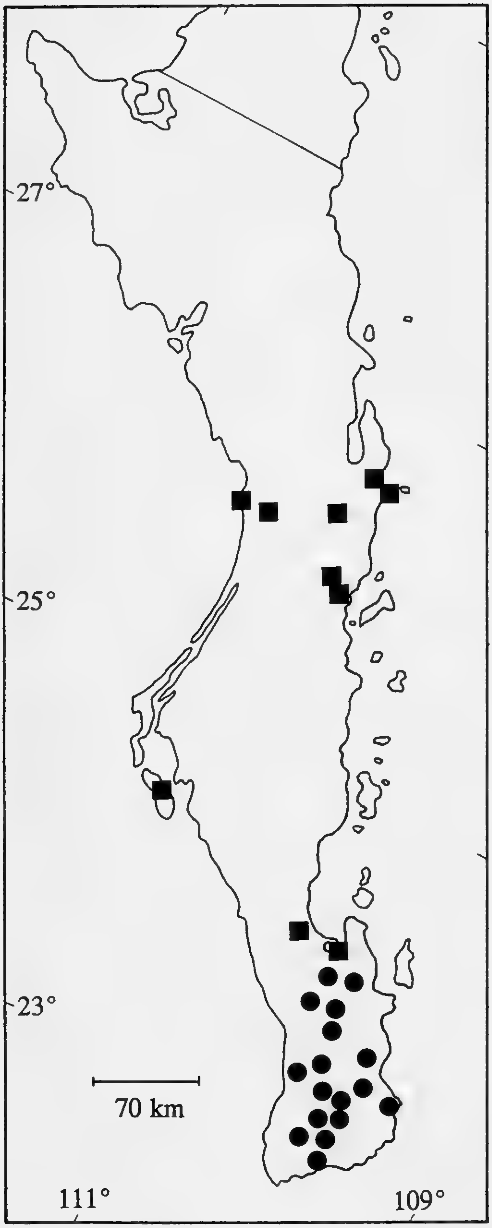


FIGURE 25. Distribution of *Justicia insolita* subsp. *insolita* (squares) and subsp. *tastensis* (circles).

of Río de la Purísima, 26°03′N, 112°08′W, *I. Wiggins 15207* (CAS, DS, UC); S side of Punta El Pulpito, 26°30′N, 111°28′W, *I. Wiggins 17444* (DS).

5b. Justicia insolita subsp. **tastensis** (Brandegee) T. F. Daniel, stat. nov. *Justicia insolita* var. *tastensis* Brandegee, Zoe 5:173. 1903. TYPE. — MEXICO. **Baja California Sur**: Sierra de la Laguna, El Taste region, Jan–Mar 1901, *C. Purpus 511* (holotype: UC!).

Branches ascending, not becoming spinescent at tips; young stems pubescent with erect to flexuose eglandular trichomes (0.2–) 0.4–1.2 mm long and sometimes (especially distally) with an understory of subsessile to stipitate glandular trichomes to 0.05 mm long, the stems not appearing pallid, epidermis clearly visible. Corolla externally pubescent with trichomes 0.1–0.5 (–1) mm long. (*n* = 12, from *Daniel & Butterwick 6938*). Fig. 24c, d, g, h.

DISTRIBUTION AND HABITAT. — Endemic to the Cape Region (south of lat. 24°05′N; Fig. 25) where the subspecies is known primarily from nondesert areas (at least one collection may have been made in a portion of the Cape Region occupied by the Central Gulf Coast subdivision of the Sonoran Desert); plants occur along watercourses and on rocky slopes mostly in thornscrub and tropical deciduous forest from 40–900 m elevation.

ADDITIONAL SPECIMENS EXAMINED. — MEXICO. **Baja CaliforniaSur:** Sierra de la Laguna, *T. Brandegee s.n.* (UC); 20 km S of Miraflores, *A. Carter et al. 2189* (DS, UC); Arroyo La Huerta, near Hwy 286 between La Paz and San Juan de los Planes, 2.7 km SE of La Huerta, ca. 24°03′N, 110°09′W, *T. Daniel & M. Butterwick 6836* (CAS); along rd from Hwy 1 across Cape Region mts to Hwy 19, 16-20 km W of Hwy 1, ca. 23°14′N, 109°55′W, *T. Daniel & M. Butterwick 6938* (BR, CAS, MEXU, MICH, SBBG, US); Rancho La Burrera, W slope of Sierra de la Laguna, ca. 22 km NE of Todos Santos, ca. 23°31′N, 110°02′W, *T. Daniel et al. 6864* (CAS, HCIB); San José del Cabo, *E. Dawson 1200* (RSA); subida a La Sierra de La Laguna, Agua el Palmillar, 23°29′N, 109°58′W, *M. Domínguez L. 367* (HCIB); near San Bartolo, *F. Gander 9774* (CAS, SD); Cape District, El Triunfo, *H. Gentry 4334* (DS); Sierra Laguna, La Burrera, *H. Gentry 4439* (DS, UC); Rancho La Huerta area, ca. 12 km SE of La Paz toward San Juan de los Planes, ca. 24°02′N, 110°09′W, *D. Harder & W. Appleby 1098* (RSA); Todos Santos, *M. Jones 24417* (POM); Laguna Mts, Cota Ranch, 14 mi E of Todos Santos, *M. Jones 24419* (POM), *24649* (GH, POM); Cañón de La Burrera cerca de Todos Santos, "El Palmillar," 23°33′N, 110°02′W, *J. León de la Luz 2334* (CAS, HCIB); Cape Region, 9.5 km N of Santiago, ca. 23°33′N, 109°42′W, *R. Moran 7107* (DS, RSA, SD);

Cape Region, 12 km SE of San Pedro, ca. 23°50′N, 110°11′W, *R. Moran 7132* (CAS, DS, SD); La Paz, *E. Palmer 40* (GH); Santiago, 3 mi S of Caduano, *R. Peters 20* (UC); 3.5 mi E of San Bartolo, *D. Porter 289* (DS), *294* (CAS, DS); Rincón, 8.7 km SE of La Ribera between Punta Arena and Cabo Pulmo, ca. 23°30′N, 109°25′W, *A. Sanders et al. 3316* (UCR); 24 mi S of La Paz, *F. Shreve 7208* (DS, UC); Cape Region, vicinity of Rancho La Burrera, ca. 11 mi E of Todos Santos, *J. Thomas 7871* (CAS, DS, SD); 16 mi S of San Pedro, *J. Whitehead 854* (DS); between La Paz and San Pedro, *I. Wiggins 5584* (CAS, DS, POM, UC); just N of San José del Viejo, *I. Wiggins 14715* (DS); 7.1 mi S of Caduano, between Santa Anita and La Palma, *I. Wiggins 14729-A* (CAS, DS).

6. Justicia palmeri Rose in Vasey & Rose, Contr. U. S. Natl. Herb. 1:75. 1890. TYPE. — MEXICO. **Baja California Sur**: vicinity of La Paz, 20 Jan–5 Feb 1890, *E. Palmer 97* (holotype: US; isotype: UC!).

Beloperone californica var. *conferta* Brandegee, Proc. Calif. Acad. Sci., ser. 2, 2:194. 1889. *Justicia californica* var. *conferta* (Brandegee) D.N. Gibson, Fieldiana, Bot. 34:67. 1972. TYPE. — MEXICO. **Baja California Sur**: San Julio Cañón, 20 Apr 1889, *T. Brandegee s.n.* (holotype: UC!; isotype: US!).

Beloperone intermedia M. E. Jones, Contr. W. Bot. 18:66. 1933. TYPE. — MEXICO. **Baja California Sur**: Sierra Giganta, Cayuca Ranch, Loreto, 23 Oct 1930, *M. Jones 27436* (holotype: POM!).

Shrubs to 3 m tall. Young stems multi-grooved (especially evident on older stems) and subterete to subquadrate, densely and evenly pubescent with retrorse to retrorsely appressed eglandular trichomes 0.2–0.3 mm long giving the stem a conspicuously pallid aspect, epidermis not (or barely) visible. Leaves petiolate, petioles to 15 mm long (petiolar stubs to 2 mm long remaining at node after leaves have fallen), blades lanceolate to ovate to elliptic, 5.5–80 mm long, 3–36 mm wide, 1.4–4.8 times longer than wide, rounded to acute to acuminate at apex, acute to subattenuate at base, surfaces sparsely pubescent with erect to antrorse eglandular trichomes, margin entire. Inflorescence of dichasia in leaf axils or in axils of subfoliose bracts along axillary sessile to pedunculate dichasiate spikes to 25 (–65) mm long, spikes (if present) opposite or alternate, rachis (if present) pubescent like young stems; dichasia alternate along spikes, 1-flowered, 1 per axil, sessile to pedunculate, peduncles to 2 mm long. Bracts (if present) subfoliose, opposite, petiolate, obovate to elliptic, (5–) 7–17 mm long, 2–8 mm wide, abaxial surface pubescent like leaves. Bracteoles subfoliose, petiolate, spatulate to oblanceolate to obovate to elliptic, 4–13 mm long, 1–4.5 (–5.5) mm wide, abaxial surface pubescent like leaves. Flowers sessile. Calyx 5-lobed, 2.2–6 mm long, lobes triangular to lance-subulate to subulate, 1.5–5 mm long, equal to subequal in length, 0.7–1.2 mm wide, abaxially pubescent with antrorse to antrorsely appressed eglandular trichomes 0.05–0.2 mm long. Corolla red to orange-red, sometimes with faint white markings on lower central lobe, (22–) 27–37 mm long, externally pubescent with erect to retrorse eglandular trichomes less than 0.05–0.2 mm long, tube gradually expanded distally, (11.5–) 15–21 mm long, 2.2–3.6 mm in diameter near midpoint, upper lip 9–19 mm long, 2-lobed at apex, lobes 0.1–1 mm long, lower lip spreading, 8–20 mm long, lobes 2.5–10 mm long, 1.5–5 mm wide. Stamens inserted near apex of corolla tube, 13–17 mm long, filaments proximally pubescent with glandular and/or eglandular trichomes, thecae 1.4–2.5 mm long (including basal appendage), subequal, parallel to subperpendicular, unequally inserted (overlapping by 0.9–2 mm), dorsally glabrous, lower theca with a ± bulbous basal appendage to 0.3 mm long; pollen (Fig. 26a) 2-aperturate, apertures flanked by 2 rows of insulae, exine reticulate. Style 20–32.5 mm long, glabrous, stigma lobes 0.2–0.3 mm long, equal. Capsule 10–16 mm long, glabrous, stipe 3.5–8 mm long, head subellipsoid, 6–9 mm long. Seeds 4, brownish or sometimes ± orangish, compressed, 3–3.8 mm long, 2.5–3.6 mm wide, 0.8–1.3 mm thick, surfaces and margin covered with rounded ± bubbly tubercles. (*n* = 14, from *Daniel & Butterwick 6843*).

PHENOLOGY. — Flowering: August–April; fruiting: September–April.

DISTRIBUTION AND HABITAT. — Endemic to Baja California Sur (Fig. 27) where the species is known from the Cape Region, the Sierra de la Giganta, and the Sonoran Desert (Central Gulf Coast and Vizcaíno subdivisions); plants occur in and along watercourses, on slopes, on sandy plains, and on barren lava in desertscrub, thornscrub, and tropical deciduous forest from near sea level to 1125 m elevation.

Additional Specimens Examined. — MEXICO. **Baja California Sur:** Todos Santos, *T. Brandegee 445* (UC); San José del Cabo, *T. Brandegee 446* (GH, UC); San José del Cabo, *T. Brandegee 447* (GH); San José del Cabo, *T. Brandegee s.n.* (UC); Cape Region, *T. Brandegee s.n.* (UC); 6-10 mi SE of Todos Santos-Cabo San Lucas Hwy on small rd to Rancho La Burrera, *D. Breedlove & D. Axelrod 43189* (CAS); Sierra de la Giganta, La Esperanza, ca. 25°48′N, 111°24′W, *A. Carter 4400* (UC); Sierra de la Giganta, vicinity of Rancho Agua Escondido (ca. 90 km E of Villa Constitución), ca. 25°06′N, 111°W, *A. Carter 4744* (UC); Sierra de la Giganta, NW slopes of Mesa de Alta Gracia, SW of La Cumbre de Alta Gracia, ca. 25°41′N, 111°21′W, *A. Carter 4889* (CAS, UC); Sierra de la Giganta, vicinity of Ojo de Agua del Carrizal, N from Rancho Viejo (on rd from Loreto to San Javier), ca. 25°59′N, 111°31′W, *A. Carter 5006* (UC); Sierra de la Giganta, N side Cerro Gabilán, S of Portezuelo de Gabilán, ca. 25°51′N, 111°25′W, *A. Carter 5091* (CAS, UC); Sierra de la Giganta, Cerro del Pinto, N of Portezuelo de San Antonio, headwaters of Arroyo el Coyote, ca. 24°50′N, 110°44′W, *A. Carter 5442* (CAS, UC); Cape Region, La Hiedra, near headwaters of arroyo NW of El Encinal, 23°10′N, 109°57′W, *A. Carter & F. Chisaki 3471* (DS, UC); Sierra de la Giganta, side arroyo heading into Mesa San Alejo, SW of Rancho El Horno (NE of San Xavier), ca. 25°53′N, 111°33′W, *A. Carter & R. Ferris 3768* (UC); Sierra de la Giganta, Arroyo Carrizal, E of Rancho El Horno (NE of San Xavier), ca. 25°53′N, 111°31′W, *A. Carter & R. Ferris 3818* (UC); near portezuelo E of La Victoria, ca. 25°52′N, 111°25′W, *A. Carter & R. Ferris 3912* (CAS, UC); Sierra de la Giganta, Cañón de Tiojo, S of La Victoria, ca. 25°51′N, 111°25′W, *A. Carter & R. Ferris 3953* (CAS, UC); Sierra de la Giganta, head of S branch of Cañada de Teojo in vicinity of Portezuelo de Peloteado (SW of Notrí), ca. 25°49′N, 111°23′W, *A. Carter & F. Leal 4650* (UC); Sierra de la Giganta, ridge of Cerro de la Palma, W of Puerto Escondido, ca. 25°49′N, 111°23′W, *A. Carter & R. Moran 5498* (CAS, UC); Sierra de la Giganta, vicinity of Cajón de la Mesa de San Alejo (W of San Javier), ca. 25°52′N, 111°34′W, *A. Carter & H. Sharsmith 4182* (UC); Arroyo Tabor, W of Puerto Escondido, ca. 25°48′N, 111°20–21′W, *A. Carter & H. Sharsmith 4249* (CAS, SD, UC); Sierra de la Giganta, El Aguaje, between Arroyo Hondo and Arroyo de Las Palmas, NW slopes of Cerro Giganta, ca. 26°08′N, 111°35′W, *A. Carter & M. Sousa S. 5189* (UC); 10.4 km SW of San José del Cabo, *A. Carter et al. 2208* (UC); Sierra de la Giganta, Picacho Humí, Mesa de Humí, crest of Sierra Giganta E from Villa Constitución, ca. 25°03′N, 110°57′W, *A. Carter et al. 5770* (CAS, UC); near base of S-most of Tres Vírgenes volcanoes, 25 mi W of Santa Rosalía, W side of pass, *K. Chambers 766* (DS, SD, UC); Central Gulf Desert Highlands, Sierra San Francisco, 6.9 mi W of Rancho San Francisco, *D. Charlton 84* (UCR); Cape San Lucas, 1 mi from beach, *T. Craig 623* (POM); Arroyo La Huerta, near Hwy 286 between La Paz and San Juan de los Planes, 2.7 km SE of La Huerta, ca. 24°03′N, 110°09′W, *T. Daniel & M. Butterwick 6843* (BR, CAS, ENCB, HCIB, K, MEXU, MICH, MO, SBBG, US); between Santiago and Agua Caliente, 2.7–5 km SW of Santiago, ca. 23°27′N, 109°45′W, *T. Daniel & M. Butterwick 6871 (CAS), 6876* (ASU, CAS, MEXU, MO); along rd from Hwy 1 across Cape Region mts to Hwy 19, ca. 3.5 km NE of San Pedro de la Soledad, ca. 23°15′N, 109°57′W, *T. Daniel & M. Butterwick 6946* (CAS); along Hwy 19, ca. 16 km NW of Cabo San Lucas, ca. 23°00′N, 110°02′W, *T. Daniel & M. Butterwick 6960* (CAS, ENCB); along Hwy 13 in the Sierra de la Laguna, ca. 0.5 mi NW of La Huerta, *T. Daniel et al. 2478* (ASU); along rd to Microondas San Bartolo, ca. 1–3 mi W of Hwy 1 in San Bartolo, *T. Daniel et al. 2531* (ASU); along Hwy 19 just S of Microondas El Carrizal, ca. 5.6 km S of jct Hwy 1 S of San Pedro, ca. 23°50′N, 110°14′W, *T. Daniel et al. 6847* (CAS, HCIB, SBBG, MEXU); San José del Cabo, *E. Dawson 1175* (RSA); 1–2 mi inland from Agua Verde Bay, *E. Dawson 6245* (RSA); "La Parrita," Rancho La Burrera, NE de Todos Santos, 23°35′N, 110°00′W, *M. Domínguez L. 259* (HCIB); Rancho Matancitas, 23°04′N, 110°01′W, *R. Domínguez C. 769* (RSA); Comondú, *F. Gander 9640* (CAS, RSA, SD); near Tres Vírgenes volcanoes, ca. 20 mi W of Santa Rosalía, *B. Hammerly 118* (CAS, DS); 2 mi W (below) Comondú, *B. Hammerly 183* (CAS, DS); between San José del Cabo and Cape San Lucas, *C. Harbison s.n.* (SD); 23.4 mi W of La Paz, along paved rd to Santo Domingo, *J. Hastings & R. Turner 64-177* (DS, SD); 2.5 mi NE of summit of Volcán Tres Vírgenes, 27°30′N, 112°33′W, *J. Henrickson 9009b* (SD); Todos Santos, *M. Jones 24420* (POM); San José del Cabo, *M. Jones 24421* (POM); Cayuca Ranch near Loreto, *M. Jones 27391* (A, DS, POM); Cayuca Ranch, Loreto, *M. Jones 87436* (UC); Cayuca Ranch, Loreto, *M. Jones 97391* (UC); Cape Region, 11 km N of Santa Anita, ca. 23°15′N, 109°42′W, *R. Moran 6928* (CAS, DS, SD); N base of Volcán las Tres Vírgenes, ca. 27°29′N, 112°36′W, *R. Moran 20465* (POM, SD); N base of Volcán las Tres Vírgenes, ca. 27°29′N, 112°36′W, *R. Moran 21371* (CAS, POM, RSA, SD); 10.1 mi N of Todos Santos on rd to La Paz, *D. Porter 80* (CAS, DS); main hwy, 21 mi W of La Paz, *D. Porter 392* (CAS, DS); Cape Region, San Felipe, *C. Purpus 470* (UC); San José del Cabo, *C.*

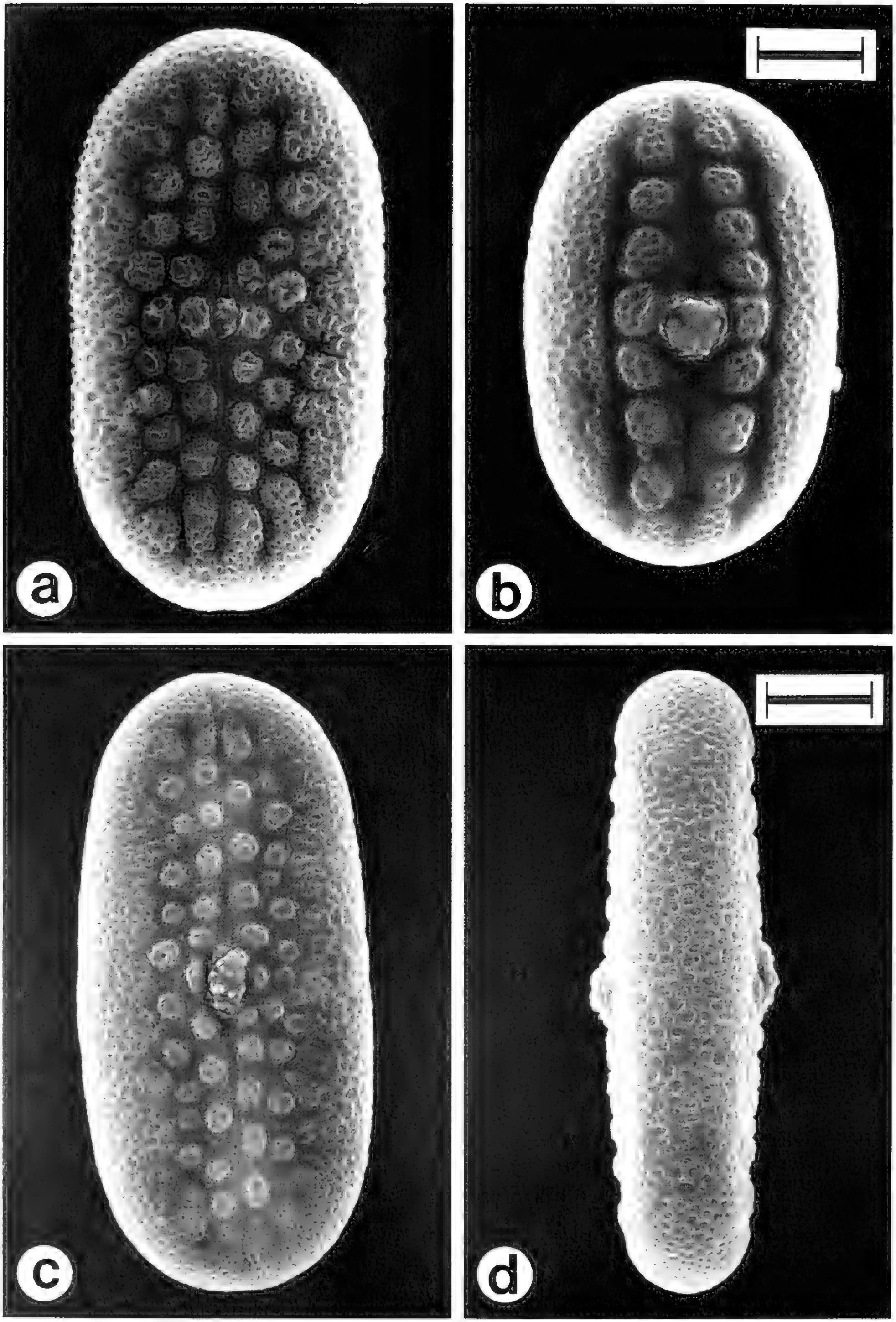


FIGURE 26. Pollen. a. *Justicia palmeri* (*Carter 5442*), apertural view; b. *J. purpusii* (*Moran 6941*), apertural view; c. *J. spicigera* from Veracruz (*Avila B. 28*), apertural view; d. *J. spicigera* (*Avila B. 28*), interapertural view. Scale for a and b = 10 µm; scale for c and d = 12.5 µm.

Purpus s.n. (UC); Juncalito Bay area, 14 mi S of Loreto, *J. Reeder & C. Reeder 7063* (SD, UC); 31 km S of La Paz near San Pedro, ca. 1 km N jct Hwys 1 and 19, ca. 23°50′N, 110°11′W, *A. Sanders et al. 3300* (UCR); Rincón, 8.7 km SE of La Ribera, between Punta Arena & Cabo Pulmo, ca. 23°30′N, 109°25′W, *A. Sanders et al. 3322* (CAS, UCR); just off Hwy 1 along rd to Juncalito, ca. 15 mi S of Loreto, *R. Spjut 5414* (CAS); 12 mi N of Todos Santos, *J. Whitehead 858* (DS); 3.8 mi E of Los Planes, *I. Wiggins 14455* (CAS, DS, UC); 0.5 mi N of fork in rd to Rancho San Pedro, near Rancho La Presa, ca. 24°51′N, 111°04′W, *I. Wiggins 15482* (CAS, DS); 10 mi S of Mission Dolores, ca. 25°00′N, 110°47′W, *I. Wiggins et al. 318* (DS, UC); .

Justicia californica var. *conferta* is included in the synonymy of *J. palmeri* for the first time. Study of the holotype of the former taxon reveals that it resembles the latter species in all of the diagnostic characteristics (especially the petiolate and spatulate to oblanceolate bracteoles) noted above in the key to species.

Justicia palmeri and similar species (e.g., *J. candicans* (Nees) L. D. Benson, *Jacobinia roseana* Leonard, and *Jacobinia mexicana* Seem.) form a widely-distributed complex that is deserving of considerable further study. *Justicia palmeri* appears to be distinct within this complex by its cauline pubescence (vs. glabrous or variously pubescent but not resembling that of *J. palmeri*) and petiolate (vs. sessile) bracteoles that vary in shape from spatulate to obovate to elliptic (vs. triangular to subulate to linear to lanceolate). It remains to be seen whether these distinctions sufficiently circumscribe a taxon deserving specific status or if subspecific status would more appropriately reflect the geographic and morphological attributes noted herein. Graham (1988) did not include *J. palmeri* in her classification of *Justicia*.

7. Justicia purpusii (Brandegee) D. N. Gibson, Fieldiana, Bot. 34:73. 1972. *Beloperone purpusii* Brandegee, Zoe 5:172. 1903. TYPE.— MEXICO. **Baja California Sur**: Cape Region, San Felipe [23°06′N, 109°50′W], Feb 1901, *C. Purpus 552* (holotype: UC!; isotypes: UC!, US).

Erect perennial herbs to shrubs to 2 m tall. Young stems multi-grooved and subterete to subquadrate, evenly pubescent with a dense understory of mostly erect eglandular (to subglandular) trichomes 0.05–0.2 mm long (often giving stems a pallid aspect) and an overstory of erect to flexuose eglandular (to subglandular) trichomes 0.3–2 mm long, epidermis not visible. Leaves petiolate, petioles to 35 mm long (petio-

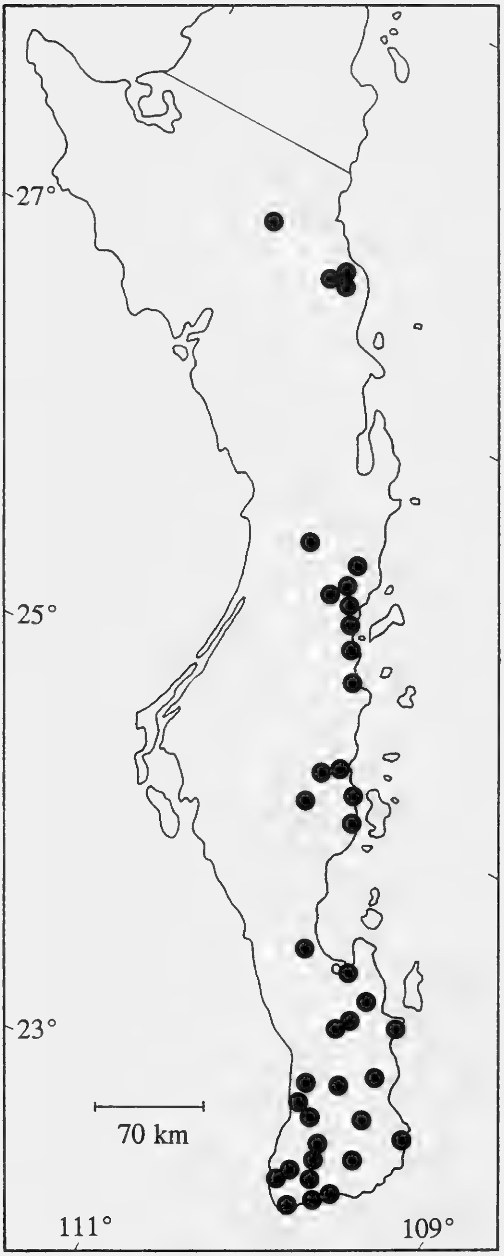


FIGURE 27. Distribution of *Justicia palmeri*.

lar stubs to 1.5 mm long remaining at nodes after leaves have fallen), blades cordate to ovate, 19–135 mm long, 12–70 mm wide, 1.4–2.2 times longer than wide, rounded to acute to acuminate at apex, cordate to truncate at base, surfaces pubescent with erect to flexuose eglandular trichomes to 1.2 mm long, margin entire to subsinuate. Inflorescence of terminal pedunculate subfoliose dichasiate thyrses to 250 mm long, rachises pubescent with an understory of mostly erect eglandular to subglandular to glandular trichomes 0.05–0.3 mm long and an overstory of coarse erect to flexuose eglandular to subglandular to glandular trichomes 0.3–4 mm long; dichasia (alternate to) opposite, 1-flowered, 1 per axil, pedunculate in axils of leaves or subfoliose bracts, peduncles to 21 mm long, pubescent like rachis. Bracts intergrading with leaves, persistent, opposite, subsessile to sessile, cordate to broadly ovate, 10–43 mm long, 8.5–36 mm wide, abaxial surface pubescent like rachis (or with both understory and overstory trichomes fewer). Bracteoles sessile, subulate to lanceolate to narrowly elliptic, 2–9 (–11) mm long, 0.3–0.7 (–1.6) mm wide, abaxial surface pubescent like bracts (except overstory trichomes often not as long). Flowers (sessile to) pedicellate, pedicels 0.5–3 mm long. Calyx 5-lobed, 9–23 mm long, lobes lanceolate, 8–22 mm long, subequal in length, 1–2.8 mm wide, abaxially and marginally pubescent like rachis. Corolla orange-red, 30–40 mm long, externally pubescent with erect to flexuose eglandular and glandular trichomes 0.05–0.7 mm long, tube expanded distally, 15–24 mm long, 3.5–5 mm in diameter near midpoint, upper lip 14–20 mm long, entire or 2-lobed at apex, lobes 0.1–1.5 mm long, lower lip spreading, 15–19 mm long, lobes 1.5–3.5 (–6) mm long, 1.5–3.5 mm wide. Stamens inserted near apex of corolla tube, 19–24 mm long, filaments proximally pubescent with eglandular trichomes, thecae 2.7–3.2 mm long (including basal appendage), equal, subparallel to subperpendicular, unequally inserted (overlapping by 1.6–2 mm), dorsally pubescent with eglandular trichomes, lower (and sometimes upper) theca with a ± bulbous basal appendage to 0.4 mm long; pollen (Fig. 26b) 2-aperturate, apertures flanked on each side by 1 row of insulae, exine reticulate. Style 28–36 mm long, glabrous or sparsely pubescent with eglandular trichomes proximally, stigma lobes 0.2 mm long, equal. Capsule 17–23 mm long, pubescent with an understory of erect to retrorse eglandular trichomes 0.2–0.3 mm long and an overstory of erect to flexuose to retrorse eglandular and glandular trichomes 0.4–2 mm long, stipe 8–12 mm long, head broadly subellipsoid to subglobose with a medial constriction, 9–11 mm long. Seeds 4, brown (often with darker brown mottling), subglobose to subcompressed, 2.6–3.6 mm long, 3–3.6 mm wide, 1.9–2.4 mm thick, surface smooth and lacking trichomes. ($n = 14$, Daniel et al. 1984).

PHENOLOGY. — Flowering: November–April; fruiting: January–April.

DISTRIBUTION AND HABITAT. — Endemic to the Cape Region of Baja California Sur (Fig. 28) where the species is known primarily (or exclusively ?) from nondesert areas; plants occur mostly in and along watercourses and on slopes in tropical deciduous forest and thornscrub from 270–1000 m elevation.

ADDITIONAL SPECIMENS EXAMINED. — MEXICO. **Baja California Sur**: Cañón de la Burrera, NE de Todos Santos, 23°32′N, 110°04′W, *R.D. C. 122* (CAS); ca. 1/3 way from Rancho San Bernardo to mouth of Arroyo de San Bernardo, E side Sierra de la Victoria, 23°24′N, 109°55′W, *A. Carter 2700* (DS, UC); Cape Region, between Rancho Palmilla and headwaters of arroyo NW of El Encinal, ca. 23°10′N, 109°58′W, *A. Carter & F. Chisaki 3594* (DS, SD, UC); Arroyo Santa Rita, from San Jorge to San Francisquito and La Chuparosa, E side Sierra de la Victoria, 23°29–31′N, 109°47–55′W, *A. Carter & R. Ferris 3317* (DS, SD, UC); SE from Rancho Poza Larga & Rancho La Ciruela, Arroyo de San Francisquito, E side Sierra de la Victoria, 23°29–31′N, 109°47–55′W, *A. Carter & R. Ferris 3396* (DS, SD, UC); along rd from Hwy 1 across Cape Region mts to Hwy 19, ca. 3.5 km NE of San Pedro de la Soledad, ca. 23°15′N, 109°57′W, *T. Daniel & M. Butterwick 6945* (CAS); along rd from Hwy 1 across Cape Region mts to Hwy 19, ca. 0.6 km W of San Pedro de la Soledad, ca. 23°14′N, 109°58′W, *T. Daniel & M. Butterwick 6950* (CAS); along rd to Microondas San Bartolo, ca. 1-3 mi W of Hwy 1 in San Bartolo, *T. Daniel et al. 2530* (ASU, CAS, K); Rancho La Burrera, W slope of Sierra de la Laguna, ca. 22 km NE of Todos Santos, ca. 23°31′N, 110°02′W, *T. Daniel et al. 6849* (BR, CAS, HCIB, MEXU, MICH, SBBG); Sierra Laguna, La Burrera, *H. Gentry 4436* (DS, UC); Miraflores, *M. Jones 24171* (A, GH, LA, SD, POM, UC); La Paz, *M. Jones 24424* (POM); Laguna Mts, Cota Ranch, 14 mi E of Todos Santos, *M. Jones 24426* (POM); SW of San

Bartolo toward microwave towers, *D. Keil et al. 16831* (UCR); "Pozas Cuatas," Cañón de La Zorra, NW de Santiago, 23°30′N, 109°52′W, *J. León de la Luz 2179* (CAS, HCIB); Sierra de la Laguna, Cañón de la Burrera, "El Palmillar," 23°29′N, 110°00′W, *J. León de la Luz 2553* (HCIB); Cape Region, 2 km below San Bartolo, ca. 23°44′N, 109°50′ W, *R. Moran 6941* (DS, RSA, SD); Cape Region, La Pastora, 9 km NE of Todos Santos, ca. 23°30′N, 110°17′W, *R. Moran 6982* (CAS, DS, SD); ca. 22 mi N of Todos Santos on coastal rd, 23°41′N, 110°33′W, *P. Mudie 903* (SD); La Paz, *E. Palmer 98* (GH); San Bartolo, base of La Ballena, near rd from San Antonio to San Bartolo, R. Peters 147 (UC); Cape Region, ca. 6 mi SW from Santiago, Arroyo San Marteo from Agua Caliente Springs and dam to ca. 0.25 mi upstream, *J. Thomas 7729* (DS, SD).

Graham (1988) treated *J. purpusii* as a species of uncertain position in the genus. Its closest relative appears to be *J. californica*. Both species have flowers in dichasiate thyrses, dorsally pubescent thecae, relatively large capsules, and subglobose to subcompressed seeds with a smooth surface. See additional discussion under *J. californica*.

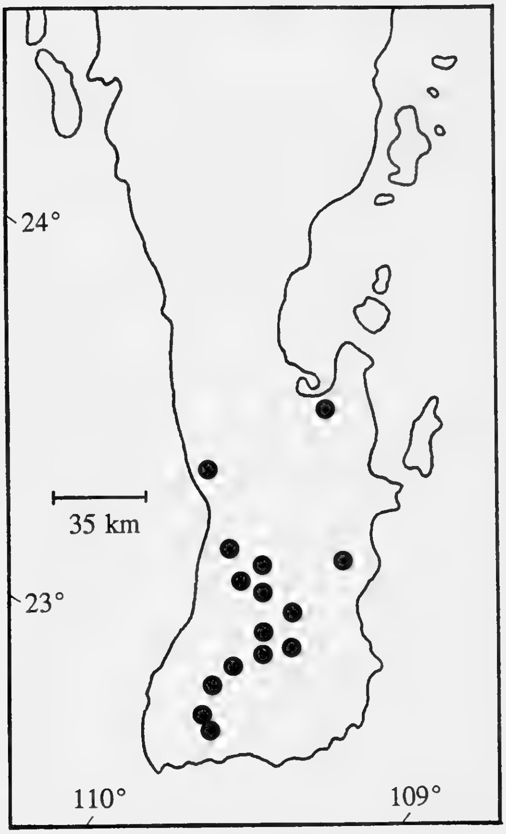


FIGURE 28. Distribution of *Justicia purpusii*.

8. Justicia spicigera Schltdl., Linnaea 7:395. 1832. *Jacobinia spicigera* (Schltdt.) L. H. Bailey, Stand. cycl. hort. 1715. 1915. TYPE.—MEXICO. **Veracruz**: Jalapa, May 1829, *A. Schiede s.n.* (syntype: B, destroyed; isosyntype: GH); cultivated at Hacienda de la Laguna, Jul 1829, *A. Schiede s.n.* (syntypes: B, destroyed, P!; isosyntype: BM!).

Justicia atramentaria Benth., Pl. hartw. 69. 1840. *Jacobinia atramentaria* (Benth.) S. F. Blake, Contr. Gray Herb. 52:103. 1917. TYPE.—MEXICO. **Oaxaca**: "Zonaguia" [Tonaguía], 1839, *T. Hartweg s.n.* (holotype: K!).

Sericographis mohintli Nees in A. DC., Prodr. 11:361. 1847, nom. illegit. (*Justicia spicigera* and *J. atramentaria* cited in synonymy). *Jacobinia mohintli* (Nees) Hemsl., Biol. cent.-amer., Bot. 2:521. 1882.

Sericographis moctli Nees in Nees & S. Schauer, Linnaea 20:715. Dec 1847. TYPE.—MEXICO. State undetermined: "in ditione Toluccana," *A. Aschenborn 101* (holotype: ?).

Sericographis neglecta Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1854:151. 1855. *Jacobinia neglecta* (Oerst.) A. Gray, Syn. fl. N. Amer. 2(1):395. 1878. *Justicia liebmanii* V.A.W. Graham, Kew Bull. 43:612. 1988, non *Justicia neglecta* T. Anders. (1863). TYPE.—MEXICO. **Veracruz**: Pital ved Río Nautla, Apr 1841, *F. Liebmann 10671* (syntype: C; isosyntype: K!); Colipa, Mar 1841, *F. Liebmann 10670* (syntype: C); Paso del Correo ved Río Tecoluta, Jun 1841, *F. Liebmann 10672* (syntype: C).

Jacobinia scarlatina S.F. Blake, Contr. Gray Herb. 52:102. 1917. *Justicia scarlatina* (S. F. Blake) V.A.W. Graham, Kew Bull. 43:612. 1988. TYPE.—BELIZE. **Belize**: near Manatee Lagoon, 12 May 1906, *M. Peck 430* (holotype: GH; isotype: K!).

Shrubs to 1 (–5) m tall. Young stems subterete to quadrate, sparsely to ± densely pubescent with antrorse to retrorse eglandular trichomes 0.5–1.2 mm long, trichomes ± evenly disposed (in ours) to concentrated in 2 lines. Leaves petiolate, petioles to 20 mm long (petiolar stubs to 0.5 mm long sometimes remaining at nodes after leaves have fallen), blades often blackening when dried, ovate-elliptic to elliptic to narrowly elliptic, 32–225 mm long, 7–67 mm wide, 2.2–4.6 times longer than wide, acute to acuminate at apex, acute to attenuate at base, surfaces pubescent (primarily along major veins) with cauline type trichomes or glabrous, margin entire to sinuate. Inflorescence of axillary pedunculate panicles of dichasiate spikes to 105 mm long (including peduncle and excluding flowers), inflorescence bracts triangular to subulate to lanceolate to obovate, 1–5 mm long, 0.5–1.3 mm wide, pubescent with cauline type trichomes (in ours) or glabrous, panicles opposite or alternate, 1 per axil, rachis glabrous or, in ours, pubescent with flexuose to antrorse to retrorse eglandular trichomes 0.1–0.5 mm long and sometimes inconspicuously glandular punctate as well, the eglandular trichomes becoming very sparse or concentrated in 2 lines distally; dichasia alternate, 1-flowered, ± secund, 1 per axil, sessile. Bracts opposite, sessile, triangular, 1–2 mm long, 0.8–1.2 mm wide, abaxial surface glabrous, inconspicuously glandular punctate, or pubescent like rachis. Bracteoles sessile, triangular to ovate to subulate, 0.9–2.2 mm long, 0.6–1 mm wide, abaxial surface glabrous or inconspicuously glandular punctate. Flowers sessile to subsessile (i.e., borne on pedicels to 1 mm long). Calyx 5-lobed, 2.8–4.5 mm long, lobes lanceolate to lance-subulate, 1.7–3.2 mm long, equal in length, 0.5–0.9 mm wide, abaxially glabrous or pubescent with subsessile to stipitate glandular trichomes to 0.1 mm long. Corolla orange, fusiform in bud, 33–55 mm long, externally pubescent with inconspicuous subsessile to stipitate glandular trichomes to 0.1 mm long proximally (i.e., near base of tube) and glabrous distally, tube gradually expanded distally, 19–32 mm long, 2.5–4 mm in diameter near midpoint, upper lip 11–21 mm long, entire at apex, lower lip recoiled, 11–21 mm long, lobes 0.8–2.5 mm long, 1–1.7 mm wide. Stamens inserted near apex of corolla tube, 14–20 mm long, filaments glabrous, thecae 1.5–3.2 mm long, equal to subequal, subparallel to subsagittate, subequally inserted, glabrous, lacking basal appendages (or with inconspicuous appendages to 0.1 mm long); pollen (Fig. 26c, d; from extralimital material) 2-aperturate, apertures flanked on each side by 2 (–3) rows of insulae, exine reticulate. Style 28–48 mm long, glabrous or with a few glands near base, stigma 0.4–0.7 mm long, lobes indistinct. Capsule 17 mm long, glabrous, stipe 8 mm long, head hourglass-shaped, 9 mm long. Seeds 4, dark brown, compressed, 2.7–3 mm long, 2.5 mm wide, 0.7 mm thick, surfaces and margin covered with subconic papillae. (chromosome number unknown).

PHENOLOGY. — Flowering: April; elsewhere flowering December–August and fruiting in March (fruiting collections rare).

DISTRIBUTION AND HABITAT. — Throughout much of Mexico, Belize, Guatemala, El Salvador, Honduras, Nicaragua, and Costa Rica; plants are commonly cultivated and are found in a variety of habitats and vegetation types. In California cultivated for ornament and in Baja California cultivated as a medicinal plant where it appears to naturalize; in our region, the species is known from a nondesert portion of the Cape Region and from the Sierra de la Giganta (Fig. 4); Wiggins (1980) noted its occurrence in arroyos and on slopes and *Carter & Moran 5644* was noted to have been collected in an arroyo.

LOCAL NAME. — "Nicle" (*Carter 2710*); "nictle" (*Carter & Moran 5644*).

USES. — Used to cure fever (*Carter 2710*); elsewhere a common medicinal and dye plant and often used in Latin America as a bluing agent for whitening clothes.

ADDITIONAL SPECIMENS EXAMINED. — MEXICO. **Baja California Sur**: E side of Sierra de la Victoria, Boca de la Sierra, ca. 6 km NW of Miraflores, mouth of Arroyo de San Bernardo, 23°23′N, 109°48′W, *A. Carter 2710* (DS, UC); Sierra de la Giganta, arroyo E of La Soledad, ca. 24°49′N, 110°52′W, *A. Carter & R. Moran 5644* (UC).

The above description has been augmented with data from other Mexican collections of *J. spicigera*. Daniel (1995) discussed the distribution of and morphological variation in this species.

The closest relatives of *J. spicigera* appear to be *Justicia leonardii* Wassh. (apparently differing only by its denser pubescence) and *Justicia colorifera* V. A. W. Graham (differing by its glabrous corollas with a spreading lower lip, and dorsally pubescent thecae). The former occurs in northeastern Mexico; the latter occurs in southern Mexico, Central America, and northern

South America. Graham (1988) treated all of these species as being peripheral to *Justicia* section *Plagiacanthus*.

RUELLIA

Ruellia L., Sp. pl. 634. 1753. LECTOTYPE (Britton and Brown, Ill. fl. n. U.S., ed. 2, 3:241. 1913). —*Ruellia tuberosa* L.

Dipteracanthus Nees in Wall., Pl. asiat. rar. 3:75, 81. 1832. LECTOTYPE (Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Tweede Sect. 45(1):15. 1948).— *Dipteracanthus prostratus* (Poiret) Nees (≡ *Ruellia prostrata* Poiret).

Aphragmia Nees in Lindl., Intr. nat. syst. bot. ed. 2, 444. 1836. TYPE.—*Aphragmia haenkei* Nees (= *Ruellia inundata* Kunth).

Cryphiacanthus Nees, Index Sem. Horti Vratislav. 1841; Linnaea 16:298. 1842. LECTOTYPE (designated fide Index Nom. Gen. Pl.).—*Cryphiacanthus barbadensis* Nees (nom. illegit.; = *Ruellia tuberosa* L.).

Decumbent to erect, subcaulescent to caulescent perennial herbs, shrubs, or (rarely) trees with cystoliths, vegetative and floral surfaces sometimes glandular punctate. Leaves opposite, sometimes anisophyllous, sessile to petiolate, margin entire to sinuate to crenate to dentate. Inflorescence of reduced or expanded dichasia in axils of leaves or bracts, sometimes forming dichasiate spikes, thyrses, or panicles; dichasia alternate or opposite, 1–many-flowered, 1 or more per axil, sessile or pedunculate. Bracts opposite, green (in ours), margin entire (in ours). Flowers usually subtended by 2 isomorphic bracteoles (sometimes absent or vestigial), chasmogamous flowers generally large and showy, cleistogamous flowers often present as well, commonly preceding or succeeding chasmogamous flowers. Calyx deeply 5-lobed, lobes homomorphic or heteromorphic, equal to unequal in length. Corolla of chasmogamous flowers blue, blue-purple, pink, red, white, yellow, or blackish, generally concolorous, sometimes with whitish or greenish markings, tube usually funnelform, often curved, gradually or abruptly expanded distally into a ± distinct throat (rarely saccate), limb bilabiate (sometimes appearing subactinomorphic), upper lip 2-lobed, lower lip 3-lobed, corolla lobes contorted in bud, corolla of cleistogamous flowers, if present, small, whitish, budlike or tubular, lobes remaining closed. Stamens 4, (homodynamous to) didynamous, usually inserted near base of corolla throat, included in corolla tube or exserted from mouth of corolla, filaments sometimes united in pairs at base, anthers 2-thecous, thecae equal in length, parallel to subsagittate, equally inserted, lacking basal appendages, dehiscing toward lower lip (i.e., flower nototribal); pollen (Figs. 29, 30) spheroidal, 3-porate, exine coarsely reticulate; staminodes 0 or 1. Style included in corolla tube or exserted from mouth of corolla, stigma 2-lobed, lobes equal or unequal, often with 1 lobe greatly reduced, rudimentary, or not evident. Capsule substipitate or stipitate, head terete or compressed, narrowly ellipsoid to broadly ellipsoid to subglobose to obovoid, retinacula present, septae with attached retinacula remaining attached to inner wall of mature capsule. Seeds 4–20 per capsule, lenticular, pubescent with hygroscopic trichomes (sometimes restricted to margin). ($x = 17$).

The generic boundaries of *Ruellia* have been debated for many years. In one broad sense it comprises approximately 250 species worldwide with species occurring primarily in the tropics and subtropics. It is the second largest genus of Acanthaceae in Mexico with about 65 species there. Thirteen or more species are native to the United States. The generic synonymy given above only includes genera in which our species have been treated previously. Daniel (1995) provided a more comprehensive generic synonymy pertaining to New World taxa.

Key to Species of *Ruellia*

1. Corolla white; young stems and leaves and external surfaces of calyx, corolla, and capsule beset with sessile patelliform glands (glandular punctate) . . . . . *Ruellia leucantha*
1. Corolla bluish, blue-purple, or pinkish; young stems and leaves and external surfaces of calyx, corolla, and capsule lacking sessile patelliform glands (although sometimes with stipitate glands).
    2. Limb of corolla 10–13.5 mm in diameter; calyx lobes unequal with one conspicuously longer and wider than others; thecae 1.7–2.4 mm long; capsule often blotched

with red, 7.5–10 mm long, glabrous .... *Ruellia inundata*

2. Limb of corolla 17–42 mm in diameter; calyx lobes equal to subequal; thecae 2.8–5 mm long; capsule never blotched with red, 11–23 mm long, pubescent (or glabrous in *R. cordata*).
    3. Perennial herbs; young stems pubescent with eglandular trichomes only; dichasia 3–many-flowered; leaves commonly constricted-attenuate at base; stipe of capsule 2–3.5 mm long; seeds 8–12 per capsule.
        4. Those dichasia in axils of distal leaves or leaflike bracts collectively forming a terminal glandular pubescent paniculiform thyrse; external surfaces of calyx and corolla pubescent with stipitate glandular trichomes; style pubescent .... *R. nudiflora*
        4. Dichasia never forming a terminal glandular paniculiform thyrse; external surfaces of calyx and corolla pubescent with eglandular trichomes only; style glabrous .. *R. intermedia*
    3. Shrubs; young stems pubescent with eglandular and stipitate glandular trichomes or glabrous-glutinous; dichasia 1–3-flowered; leaves never constricted-attenuate at base; stipe of capsule 3.5–7 mm long; seeds 4 per capsule.
        5. Calyx lobes (linear to) oblanceolate to spatulate (i.e., widest at or above middle); bracteoles subcordate to broadly ovate to subcircular, 7–10 mm wide; leaf blades (ovate to) broadly ovate to cordate to reniform; capsule glabrous .... *R. cordata*
        5. Calyx lobes lance-subulate (i.e., widest at base); bracteoles linear to lanceolate to lunate to ovate to elliptic to obovate, 0.3–2.5 (–4) mm wide; leaf blades elliptic to ovate (to broadly ovate); capsule pubescent .. .. *R. californica*

1. **Ruellia californica** (Rose) I. M. Johnst., Proc. Calif. Acad. Sci., ser. 4, 12:1171. 1924. *Calophanes californica* Rose, Contr. U. S. Natl. Herb. 1:85. 1890. TYPE. — MEXICO. **Baja California Sur**: Santa Rosalía, 24 Feb–3 Mar 1889, *E. Palmer 190* (holotype: US; isotypes: GH!, NY, UC!).

Shrubs to 1.5 m tall, herbage mephitic and often glutinous (i.e, with a sticky and shiny surface). Young stems subterete to quadrate, glabrous or densely and evenly pubescent with erect to flexuose glandular (and often with a few inconspicuous eglandular) trichomes 0.1–1.5 mm long (glandular pubescent). Leaves petiolate, petioles to 10 (–15) mm long, blades ovate to broadly ovate to elliptic (to cordate), 6–55 mm long, 3–32 mm wide, (1.1–) 1.3–2.6 times longer than wide, acute to acuminate at apex, acute to rounded to truncate to subcordate at base, surfaces either lacking eglandular and stipitate glandular trichomes or glandular pubescent, glandular punctate, punctae often inconspicuous and usually exuding a clear, shiny, and sticky substance (i.e., glutinous) and giving the appearance of either glistening dots or a general shiny coating, margin entire to angulate-sinuate. Inflorescence of axillary dichasia; dichasia alternate or opposite, 1–3-flowered, 1 per axil, pedunculate in leaf axils, peduncles 1–17 mm long, subterete, glabrous or glandular pubescent. Bracteoles often subfoliose, sometimes petiolate, linear to lanceolate to lunate to elliptic to oblanceolate to obovate (to ovate), 1–14 mm long, 0.3–2.5 (–4) mm wide, abaxial surface glabrous or glandular pubescent, secondary bracteoles (if present) similar to bracteoles except smaller. Flowers sessile to pedicellate, pedicels (if present) to 2.5 mm long. Calyx (4–) 6–22 mm long, tube 1.5–4.7 mm long, lobes lance-subulate, (1.5–) 3.3–20 mm long, often subequal to unequal in length, 1.1–10 times longer than tube, 1–1.9 mm wide, abaxially glabrous, sparsely pubescent with antrorse eglandular trichomes to 0.1 mm long, or glandular pubescent, margin glandular pubescent. Corolla blue-purple (rarely pinkish), sometimes with yellowish markings in throat or the throat lighter purple than the limb and streaked with darker purple, (26–) 33–51 mm long, externally pubescent with erect to flexuose glandular trichomes 0.05–0.2 mm long, tube (18–) 24–42 mm long, narrow proximal portion 6–20 mm long, abruptly expanded distally into throat, throat 12–23 mm long, longer than (or rarely equal to) the narrow proximal portion of the tube, 6–15 mm in diameter near midpoint, limb (17–) 23–42 mm in diameter,

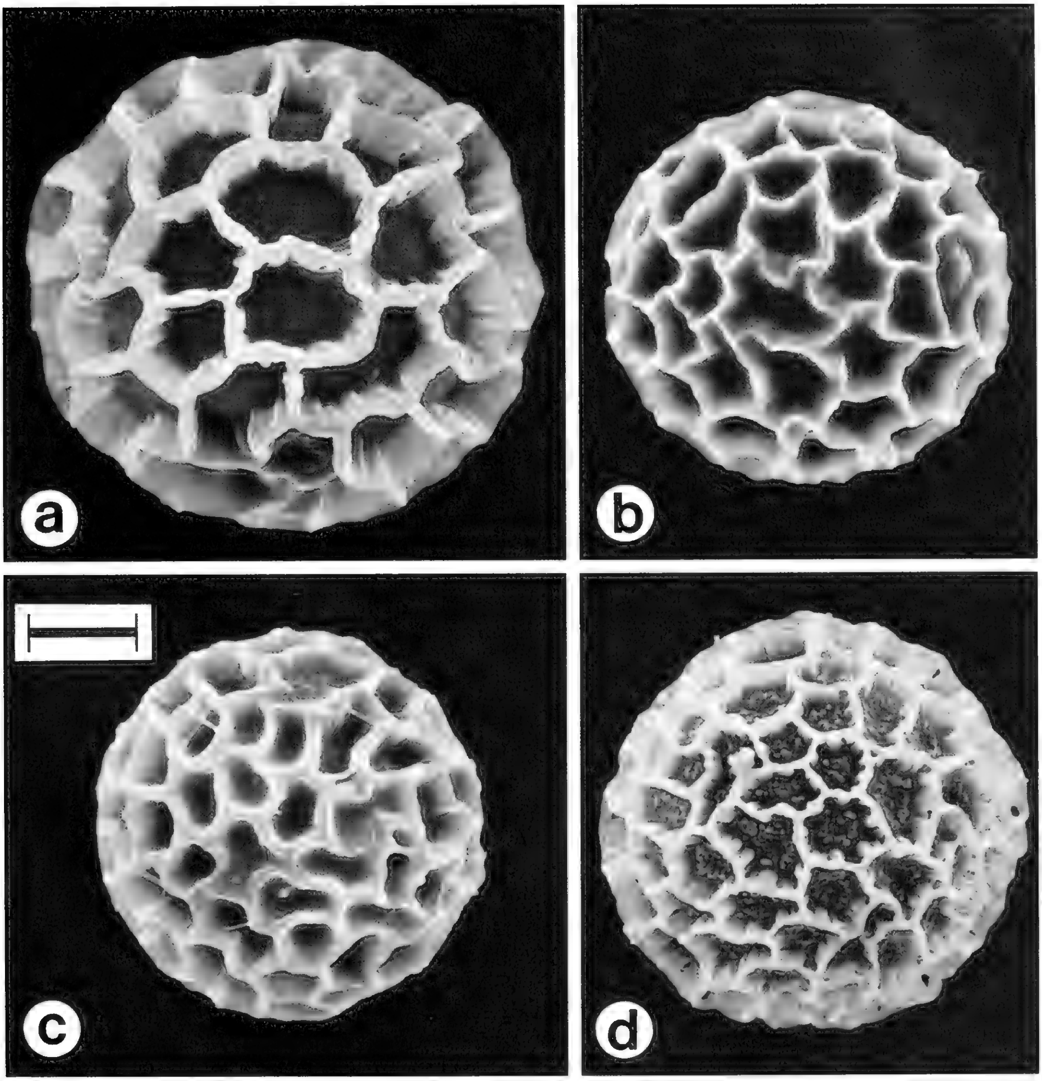


FIGURE 29. Pollen. a. *Ruellia californica* subsp. *californica* (*Wiggins 11411*); b. *R. californica* subsp. *peninsularis* (*Daniel & Butterwick 6844*); c. *R. cordata* (*Boyd & Ross 5934*); d. *R. intermedia* (*Jenkins et al. s.n.*). Scale for a–d = 15 µm.

lobes 6–14 mm long, 6.5–18 mm wide. Stamens included, longer pair 8–18 mm long, shorter pair 5.5–13 mm long, thecae 3–5 mm long. Style 15–37 mm long, pubescent with eglandular and usually glandular (at least proximally, sometimes inconspicuous) trichomes, stigma unequally 2-lobed, 1 lobe 1.5–5 mm long, other lobe 0.3–0.7 mm long. Capsule stipitate, 14–19 mm long, pubescent with erect glandular trichomes 0.05–0.2 mm long, stipe 4.5–7.5 mm long, head subovoid to ellipsoid to obovoid. Seeds 4, 2.5–4.5 mm long, 2.5–3.5 mm wide, surfaces covered with appressed hygroscopic trichomes. (n = 17, Daniel et al. 1984). Fig. 31.

PHENOLOGY. — Flowering and fruiting throughout the year.

DISTRIBUTION. — Northwestern Mexico (Baja California, Baja California Sur, and Sonora); in our region the species is known from southern Baja California and from throughout Baja Cali-

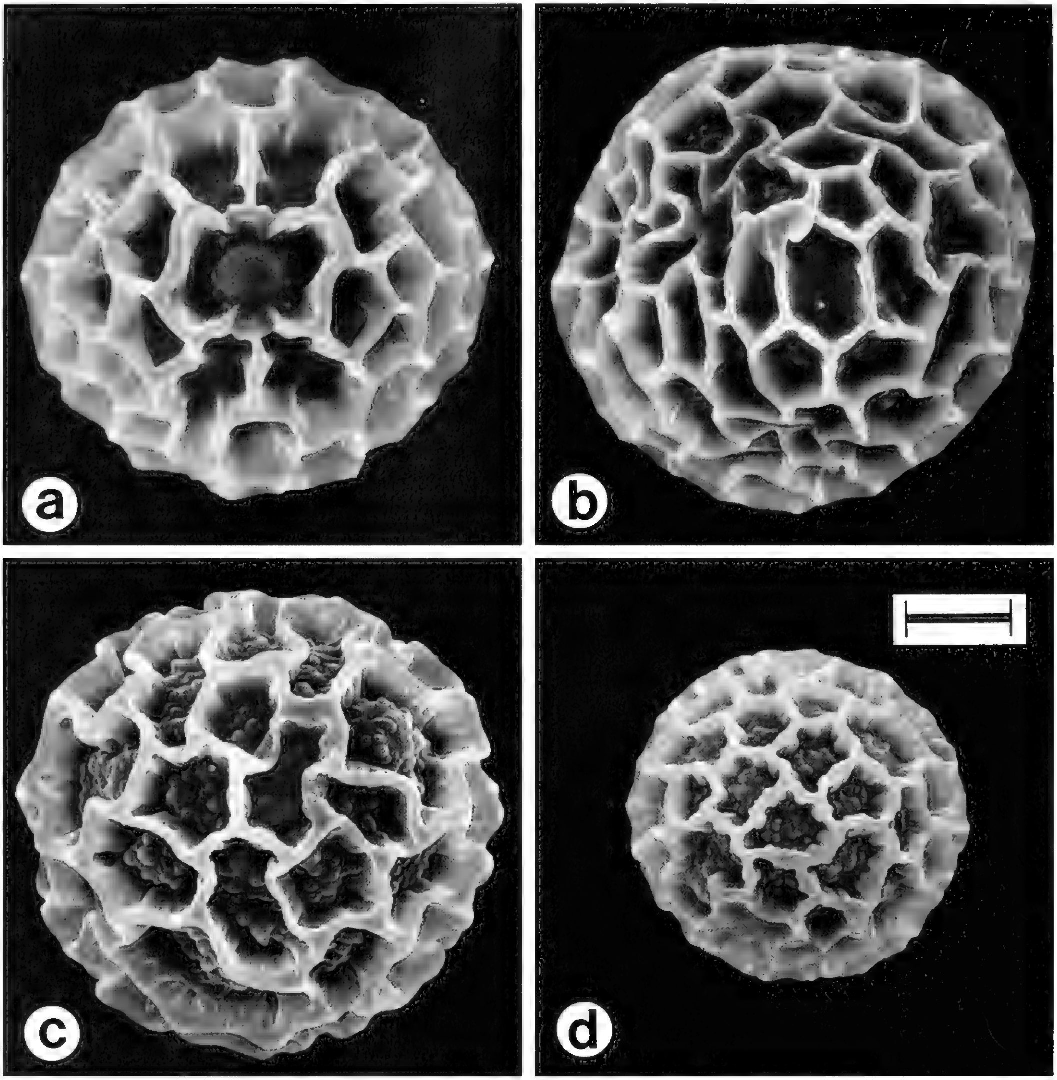


FIGURE 30. Pollen. a. *Ruellia inundata* (*Daniel & Butterwick 6952*); b. *R. leucantha* subsp. *leucantha* (*Daniel & Butterwick 6940*); c. *R. leucantha* subsp. *postinsularis* from Sinaloa (*Brandegee s.n.*); d. *R. nudiflora* from Sonora (*Wiggins & Rollins 136*). Scale for a–d = 15 µm.

fornia Sur (Figs. 32, 33) where it occurs in the Cape Region, the Sierra de la Giganta, and the Sonoran Desert (Central Gulf Coast, Vizcaíno, and Magdalena subdivisions).

There is no recent taxonomic treatment of Mexican *Ruellia*. Among species with which I am familiar, *R. cordata* is most similar to *R. californica* on the basis of morphological characteristics.

Felger and Moser (1985) considered *R. peninsularis* to be conspecific with *R. californica*. Johnston (1924) discussed the differences between these taxa and other peninsular species of *Ruellia*. Gentry (1949) noted that *R. californica* is closely related to *R. peninsularis*, the primary difference being the presence of clavate glands on the calyx of the former and the absence of them on the latter. He also noted that *R. peninsularis* appeared to be limited in distribution to the peninsula. The two taxa are indeed very similar to one another and herbariums specimens of them have often been misidentified. They differ primarily in the presence of conspicuous, stipitate glandular pubescence on vegetative organs of *R. californica*. As noted by previous investigators (Johnston 1924, Gentry 1949, Turner et al. 1995) this difference in pubescence has a geographic basis. Specimens treated as *R. californica* and *R. peninsularis* were sorted based on the distinction noted above and their distributions were plotted on maps. The maps reveal that in Baja California (Figs. 32, 33) plants treated as *R. californica* occur only to the north of lat. 25°30′N (see discussion of *Craig 757*, presumably from Cape Region, below) and that plants formerly treated as *R. peninsularis* occur only to the south of lat. 26°13′N. Furthermore, only plants with stipitate glandular trichomes (see additional discussion below) are known from Sonora. The only known region where the ranges of these taxa overlap occurs between about lat. 25°30′N and lat. 26°13′N in the Central Gulf Coast subdivision of the Sonoran Desert and the Sierra de la Giganta.

In addition to the difference in pubescence, several morphological tendencies can be useful for further distinguishing these taxa. Lengths of the calyces, corollas, and styles are usually relatively shorter in plants treated as *R. peninsularis* than in those treated as *R. californica*: calyces (4–) 6–12.3 vs. 7–22 mm long, corollas 27–40 vs. (26–) 33–51 mm long, and styles 15–20 vs. 20–37 mm long.

My studies show that the differences between *R. californica* and *R. peninsularis* are slight and that their distributions are predominately allopatric. The minor difference in pubescence between these taxa, which has a geographic basis, is more suggestive of the differences between subspecies of *Justicia insolita* and *Holographis virgata* than between other species of *Ruellia*. For this reason, *R. peninsularis* is here treated as a subspecies of *R. californica*.

Several specimens from at least two regions are somewhat intermediate between these subspecies. Some collections from the vicinity of Guaymas in Sonora (e.g., *Blakley B-1640*, *Daniel 3987*, *Dawson 1002*, and *Phillips et al. 76-183*) and the northern Sierra de la Giganta in Baja California Sur (e.g., *Boyd & Ross 5944* and *Carter 4399*) exhibit varying amounts of stipitate glandular and eglandular trichomes on the herbage. These trichomes, which are absent in subspecies *peninsularis* and usually dense in subspecies *californica*, vary from very sparse to somewhat dense (usually only on the newest growth) on various internodes of each of these collections. For example, *Dawson 1002* contains individuals with typical densely glandular shoots as well as less glandular individuals. Because stipitate glandular and eglandular trichomes are evident on all of these collections, they are treated as subspecies *californica*. The lengths of floral organs in all of these collections except *Carter 4399* also suggest that they are better treated as subspecies *californica*. *Carter 4399* has some shoots very sparsely glandular and others rather densely glandular. Lengths of the calyx (10.5–12 mm), corolla (26–30 mm), and style (18–20 mm) of plants represented by this collection are more suggestive of subspecies *peninsularis*. It is not known whether any or all of these collections represent hybrids (which might be expected in the northern Sierra de la Giganta based on present day distributions of the two taxa) or merely morphological variation in one or both subspecies. *Zippin 20* from the vicinity of San Isidro (i.e., near where there is overlap in the ranges of the subspecies) contains numerous separate shoots, some of which are referable to subsp. *californica* and others of which are referable to subsp. *peninsularis*.

Key to the Subspecies of *Ruellia californica*

1. Stems and leaves covered with stipitate glandular and eglandular trichomes (youngest growth lacking stellate trichomes); calyx 8–22 mm long, lobes abaxially pubescent with stipitate glandular and eglandular trichomes . . . . subsp. *californica*
1. Stems and leaves lacking stipitate glandular and eglandular trichomes (youngest growth sometimes with scattered stellate eglandular trichomes); calyx 5–12.3 mm long, lobes abaxially glabrous. . . . . subsp. *peninsularis*

1a. **Ruellia californica** subsp. **californica**

Young stems evenly pubescent with erect to flexuose glandular (and often with a few inconspicuous eglandular) trichomes 0.1–1.5 mm long (glandular pubescent). Leaf blades ovate to ellip-

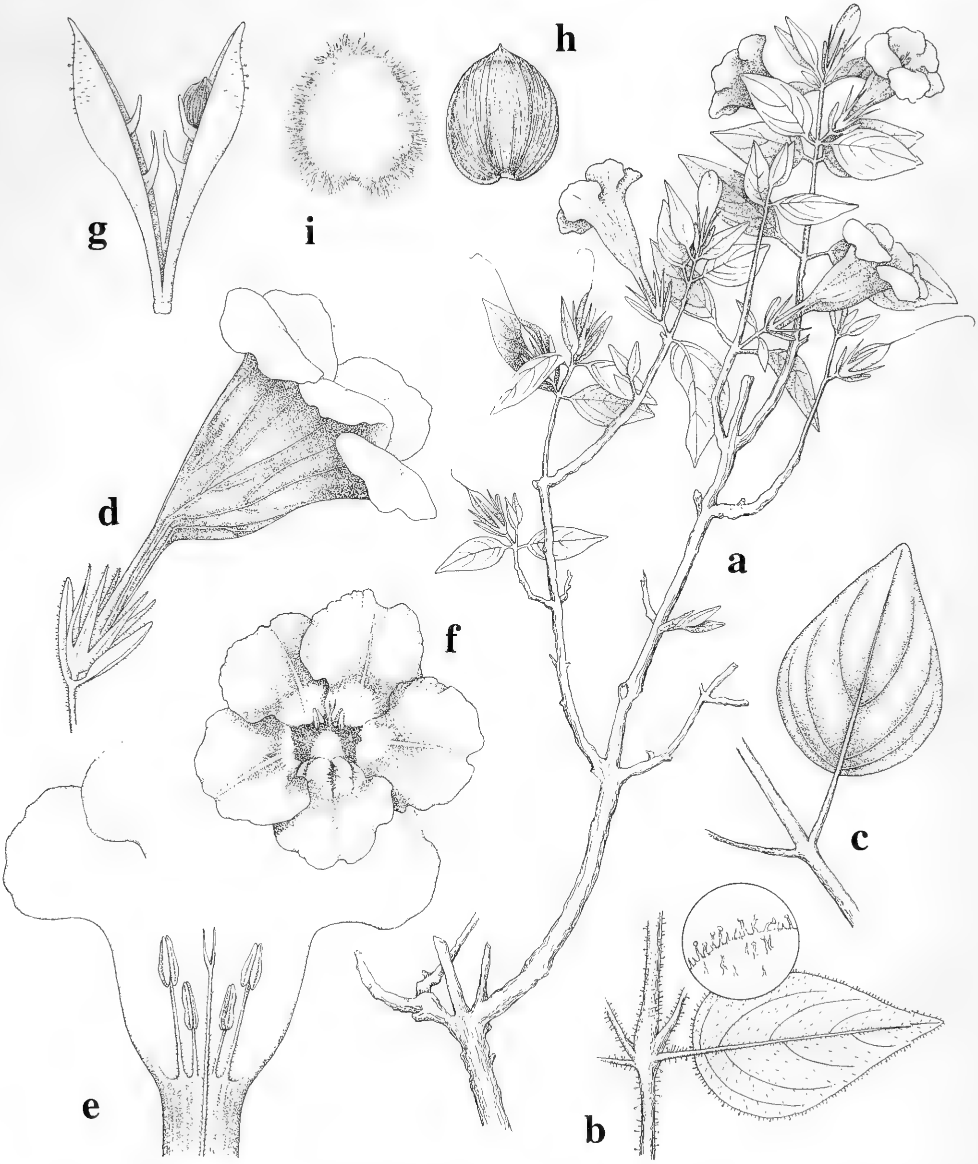


FIGURE 31. *Ruellia californica*. (a, b, d–i from subsp. *californica*, c from subsp. *peninsularis*). a. habit (*Hammerly 134* and *Daniel 1884*), × 0.5; b. vegetative node (*Wiggins 17944*), × 1; c. vegetative node (*Daniel et al. 6844*), × 1.5; d. flower (*Hammerly 134* and *Wiggins 11411*), × 1.2; e. distal portion of flower cut open (*Hammerly 134*), × 1.5; f. front view of flower (*Hammerly 134*), × 1.1; g. capsule (*Daniel 1884*), × 2.7; h. dry seed (*Thomas 8318A*), × 5; i. moistened seed (*Thomas 8318A*), × 5. Drawn by Jenny Speckels.

tic, surfaces glandular pubescent. Peduncles of inflorescence glandular pubescent. Bracteoles linear to narrowly elliptic to lanceolate to lunate, abaxial surface glandular pubescent. Calyx 7–22 mm long, tube 1.5–3 mm long, lobes 4–20 mm long, 3–10 times longer than tube, abaxially and marginally glandular pubescent. Corolla (26–) 33–51 mm long, tube (18–) 24–42 mm long, narrow proximal portion (6–) 10–20 mm long. Longer pair of stamens 11.5–18 mm long, shorter pair of stamens 9–13 mm long. Style 20–37 mm long, stigma with 1 lobe 3.5–5 mm long, other lobe 0.4–0.7 mm long. (*n* = 17, Daniel et al. 1984). Fig. 31a, b, d–i.

PHENOLOGY. — Flowering and fruiting throughout the year.

DISTRIBUTION AND HABITAT. — Northwestern Mexico (Baja California, Baja California Sur, and Sonora); in our region the subspecies occurs in southern Baja California and extends southward in Baja California Sur to about latitude 25°30′N (Fig. 32) and is known from the Sonoran Desert (Central Gulf Coast, Vizcaíno, and Magdalena subdivisions) and the Sierra de la Giganta; plants occur along sandy and rocky watercourses, on slopes, on rocky flats, and on sand dunes in desertscrub and thornscrub from near sea level to 800 (–1300) m elevation.

LOCAL NAME. — "Rama parda" (numerous herbarium labels).

ADDITIONAL SPECIMENS EXAMINED. — MEXICO. **Baja California**: 11 km N of junction of El Barril and San Francisquito rds, ca. 28°27′N, 113°15′W, *A. Carter 5821* (CAS, UC); ca. 30 mi E of Pozo Alemán on Calmallí-San Ignacio Rd, *R. Ferris 8620* (DS); Rancho Miraflores, (El Arco), *C. Harbison s.n.* (SD); ca. 27 mi S of Bahía de los Angeles, *J. Henrickson 1129* (RSA); 9 mi SE of Las Flores, ca. 28°44′N, 113°29′W, *R. Moran 10258* (DS, SD, UC); ca. 8 mi ESE of La Bocana, 28°28′N, 113°18′W, *R. Moran 11558* (SD); Calmallí, *C. Purpus 85* (DS, UC); 14 mi N of Los Angeles, *I. Wiggins 5425* (DS, POM, UC). **Baja California Sur**: Concepción Bay, *E. Berry 102* (CAS, DS); Arroyo San Bruno, SE of Santa Rosalía, 4.8 mi W of Hwy 1 on rd to San José de Magdalena, ca. 27°04′N, 112°12′W, *S. Boyd & T. Ross 5836* (RSA, UCR); N Sierra La Giganta, S of Mulegé, 11.2 mi W of Hwy 1 on rd from Rosarito to San Isidro, ca. 26°21′N, 111°45′W, *S. Boyd & T. Ross 5944* (CAS, RSA); without locality, *T. Brandegee s.n.* (UC); 24 km N of San Ignacio, *D. Breedlove & C. Burns 72723* (CAS, MEXU); 43 km N de Loreto, carr. a Mulegé, 26°19′N, 111°33′W, *A. Campos V. 4486* (CAS); Sierra de la Giganta, Valle de Los Encinos (S side of Cerro Giganta), ca. 26°04′N, 111°34′W, *A. Carter 4136* (CAS, UC); Pilón de las Parras, 25°58′N, 111°30′W, *A. Carter 4212* (SD, UC); Sierra de la Giganta, La Esperanza, ca. 25°48′N, 111°24′W, *A. Carter 4399* (CAS, UC); W of cemetery, "Las Lomas de Anita," Loreto, ca. 26°00 N, 111°21 W, *A. Carter 4421* (UC); Sierra de la Giganta, saddle between N and S peaks of Cerro Gabilán, ca. 25°55′N, 111°25′W, *A. Carter 4461a* (UC); ridge S of Tinaja de Naucajoa, Cerros de Naucajoa (W of Llanos de San Juan), ca. 26°15′N, 111°38′W, *A. Carter 4479a* (UC), *4479b* (UC); Sierra de la Giganta, Cañón de la Cumbre, a branch of Arroyo de Agua Verde on trail to San José de Agua Verde, ca. 25°30′N, 111°07′W, *A. Carter 4846* (UC), *4846a* (UC); Isla Carmen, Puerto Balandra, ca. 26°00′N, 111°10′W, *A. Carter & R. Ferris 3724* (CAS, UC), *3724A* (CAS, UC); Sierra de la Giganta, ridge S of La Victoria, ca. 25°52′N, 111°25 W, *A. Carter & R. Ferris 3897* (CAS, UC); Cuesta de Chuenque, ca. 22 km S of Loreto, 25°53′N, 111°20′W, *A. Carter & L. Kellogg 2926* (DS, SD, UC); Isla Carmen, Puerto Balandra, ca. 26°05′N, 111°10′W, *A. Carter & J. Reese 4550* (CAS, UC); Sierra de la Giganta, Arroyo Tabor, W of Puerto Escondido, ca. 25°48′N, 111°20–21′W, *A. Carter & H. Sharsmith 4245* (CAS, UC); Sierra de la Giganta, mouth of Arroyo Tabor, W of Puerto Escondido, ca. 25°48′N, 111°20′W, *A. Carter & H. Sharsmith 4259* (UC); W of Bahía de la Concepción, 40.6 km S of Mulegé, *A. Carter et al. 1985* (DS, UC); near base of S-most of Tres Vírgenes, 25 mi W of Santa Rosalía on W side of pass, *K. Chambers 768* (DS, SD, UC); Arroyo de la Purísima, 16 mi above La Purísima, *L. Constance 3152* (DS, UC); S end of Bahía Coyote, across from Rancho El Coyote, 16.7 mi S of Puente Mulegé, ca. 26°42′N, 111°55′W, *T. Daniel 204* (ASU, CAS); along Mex. Hwy 1, 4.1 mi E of San Ignacio, *T. Daniel 1884* (ASU, CAS); above Playa El Coyote on W side of Bahía Concepción, 18.5 mi S of Mulegé, *T. Daniel 1891* (ASU, CAS); along Hwy 1 by Bahía Concepción, 14.1 mi N of Microondas Rosarito, *T. Daniel et al. 2396* (ASU, MICH, CAS); 1–2 mi inland from Agua Verde Bay, *E. Dawson 6279* (RSA); Bargo Island, Concepción Bay, *E. Dawson 6360* (RSA); Puerto Escondido, SW side of lagoon, *E. Dawson 6408* (RSA); Mpio. Comondú, Ejido Los Naranjos, 26°20′N, 111°53′W, *M. Domínguez L. 192* (HCIB); Sierra de la Giganta, San Javier Rd, 8.8 mi SW of Hwy 1, *J. Donahue 73095* (RSA); Isla del Carmen, 3–4 km al lado SE, *G. Flores F. 492* (RSA); Sierra Giganta, Arroyo Hondo, *H. Gentry 4133* (DS, UC); Desierto Viscaíno Region, between San Ignacio and Los Martiles, *H. Gentry 7874* (DS, RSA, UC); Coyote, Bahía Conception, *H. Gentry & B. Gentry 23180* (CAS); S end of Vizcaíno Desert, ca. 15 mi N of San Ignacio, *B. Hammerly 97* (CAS); overlooking Coyote Cove on Concepción Bay, *B. Hammerly 134* (CAS, DS); Loreto, *C. Harbison s.n.* (CAS, SD); between Santa Agueda and Santa Rosalía, *C. Harbison s.n.* (SD); Isla Carmen, Puerto Balandra, 26°00′N, 111°12′W, *J. Hastings 71-124* (SD); 27 mi SE of El Arco, *J. Hastings & R. Turner 63-275* (DS, SD); 16.1 mi W of San Ignacio, *J. Hastings & R. Turner 63-291* (DS, SD); Rancho Mezquital, S ofVolcán Las Tres Vírgenes, 27°26′N, 112°39′W, *D. Howe 3731* (SD); Mulegé, *I.

Johnston 3681 (CAS, DS, UC); San Nicholas Bay, *I. Johnston 3725* (CAS); Loreto, *I. Johnston 3781* (CAS); Arroyo de Arce, 15 mi N of Loreto, *I. Johnston 3793* (CAS); Carmen Island, Puerto Balandra, *I. Johnston 3808* (CAS, UC); Carmen Island, Puerto Balandra, *I. Johnston 3830* (CAS); Arroyo Undo Ranch, Loreto, *M. Jones 27393* (POM); Bahía del Coyote, *D. Keil et al. 16637* (UCR); Sierra de Santa Marta, 27°30′N, 112°58′W, *J. León de la Luz 3238* (HCIB); Carmen Island, Balandra Bay, 26°00′N, 111°10′W, *R. Moran 3922* (DS, SD, UC); San Bruno, ca. 27°09′N, 112°11′W, *R. Moran 7473* (CAS, DS, SD, UC); W side of Conception Bay, SE of Santispaquis, ca. 26°44′N, 111°57′W, *R. Moran 9044* (DS, SD); Danzante Island, ca. 25°48′N, 111°15′W, *R. Moran 9237* (DS, SD); 4 mi SW of Canipole, 26°23′N, 111°43′W, *R. Moran 20043* (SD); Sierra de la Giganta, Arroyo de la Zorra, *C. Mullinex s.n.* (CAS); 10 mi N of Santa Rosalía, *F. Reed 6223* (POM); Juncalito Bay, 14 mi S of Loreto, *J. Reeder 7066* (SD); Agua Verde Bay, *P. Rempel 133* (RSA), *138* (RSA); island in Conception Bay, *P. Rempel 193* (RSA); Arroyo El Infiemo, 4 mi NW of Gulf of California, near Santa Rosalía, ca. 27°23′N, 112°22′W, *A. Sanders 6340* (UCR); 2.3 mi ENE of Ejido Alfredo V. Bonfil, 30 mi NW of Santa Rosalía, ca. 27°22′N, 112°28′W, *A. Sanders 6395* (UCR); Bahía Concepción, SE corner of bay at base of peninsula, 26°35′N, 111°41′W, *A. Sanders 7499* (RSA, SD, UCR); Isla del Carmen (26°01′N, 111°11′W), lado W de la isla, Puerto Balandra, *M. Sousa P. 240* (CAS, RSA); Bahía Concepción, along Mexico 1, *D. Taylor 6303* (UC); ca. 3 mi N of El Coyote, just inland from Bahía de la Concepción, *J. Thomas 7968* (CAS, DS); ca. 1.5 mi SW of Los Martires on rd to San Ignacio, *J. Thomas 8318A* (CAS, DS); 27.7 mi S of Pozo Alemán, *I. Wiggins 7875* (DS); foot of Coyote Grade (Cuesta de Coyote), 20 mi S of Mulegé, *I. Wiggins 11411* (DS, RSA, UC); 9 mi N of San Ignacio, 27°20′N, 112°54′W, *I. Wiggins 16229* (DS); Marques Bay, Isla Carmen, 26°01 N, 111°11 W, *I. Wiggins 17509* (DS); Isla Danzante, near N end of island, 25°45′N, 111°15′W, *I. Wiggins 17565* (DS); Bahía de la Concepción, E end of Club Aereo landing strip, Mulegé, *I. Wiggins & D. Wiggins 17944* (DS); Bahía de la Concepción, near Punta San Ignacio, *I. Wiggins & D. Wiggins 18034* (DS); Santispaquis Cove, Bahía de la Concepción, *I. Wiggins & D. Wiggins 18243* (CAS, DS); ca. 2 mi N of Santispaquis Cove, Bahía de la Concepción, *I. Wiggins & D. Wiggins 18282* (CAS, DS); N of Loreto, *W. Wisura 3737* (RSA); along La Purísima River at San Isidro, *D. Zippin 20* (SD).

Plants of *Ruellia californica* subsp. *californica* have stipitate glandular trichomes varying from long (i.e., 1.5 mm) and dense (e.g., *Daniel 1891*) to short (i.e.,0.1–0.2 mm) and somewhat sparser (e.g., *Boyd & Ross 5944*); however, stipitate glands are always evident and more or less conspicuous. The subspecies sometimes becomes a dominant or codominant shrub in portions of its range. Pink-flowered individuals are known only from Isla Carmen. Occasional plants with pink corollas were noted to grow there among typical plants with "violet" corollas (fide *Johnston 3830*).

A specimen from the Cape Region [Cape San Lucas, 1 mi from beach, *T. Craig 757* (POM)] is referable to this subspecies on the basis of its shoots with dense stipitate glandular pubescence. In the same month of 1928, Craig also collected material of subspecies *peninsularis* at this same locality and material of subspecies *californica* in Sonora. Subspecies *californica* is not otherwise known from the Cape Region. It remains to be determined whether this collection represents a natural occurrence of subspecies *californica* in the Cape Region, a cultivated individual, or a mislabeled specimen. Until additional evidence is available concerning the presence of subspecies *californica* near Cabo San Lucas, this specimen is excluded from consideration.

1b. Ruellia californica subsp. **peninsularis** (Rose) T. F. Daniel, stat. nov. *Ruellia peninsularis* (Rose) I. M. Johnst., Proc. Calif. Acad. Sci., ser. 4, 12:1172. 1924. *Calophanes peninsularis* Rose, Contr. U. S. Natl. Herb. 1:75. 1890. TYPE. — MEXICO. **Baja California Sur**: mesas about La Paz, 20 Jan–5 Feb 1890, *E. Palmer 20* (holotype: US; isotypes: GH!, NY).

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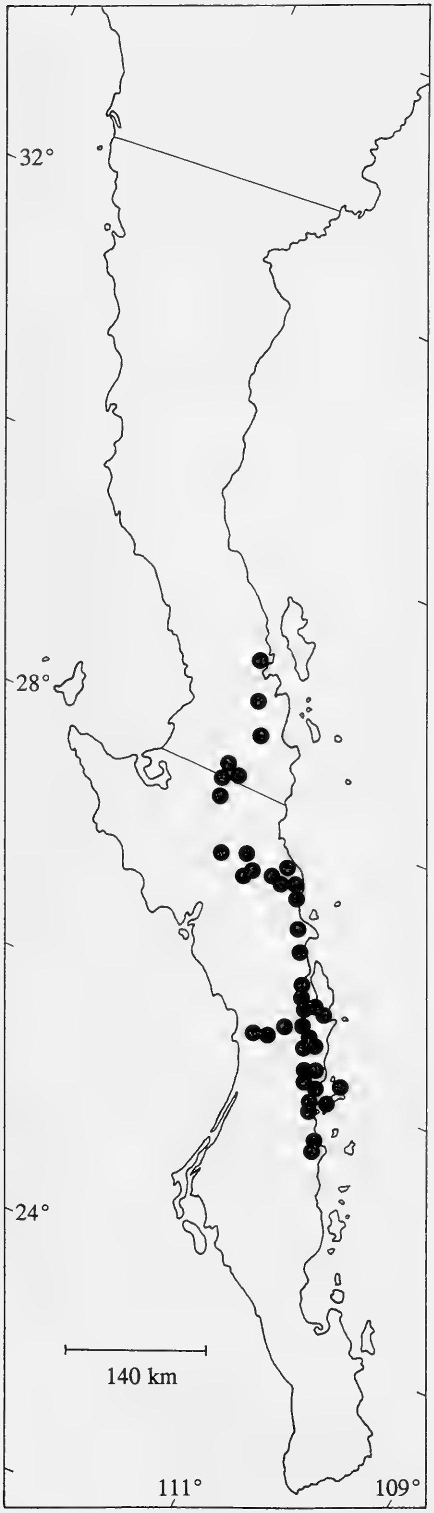
FIGURE 32. Distribution of *Ruellia californica* subsp. *californica* in the peninsula of Baja California.



Young stems glabrous but usually ± glutinous (i.e., sticky and shiny), youngest growth sometimes with scattered stellate eglandular trichomes to 0.2 mm long or with inconspicuous sessile patelliform glands (i.e., glandular punctate). Leaf blades ovate to broadly ovate (to cordate), surfaces lacking eglandular or stipitate glandular trichomes. Peduncles of inflorescence glabrous. Bracteoles (ovate to) linear to elliptic to oblanceolate to obovate, abaxial surface glabrous but glutinous. Calyx (4–) 6–12.3 mm long, tube (1.5–) 2.5–4.7 mm long, lobes (1.5–) 3.3–9 mm long, 1.1–3.2 times longer than tube, abaxially glabrous (or sparsely pubescent with antrorse eglandular trichomes to 0.1 mm long) and glutinous, margin pubescent with eglandular and glandular trichomes 0.05–0.1 mm long. Corolla 27–40 mm long, tube 19–27 mm long, narrow proximal portion 6–10 mm long. Longer pair of stamens 8–13.5 mm long, shorter pair of stamens 5.5–10 mm long. Style 15–20 mm long, stigma with 1 lobe 1.5–3 mm long, other lobe 0.3–0.5 mm long. (*n* = 17, Daniel et al. 1984). Fig. 31c.

Phenology. — Flowering and fruiting: October–May.

Distribution and Habitat. — Endemic to Baja California Sur (Fig. 33); the subspecies is common in the Cape Region (both desert and nondesert portions) and extends northward to about latitude 26°13′N where it is found in the Sierra de la Giganta and the Sonoran Desert (Central Gulf Coast and Magdalena subdivisions); plants occur on slopes, along watercourses, and on sandy flats in desertscrub and thornscrub from near sea level to 750 m elevation.

Local Names. — "Rama parda" (numerous herbarium labels); "rama prieta" (*León de la Luz 2603*, *Peters 120*); "viuda del monte" (*Peters 1*).

Additional Specimens Examined. — MEXICO. **Baja California Sur:** San José del Cabo, *T. Brandegee 441* (UC), *s.n.* (UC); 2.6 mi S of Todos Santos on hwy to Cabo San Lucas, *D. Breedlove 43136* (CAS); Sierra de la Giganta, Llano de San Julio, E of Comondú, ca. 26°03′N, 111°45′W, *A. Carter 4316* (CAS, UC); Sierra de la Giganta, NW of Portezuelo de la Cuesta de los Dolores (W from N end of Isla de San José), ca. 25°07′N, 110°57–58′W, *A. Carter 4784* (UC); Sierra de la Giganta, vicinity of Rancho Tasajera, ca. 3.5 km NE of San José de Agua Verde, ca.

25°30′N, 111°10′W, *A. Carter 4828* (UC); Sierra de la Giganta, NW slopes of Mesa de Alta Gracia, SW of La Cumbre de Alta Gracia, ca. 25°41′N, 111°21′W, *A. Carter 4888* (UC); Sierra de la Giganta, Aguaje de San Antonio, Arroyo el Coyote (SE of La Soledad and N of Cerro Mechudo), ca. 24°49 N, 110°46 W, *A. Carter 5421* (CAS, UC); Sierra de la Giganta, KM 69, E of Villa Insurgentes on hwy to Loreto (2 km W of Estación Microondas Liguí), ca. 25°26′N, 111°12′W, *A. Carter 5810* (CAS, UC); vicinity of Rancho Los Burros, E of Llanos de San Pedro, NE of Comondú, 26°05′N, 111°40′W, *A. Carter & R. Ferris 3429* (DS, SD, UC); Sierra de la Giganta, Mesa San Alejo, SW of Rancho El Horno (NE of San Xavier), ca. 25°53′N, 111°33′W, *A. Carter & R. Ferris 3766* (CAS, SD, UC); Sierra de la Giganta, vicinity of La Tinaja, Mesa de San Alejo (W of San Javier), ca. 25°51′N, 111°34′W, *A. Carter & H. Sharsmith 4169* (UC); Sierra de la Giganta, between Tinaja del Cajón and summit of Mesa de San Alejo (W of San Javier), ca. 25°53′N, 111°33′W, *A. Carter & H. Sharsmith 4193* (CAS, UC), *4193A* (CAS, UC); Sierra de la Giganta, Mesa de San Alejo (N of Rancho el Horno), ca. 25°53′N, 111°33′W, *A. Carter & H. Sharsmith 4202* (CAS, UC), *4202A* (CAS, UC); Sierra de la Giganta, trail from San José de Agua Verde to Bahía Agua Verde, W of crest of ridge, ca. 25°30′N, 111°09′W, *A. Carter & H. Sharsmith 4938* (UC); 8.3 km N of San José del Cabo, *A. Carter et al. 2195* (DS, UC); San Lucas Bay, 1 mi from beach, *T. Craig 625* (POM); along Hwy 286 between La Paz and San Juan de los Planes, near Paraje Los Chinos (8.3 km NW of La Huerta), ca. 24°06′N, 110°15′W, *T. Daniel & M. Butterwick 6814* (CAS, MEXU, MICH, SBBG); along rd from Hwy 1 across Cape Region mts to Hwy 19, ca. 9.7 km E of Hwy 19, ca. 23°16′N, 110°04′W, *T. Daniel & M. Butterwick 6957 (CAS, HCIB); Hwy 1, 83.7 mi SE jct Hwy 22 in Cd. Constitución, T. Daniel et al. 2441* (ASU, MICH, CAS); along Hwy 19 just S of Microondas El Carrizal, ca. 5.6 km S of jct Hwy 1 S of San Pedro, ca. 23°50′N, 110°14′W, *T. Daniel et al. 6844* (CAS); San José del Cabo, *E. Dawson 1163* (RSA); Hwy 19, ca. 1 km ESE of Santa Ines, ca. 9 km ENE of Todos Santos, 23°31′N, 110°11′W, *J. Dice 557* (RSA, SD); El Centenario, La Paz, 24°11′N, 110°20′W, *M. Domínguez L. 388* (CAS); Isla Espiritu Santo, 1 km O de la Bahía, enfrente del Islote del Gallo, 24°30′N, 110°22′W, *G. Flores F. 402* (RSA); San José del Cabo, *F. Gander 9733* (CAS, SD); Sauce, Magdalena Plain, *H. Gentry 4186* (DS, UC); SE La Paz, *C. Harbison s.n.* (CAS); Comondú, between San Miguel and San José, *C. Harbison & Higgins s.n.* (SD); ca. 5 km E of San José Comondú along rd to Loreto, ca. 26°03′N, 111°46′W, *D. Harder & W. Appleby 1081* (RSA); 23.4 mi W of La Paz, along rd to Santo Domingo, *J. Hastings & R. Turner 64-170* (DS, SD); 16 km N of La Paz, 2 km S of Pichilingue, *J. Henrickson 2188* (RSA); 6.6 mi N of Todos Santos, ca. 23°31′N, 110°12′W, *D. Howe 4438* (SD); Cape Region, Boca de Tinaja, *D. Johansen s.n.* (DS); La Paz, *I. Johnston 3037* (CAS); San José del Cabo, *D. Johansen 517* (DS); La Paz, *M. Jones 22582* (POM); Todos Santos, *M. Jones 24089* (CAS, DS, POM); San José del Cabo, *M. Jones 24350* (POM); "El Comitán," 24°07′N, 110°12′W, *J. León de la Luz 2122* (HCIB); "El Comitán," NW de La Paz, 24°13′N, 110°20′W, *J. León de la Luz 2603* (HCIB); "El Comitán," 17 km NW de La Paz, 24°10′N, 110°26′W, *J. León de la Luz 3432* (HCIB); Cape Region, San Pedro, ca. 23°23′N, 110°12′W, *R. Moran 6996* (CAS, DS, SD); Arroyo de Aguada, NE side of San José Island, ca. 25°03′N, 110°39′W, *R. Moran 9400* (CAS, RSA, SD); La Sabanilla, 24°49′N, 110°44′W, *R. Moran 18871* (SD, UC); La Paz, 8 mi from Las Cruces Ranch, *R. Peters 1* (UC); Los Planes, E side of Los Planes Valley, *R. Peters 120* (UC); San José del Cabo, *C. Purpus 401* (UC); 55 km NW de La Paz, sobre la carretera a Santo Domingo, *J. Rzedowski 26565* (DS); 33 mi S of El Refugio, *F. Shreve 7185* (DS); ca. 12 mi W of La Paz near El Centenario, *R. Spjut & C. Edson 5310* (CAS); ca. 15–20 mi E of San José del Cabo, *R. Spjut & C. Edson 5327* (CAS); Mpio. San Antonio, 4 km SE de San Pedro, carr. a Cabo San Lucas, 23°55′N, 110°15′W, *P. Tenorio L. & C. Romero de T. 12821* (CAS); near KM 40 on hwy between La Paz and Santo Domingo, *J. Thomas 8461* (CAS, DS); near KM 24 on hwy between La Paz and Santo Domingo, *J. Thomas 8471* (CAS, DS); ca. 23 mi NW of La Paz, 24°10′N, 110°30′W, *G. Webster 19563* (SD); 1 mi N of Flor de Malva Arroya, *J. Whitehead 827* (DS); 9 mi W of La Paz, *I. Wiggins 11500* (DS, RSA, UC); SE of La Paz, 18.5 mi SE of airport along rd to Los Planes, *I. Wiggins 14410* (DS); 0.6 mi NW of Aripes, 10.3 mi W of La Paz, *I. Wiggins 14613* (CAS, DS); 3.6 mi N of Punta del Cerro, ca. 24°40′N, 111°07′W, *I. Wiggins 15465* (CAS, DS); near KM 123 NW of La Paz, ca. 24°28′N,

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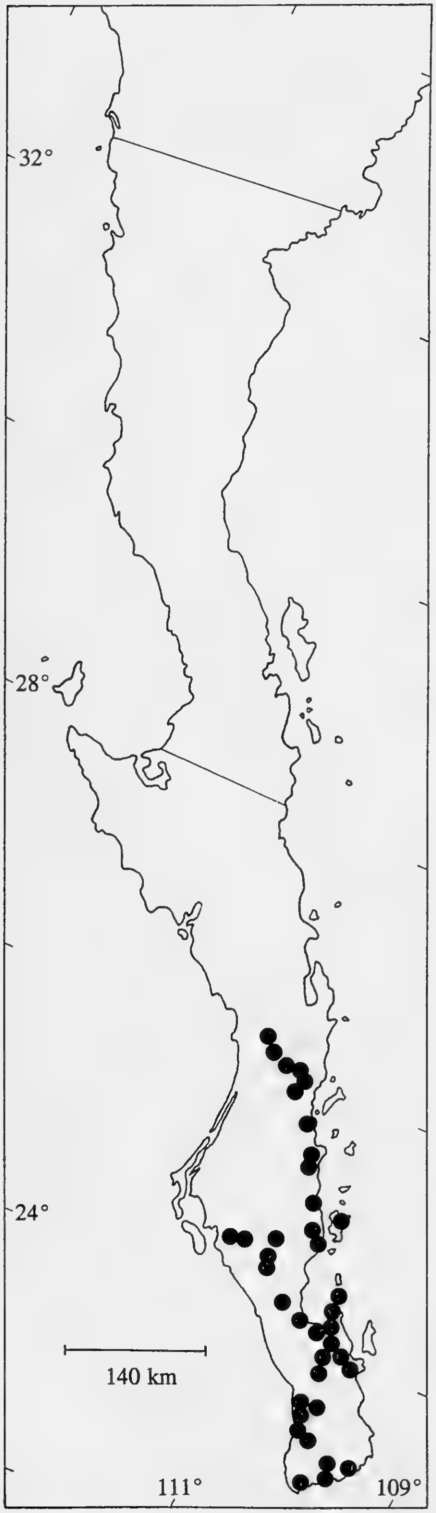
FIGURE 33. Distribution of *Ruellia californica* subsp. *peninsularis*.



111°12′W, *I. Wiggins 15585* (CAS, DS); along La Purísima River at San Isidro, *D. Zippin 20* (SD).

Harbison & Higgins s.n. 18 Nov. 1956 from Comondú, *Hastings & Turner 64-170* from west of La Paz, and *Howe 4438* from the vicinity of Todos Santos have herbage that generally lacks stipitate glands, has relatively short (i.e., 26–34 mm long) corollas, and relatively short (i.e., 6.5–9 mm long) calyces suggestive of subsp. *peninsularis*. They differ from most other collections of this subspecies by having a few scattered stipitate glands on some leaves and internodes. These collections are treated as subsp. *peninsularis* based on the general absence of glandular pubescence and the relatively short floral organs.

The identity of *Johnston 3037* (CAS), a collection from the vicinity of La Paz, remains in doubt. It is a poorly preserved specimen that resembles subspecies *peninsularis* in the length of its floral organs (i.e., calyx 6–8 mm long, corolla 35–37 mm long) but resembles subspecies *californica* by having some herbage with scattered glandular trichomes and irregular patches of trichomes elsewhere. This collection is treated as aberrant and is not included herein.

Most specimens have typical dark purple (violet) corollas; however, *Carter & Sharsmith 4202* is noted to have white flowers with blue veins. They considered this form, which grew among purple-flowered individuals, to be albinic.

Flowers of *Daniel & Butterwick 6814* were visited by honey bees, a non-native hymenopteran. The form of flowers in this species is certainly suggestive of pollination by large bees. Freeman (1986) found that nectar sugar from flowers of an individual of *R. californica* var. *peninsularis* (as *R. peninsularis*) changed from sucrose-dominant to sucrose-rich over a 24 hour period.

This subspecies sometimes becomes a dominant or codominant shrub in portions of its range.

2. Ruellia cordata Brandegee, Zoe 5:173. 1903. TYPE. — MEXICO. **Baja California Sur:** Comondú, 26 Mar 1889, *T. Brandegee s.n.* (holotype: UC!; isotype: US).

Shrubs to 3 dm (or more?) tall. Young stems subterete to subquadrate, densely and evenly pubescent with erect (to flexuose) glandular and eglandular trichomes 0.1–0.7 (–1.5) mm long (glandular pubescent). Leaves petiolate, petioles to 6 mm long, blades (ovate to) broadly ovate to cordate to reniform, 4.5–20 mm long, 4–20 mm wide, 0.8–1.6 (–1.8) times longer than wide, (emarginate to) rounded to acute at apex, (acute to) truncate to cordate at base, surfaces glandular pubescent, margin entire. Inflorescence of axillary dichasia; dichasia alternate or opposite, 1-flowered, 1 per axil, pedunculate in leaf axils, peduncles 11–27 mm long, subterete, glandular pubescent. Bracteoles foliose, subpetiolate to petiolate, subcordate to broadly ovate to subcircular, 8–10 mm long, 7–10 mm wide, abaxial surface glandular pubescent. Flowers sessile to subsessile (i.e., borne on pedicels to 1 mm long). Calyx 13–17 mm long, tube 2–2.5 mm long, lobes (linear to) oblanceolate to spatulate (i.e., widest at or above middle), 11–14.5 mm long, subequal to equal in length, 4.4–5.8 times longer than tube, (0.8–) 1.7–4 mm wide, abaxially and marginally glandular pubescent. Corolla dark purple, 29–45 mm long, externally glandular pubescent (the trichomes sometimes sparse and mostly flexuose), tube 21–32 mm long, narrow proximal portion 8–12 mm long, abruptly expanded distally into throat, throat 14–21 mm long, longer than narrow proximal portion of tube, 7–8.5 mm in diameter near midpoint, limb 17–29 mm in diameter, lobes 6–14 mm long, 7.5–14 mm wide. Stamens included, longer pair 9–15 mm long, shorter pair 5–10 mm long, thecae 3–3.2 mm long. Style 19–25 mm long, pubescent with glandular and eglandular trichomes, stigma unequally 2-lobed, 1 lobe 2.5 mm long, other lobe 0.7 mm long. Capsule stipitate, 12 mm long, glabrous, stipe 3.5 mm long. Seeds apparently 4, surfaces covered with appressed hygroscopic trichomes. (Chromosome number unknown.)

PHENOLOGY. — Flowering: February–April; fruiting: April.

DISTRIBUTION AND HABITAT. — Endemic to central Baja California Sur (Fig. 34) where the species is known from the Sierra de la Giganta; plants occur on rocky slopes from 200–400 m elevation.

ADDITIONAL SPECIMENS EXAMINED. — MEXICO. **Baja California Sur**: NW Sierra de la Giganta, 1.4 mi NE of San Isidro on rd to Rosarito, ca. 26°15′N, 112°00′W, *S. Boyd & T. Ross 5934* (CAS, RSA, UCR); 20 mi W of jct Hwy 1 on rd between La Purísima and Rosarito near La Laguna, *D. Zippin 14* (SD).

Zippin 14 differs from the other collections of *R. cordata* by its calyx lobes which are more linear (i.e., widest at middle) than oblanceolate (i.e., widest distal to the middle). In other respects, this collection resembles others of *R. cordata.*

This species is most similar to *R. californica*, particularly *R. californica* subsp. *californica*, with which it shares the feature of conspicuously glandular herbage.

3. Ruellia intermedia Leonard, J. Wash. Acad. Sci. 17:512. 1927. TYPE. — MEXICO. **Jalisco**: Bolaños, 10–19 Sep 1897, *J. Rose 2915* (holotype: US!; isotype: NY).

Erect to ascending perennial herbs to 5 dm tall. Young stems quadrate to quadrate-sulcate, ± evenly pubescent with retrorse eglandular trichomes 0.05–0.4 mm long (and rarely with a sparse overstory of coarse flexuose eglandular trichomes 0.5 mm long as well). Leaves petiolate, petioles (naked portion) to 15 mm long, blades ovate to elliptic to obovate, 17–60 mm long, 11–40 mm wide, 1.1–1.9 times longer than wide, rounded to subacute at apex, acute and ± abruptly attenuate at base, surfaces pubescent with eglandular trichomes, margin entire to subsinuate to subcrenate. Inflorescence of ± expanded axillary dichasia; dichasia opposite or alternate, (1–) 3–many-flowered, 1 per axil, pedunculate in axils of leaves ± throughout plant or confined to distal leaves, peduncles 6–43 mm long, quadrate to quadrate-sulcate, pubescent like young stems. Bracteoles usually subfoliose, lance-ovate to ovate to elliptic to linear to obovate, 3.5–9.5 mm long, 0.9–5.5 mm wide, abaxial surface pubescent like leaves, secondary bracteoles (if present) linear to narrowly elliptic, 1.5–4 mm long, 0.8–1 mm wide. Flowers pedicellate, pedicels 3–9 mm long. Calyx 12.5–20 mm long, tube 1.5–3 mm long, lobes linear to subulate, 9–23 mm long, subequal in length, 5–11.5 times longer than tube, 0.7–1.6 mm wide, abaxially and marginally pubescent with erect to flexuose eglandular (extralimitally sometimes glandular as well) trichomes 0.1–0.3 mm long. Corolla bluish, 41–65 mm long, externally pubescent with flexuose to retrorse eglan-

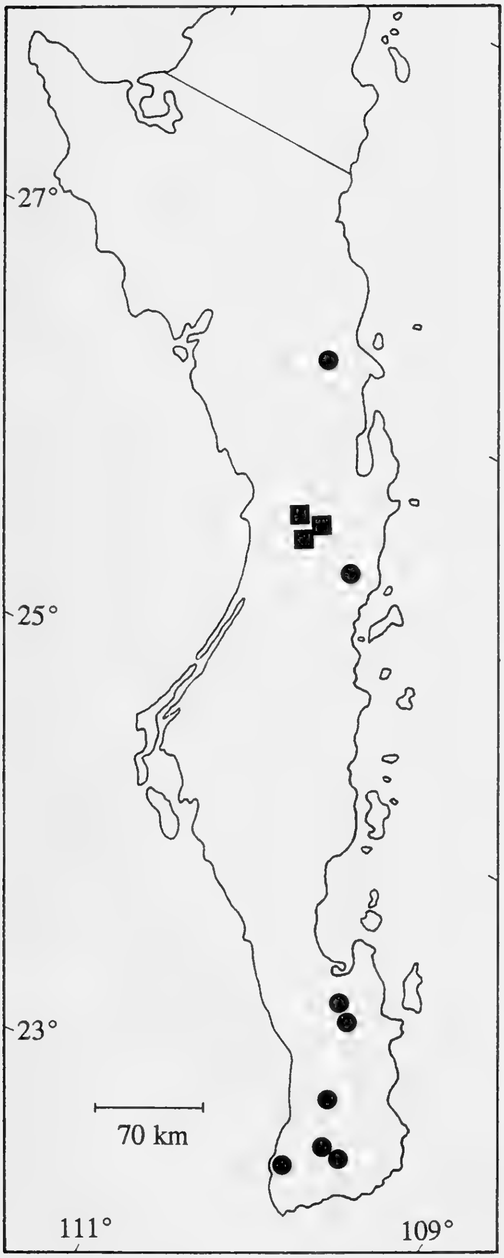


FIGURE 34. Distribution of *Ruellia cordata* (squares) and of *Tetramerium nervosum* (circles) in the peninsula of Baja California.

dular trichomes to 0.3 mm long, tube (25–) 30–52 mm long, narrow proximal portion (9–) 19–34 mm long, abruptly expanded distally into throat, throat 17–21 mm long, shorter than (or extralimitally sometimes longer than) narrow proximal portion of tube, 8–12 mm in diameter near midpoint, limb 30–42 mm in diameter, lobes (11–) 14–18 mm long, 11–16 mm wide. Stamens included, longer pair 13–15 mm long, shorter pair 9–10 mm long, thecae 3 mm long. Style 22–41 mm long, glabrous, stigma 2 mm long, only 1 lobe evident. Capsule substipitate, 12–23 mm long, glabrous proximally, pubescent at apex with erect to antrorse eglandular (and sometimes glandular) trichomes 0.1–0.4 mm long, stipe 2–2.5 mm long, head narrowly ellipsoid. Seeds 12 (extralimitally to 20), 3.2–3.4 mm long, 2–3 mm wide, surfaces and margin covered with appressed hygroscopic trichomes. ($n = 17$, Grant 1955).

PHENOLOGY. — Flowering: August–October; fruiting: October.

DISTRIBUTION AND HABITAT. — Mexico (Baja California Sur, Chiapas, Chihuahua, Colima, Guerrero, Jalisco, México, Michoacán, Morelos, Nayarit, Sinaloa, Sonora); in our region the species is known only from nondesert portions of the Cape Region (Fig. 16); plants occur on rocky slopes and in watercourses in tropical deciduous forest and thornscrub from 450–600 m elevation.

ADDITIONAL SPECIMENS EXAMINED. — MEXICO. **Baja California Sur**: La Parrita, Rancho La Burrera, 23°29′N, 110°03′W, *M. Domínguez L. 405* (HCIB); San Bartolo, *F. Gander 9677* (SD); Arroyo El Zacatón, 12 km NE de Todos Santos, cerca del Rancho Sta. Gertrudis, 23°38′N, 110°04′W, *J. León de la Luz 3022* (HCIB, MEXU, SD); 5 mi S of San Antonio, *C. Mullinex s.n.* (CAS).

The above description has been augmented with data from other Mexican collections. Exceptions are noted where extralimital collections differ from those in our region. This is the first report of the species from the peninsula of Baja California.

Ruellia intermedia is superficially similar to *R. nudiflora*, with which it is sometimes confused (see discussion under *R. nudiflora*). In addition to the distinctions noted in the key, plants of *R. intermedia* tend to have smaller leaf blades and shorter petioles than those of *R. nudiflora* from northwestern Mexico. Also, pubescence on the capsules of *R. intermedia* is restricted to the apex and sometimes lacks glands whereas that of *R.*

nudiflora is distributed over the entire surface of the capsule and always includes some glands (at least near apex).

4. **Ruellia inundata** Kunth, Nov. gen. sp. 2:239. 1817. *Aphragmia inundata* (Kunth) Bremek., Verh. Kon. Ned. Akad. Wetensch. Afd. Natuurk., Tweede Sect. 45:10. 1948. TYPE. — COLOMBIA. "In ripa fluminis Magdalenae prope Mompox et Badillas," May, (fide protologue), *A. von Humboldt & A. Bonpland mss. n. 3711* (holotype: P-Bonpl.!).

Ruellia albicaulis Bertero in Spreng., Syst. veg. 2:822. 1825. TYPE. — COLOMBIA. "Ad fl. Magdalen.," no specimens have been seen.

Aphragmia haenkei Nees in Lindl., Intr. nat. syst. bot., ed. 2, 444. 1836. *Dipteracanthus haenkei* (Nees) Nees in A. DC., Prodr. 11:141. 1847. TYPE. — MEXICO. **Guerrero**: Acapulco, 1791, *T. Haenke s.n.* (no type designated nor place of deposition noted; probable type material: K, PR!, PRC!).

Ruellia galeottii Leonard, Kew Bull. 1938:59. 1938. TYPE. — MEXICO. **Oaxaca**: Sola, Oct 1844, *H. Galeotti 510J* (holotype: US!; isotype: NY).

Erect to ascending perennial herbs or shrubs to 0.5 (–1) m tall, herbage mephitic. Young stems subterete to quadrate, at first evenly pubescent with erect to flexuose eglandular and glandular trichomes 0.2–2 mm long, pubescence soon consisting of flexuose-retrorse eglandular trichomes only. Leaves petiolate, petioles to 85 mm long, blades ovate to elliptic, 33–190 mm long, 13–105 mm wide, 1.5–2.5 times longer than wide, acuminate at apex, acute to attenuate at base, surfaces pubescent with glandular (absent on mature leaves) and eglandular trichomes, margin entire to crenate. Inflorescence of sessile to pedunculate expanded dichasia (or inflorescence seemingly derived from a compound dichasium where the central flower is displaced to a lateral position and one dichasial branch appears central or terminal) to 40 mm long from leaf axils, collectively sometimes forming a terminal leafy panicle; dichasia alternate or opposite, (1–) 3–many-flowered, 1 (–3) per axil, peduncles (if present) 1–8 (–30) mm long, terete to subquadrate, pubescent with erect to flexuose glandular and eglandular trichomes 0.1–1.5 (–2) mm long (glandular pubescent), secondary peduncles to 22 mm long, glandular pubescent. Bracteoles and secondary bracteoles sessile to petiolate, lanceolate to lance-ovate to narrowly elliptic to oblanceolate, 4–14 mm long, 0.8–2.8 (–4) mm wide, abaxial surface glandular pubescent. Flowers sessile to subsessile (i.e., borne on pedicels to 0.5 mm long). Calyx 9–17 mm long, tube 1–2 mm long, lobes linear to oblanceolate, (5–) 7–15 mm long, unequal in length (longest lobe 1.2–1.7 times longer than shortest lobe), 6.5–24 times longer than tube, 0.2–2 mm wide, abaxially and marginally glandular pubescent. Corolla blue-purple (extralimitally sometimes pink), 20–35 mm long, externally glandular pubescent, tube 14.5–27 mm long, narrow proximal portion 8–16 mm long, gradually to ± abruptly expanded into throat, throat 6.5–17 mm long, longer or shorter than narrow proximal portion of tube, 3.5–6 mm in diameter near midpoint, limb 10–13.5 mm in diameter, lobes 4–7 mm long, 4–7.5 mm wide. Stamens included or slightly emergent, longer pair 6–12 mm long, shorter pair 4–10.5 mm long, thecae 1.7–2.4 mm long. Style 13–22 mm long, pubescent throughout with eglandular trichomes, stigma unequally 2-lobed, 1 lobe 0.2–0.5 mm long (or sometimes not evident), other lobe 0.9–1.8 mm long. Capsule stipitate, often blotched with red, 7.5–10 mm long, glabrous, stipe 2.2–3.3 mm long, head broadly ellipsoid to subcircular to obovoid. Seeds 4, 2.7–3.5 mm long, 2–3 mm wide, surfaces and margin pubescent with appressed hygroscopic trichomes. ($n = 17$, Daniel and Chuang 1993).

PHENOLOGY. — Flowering and fruiting: May, December (elsewhere flowering and fruiting: October–March).

DISTRIBUTION AND HABITAT. — Mexico (Baja California Sur, Campeche, Chiapas, Colima, Guerrero, Jalisco, México, Michoacán, Morelos, Oaxaca, Puebla, Quintana Roo, Sinaloa, Sonora, Veracruz, Yucatán), Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Ecuador, and Brazil; in our region the species is known only from nondesert portions of the Cape Region (Fig. 21); plants occur on rocky slopes and in sandy watercourses in thornscrub from near sea level to 310 m elevation.

ADDITIONAL SPECIMENS EXAMINED. — MEXICO. **Baja California Sur**: along rd from Hwy 1 across

Cape Region mts to Hwy 19, ca. 4.5 km W of San Pedro de la Soledad, ca. 23°15′N, 110°01′W, *T. Daniel & M. Butterwick 6952* (CAS, HCIB, MEXU); vicinity of Punta Lobo, *F. Hrusa 8421* (DAV).

Ruellia inundata is a widely distributed and sometimes weedy species that occurs in many habitats throughout its range. This is the first report of the species from the peninsula of Baja California where it appears to be rare. In other portions of its range, *R. inundata* sometimes has pink corollas. The above description has been augmented with data from other Mexican collections. Daniel (1995) discussed the use of this name for these plants relative to the type. *Hrusa 8421* was collected in a wash along a beach ("apparently washed downstream from adjacent mountains") and consists entirely of greatly expanded dichasia (i.e., comprising 20 or more flowers with elongate secondary peduncles). *Daniel & Butterwick 6952* comprises plants with considerably less floriferous dichasia.

Ruellia inundata is often confused with *R. paniculata* L., a similar species that occurs in similar habitats, that could also occur in the tropical deciduous forests of the Cape Region. *Ruellia paniculata* differs from *R. inundata* by its longer (11–16 mm) capsule with a narrowly ellipsoid head, its seeds which are more numerous (8–12 per capsule) and which have the trichomes restricted to the periphery, longer (2.5–3.5 mm) thecae, and subulate to linear-subulate calyx lobes which are subequal.

5. **Ruellia leucantha** Brandegee, Zoe 5:109. 1901. TYPE. — MEXICO. **Baja California Sur**: Todos Santos, 21 Jan 1890, *T. Brandegee s.n.* (lectotype, designated here: UC!).

Shrubs to 1.5 m tall, herbage often mephitic. Young stems subquadrate to quadrate, evenly and densely pubescent with erect to flexuose eglandular trichomes 0.3–1.5 mm long and glandular punctate as well, the youngest growth sometimes floccose and including stellate trichomes. Leaves subsessile to petiolate, petioles to 16 mm long, blades ovate to elliptic to subcircular, 11–110 mm long, 6–62 mm wide, 1.2–2.6 times longer than wide, acute to subacuminate at apex, acute to subattenuate at base, surfaces pubescent with eglandular trichomes (youngest growth sometimes floccose and including stellate trichomes) and glandular punctate, margin entire to subsinuate. Inflorescence of axillary dichasia; dichasia alternate or opposite, 1-flowered, 1 per axil, sessile to subsessile (i.e., peduncles to 1 mm long) in axils of distal leaves. Bracteoles petiolate, linear to elliptic to oblanceolate, 7.5–37 mm long, 0.9–7 mm wide, abaxial surface pubescent with ± flexuose eglandular (sometimes stellate) trichomes 0.1–0.5 mm long and glandular punctate, margin ciliate with flexuose eglandular trichomes to 1.5 mm long. Flowers sessile to subsessile (i.e., pedicels to 1 mm long). Calyx 10.3–17 mm long, tube 1.5–2.5 mm long, lobes subulate, 8–15 mm long, equal to subequal in length, 3.5–7.3 times longer than tube, 1–1.5 mm wide, abaxially and marginally pubescent with flexuose eglandular trichomes 0.3–1.1 mm long and glandular punctate. Corolla white, (45–) 55–75 (–90) mm long, externally pubescent with flexuose eglandular trichomes 0.2–0.4 mm long and glandular punctate, tube (36–) 40–54 (–65) mm long, narrow proximal portion (20–) 22–35 (–40) mm long, abruptly expanded distally into throat, throat 16–25 mm long, nearly equaling or shorter than narrow proximal portion of tube, 8–12.5 mm in diameter near midpoint, limb 28–50 mm in diameter, lobes 9–28 mm long, 7.5–21 mm wide. Stamens included, longer pair 13–18 (–25) mm long, shorter pair 11–15 (–23) mm long, thecae 4.5–5 mm long. Style 42–45 (–65) mm long, pubescent with eglandular trichomes, stigma unequally 2-lobed, 1 lobe 2–2.6 mm long, other lobe 0.2–0.3 mm long. Capsule stipitate, 12–15 mm long, pubescent with erect to flexuose eglandular trichomes 0.2–0.3 mm long and glandular punctate, stipe 3–3.5 mm long, head subellipsoid to obovoid. Seeds (4–) 6–8, 4–5 mm long, 3.7–5 mm wide, surfaces and margin covered with appressed hygroscopic trichomes. ($n = 17$, from *Daniel & Butterwick 6913cv*).

PHENOLOGY. — Flowering: August–January, April–May; fruiting: September–January, May.

DISTRIBUTION AND HABITAT. — Northwestern Mexico (Baja California Sur, Sinaloa); in our region the species is restricted to the Cape Region (Fig. 35), primarily outside of the desert (only one or two collections appear to have been made in regions of desertscrub); plants occur in and along watercourses and on rocky slopes mostly in thornscrub and tropical deciduous forest from near sea level to 900 m elevation.

LOCAL NAMES. — "Conpinturia" (*Carter et al. 2697*); "petunia del monte" (*Peters 230*).

ADDITIONAL SPECIMENS EXAMINED. — MEXICO. **Baja California Sur:** near La Palmilla, W of San José del Cabo, *K. Bechtel s.n.* (DS); San José del Cabo, *T. Brandegee 442* (UC), *s.n.* (UC); Sierra de la Laguna, *T. Brandegee s.n.* (UC); Cape Region, San Felipe, *T. Brandegee s.n.* (UC); San Pedro, *T. Brandegee s.n.* (GH); between Rancho Palmilla and headwaters of arroyo NW of El Encinal, ca. 23°10′N, 109°58′W, *A. Carter & F. Chisaki 3595* (DS, UC); Rancho Poza Larga, Arroyo de San Francisquito, E side of Sierra de la Victoria, 23°29–31′N, 109°47–55′W, *A. Carter & R. Ferris 3384* (DS, SD, UC); Cabo San Lucas, *A. Carter & D. Noack 4441a* (UC); ca. 1/3 of way from Rancho San Bernardo to mouth of Arroyo de San Bernardo, E side of Sierra de la Victoria, 23°24′N, 109°55′W, *A. Carter et al. 2697* (UC); Cape Region, 24 km NW of Cabo San Lucas, ca. 23°02′N, 110°01′W, *A. Carter et al. 5896* (CAS, UC); 47.5 mi S of Todos Santos on rd to Cabo San Lucas, *K. Chambers 871* (DS); along rd from Hwy 1 across Cape Region mts to Hwy 19, ca. 9–10 km W of Hwy 1, ca. 23°13′N,109°50′W, *T. Daniel & M. Butterwick 6913* (CAS, MEXU, MICH, SBBG); along rd from Hwy 1 across Cape Region mts to Hwy 19, 16–20 km W of Hwy 1, ca. 23°14′N, 109°55′W, *T. Daniel & M. Butterwick 6940* (CAS, HCIB); Rancho La Burrera, W slope of Sierra de la Laguna, ca. 22 km NE of Todos Santos, ca. 23°31′N, 110°02′W, *T. Daniel et al. 6863* (CAS); Punta Frailes, *E. Dawson 1135* (RSA); Cape San Lucas, *E. Dawson 6430* (RSA); cima de la cuesta de San Antonio, 23°45′N, 110°02′W, *R. Domínguez C. 613* (HCIB); Sierra de La Laguna, Rancho San Antonio de La Sierra, 11.6 mi SE of KP 147.6 on Hwy 1, *J. Donahue 97.169* (RSA); San José del Cabo, *F. Gander 9729* (CAS, SD); Sierra de la Laguna, Las Animas, ranch at river-fork near base of El Picacho Peak, *B. Hammerly 266* (CAS, DS); half way between Cape San Lucas and Todos Santos, *C. Harbison s.n.* (CAS, SD); San Pedro, 17 mi S of La Paz, 23°55′N, 110°16′W, *C. Harbison s.n.* (SD); 5 mi W of San Bartolo, *J. Hastings & R. Turner 64-250* (DS, SD); 15 mi N of Cabo San Lucas, *J. Hastings & R. Turner 64-350* (DS, SD); 4 mi W of San Bartolo, 23°45′N, 109°52′W, *D. Howe 4397* (SD); Todos Santos, *M. Jones 24428* (POM); W side of the Lagunas, *M. Jones 27434* (POM); Triunfo, *M. Jones 27435* (DS, POM, UC); Sol de Mayo, NW de Santiago, 23°28′N, 109°50′W, *J. León de la Luz 2770* (CAS, HCIB); Mpio. Los Cabos (Las Bahías), camino a Matancitas, 23°08′N, 110°04′W, *J. León de la Luz 3027* (HCIB); mesa "San Martin," Rancho La Burrera, 16 km NE de Todos Santos, 23°28′N, 110°07′W, *J. León de la Luz 4758* (HCIB); Cape Region, Arroyo San Bartolo, 2.5 km above San Bartolo, 23°43′N, 109°53′W, *R. Moran 6952* (SD); Cape Region, San Pedro, ca. 23°23′N, 110°12′W, *R. Moran 7000* (DS); Cape Region, S of Cabo San Lucas, *R. Moran 7051* (DS); San Pedrito, S of Todos Santos, 23°24′N, 110°13′W, *R. Moran 21340* (SD); Santiago, above Arroyo San Ignacio, *R. Peters 230* (UC); Cape Region, Arroyo San Lázaro, from its mouth (ca. 10 mi NW of San José del Cabo) to ca. 3 mi upstream, *J. Thomas 7775a* (DS); between Triunfo and San Bartolo, *I. Wiggins 5619* (CAS, DS, POM, UC); 13.5 mi E of La Paz airport along rd to Los Planes, ca. 24°02′N, 110°07′W, *I. Wiggins 15307-A* (DS); higher slopes of Calaveras, *A. Zwinger 477* (RSA).

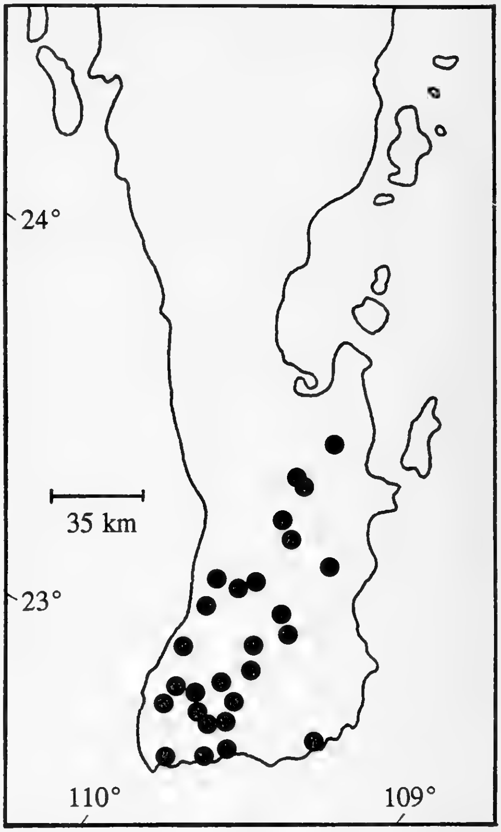


FIGURE 35. Distribution of *Ruellia leucantha.*

No collections or specific localities were cited in Brandegee's (1901) protologue. He stated that the species was, "common along the slopes of the Cape Region Mountains" and that "flowers can be found at any time of the year." Four collections from the Cape Region that were collected prior to 1901 are present in the Brandegee herbarium at UC: *Brandegee 442*, *Brandegee s.n.* (21 Jan 1890, Todos Santos), *Brandegee s.n.* (9 Sep 1893), and *Brandegee s.n.* (21 Jan 1890, Sierra de la Laguna). Brandegee labeled the former three of these specimens with his name, *Ruellia leucantha*; the latter specimen was labeled by him as simply "*Ruellia*." At least the three specimens that he labeled are syntypes of *R. leucantha*. One of these specimens (*Brandegee s.n.* 21 Jan 1890, Todos Santos) has been annotated as the type in handwriting other than that of Brandegee, but such designation of a lectotype has apparently never been published. This specimen is herewith so designated. It is a flowering and fruiting specimen that Brandegee annotated with his name and that agrees well with the protologue.

Ruellia leucantha is unusual among species of the genus occurring in northwestern Mexico by its white corollas. Although white corollas are commonly encountered among species of *Ruellia* section *Chiropterophila* Ramamoorthy from central and southern Mexico, these possess a gibbous throat and tend to open at night. The southern Mexican species *Ruellia pringlei* Fernald has white corollas that are similar in form to those of *R. leucantha* but that lack the punctate glands. It remains to be determined whether *R. pringlei* is closely related to *R. leucantha* or merely has similar corollas in response to a similar pollinator.

A mainland variety of this species was described by Gentry (1948) as *R. leucantha* var. *postinsularis* Gentry. Daniel (1996) elevated this taxon to subspecific rank. Pollen of both subspecies is shown in Fig. 30. The two subspecies can be distinguished by the following couplet:

Cauline trichomes erect to flexuose, 0.3–1.5 mm long; capsules 12–15 mm long; Baja California Sur .... subsp. *leucantha*.
Cauline trichomes erect to retrorse, 0.05–0.2 mm long; capsules 9–12 mm long; Sinaloa .. .. subsp. *postinsularis*.

Our subspecies is endemic to the Cape Region of Baja California Sur and becomes a dominant shrub in some parts of its range.

6. Ruellia nudiflora (Engelm. & A. Gray) Urb., Symb. antill. 7:382. 1912. *Dipteracanthus nudiflorus* Engelm. & A. Gray, Boston J. Nat. Hist. 5:229. 1845. TYPE. — UNITED STATES. **Texas:** Sim's Bayou near Houston, May–Jul 1843, *F. Lindheimer 157* (syntypes: GH!, UC!; isosyntype: K!); without locality, 1835, *T. Drummond coll. 2, no. 221* (syntype: GH!; isosyntype: K!), *coll. 3, no. 257* (syntype: GH!; isosyntype: K!). Leonard (J. Wash. Acad. Sci. 27:514. 1927) indicated that Lindheimer's collection from Sim's Bayou was the type. Because he did not cite a specimen, his choice would not appear to constitute a lectotypification.

Ruellia tuberosa L. var. *occidentalis* A. Gray, Syn. fl. N. Amer. 2(1):325. 1878. *Ruellia nudiflora* var. *occidentalis* (A. Gray) Leonard, J. Wash. Acad. Sci. 17:516. 1927. *Ruellia occidentalis* (A. Gray) Tharp & F. A. Barkley, Amer. Midl. Naturalist 42:25. 1949. TYPE. — Collections of Berlandier, Wright, Rothrock, and Coulter from the southwestern United States were cited by Gray. Leonard (J. Wash. Acad. Sci. 17:516. 1927) indicated that the type was collected in Texas by Berlandier. Because he did not cite a specimen, his choice would not appear to constitute a lectotypification.

Ruellia nudiflora var. *glabrata* Leonard, J. Wash. Acad. Sci. 17:518. 1927. *Ruellia glabrata* (Leonard) Tharp & F. A. Barkley, Amer. Midl. Naturalist 42:13. 1949. TYPE. — MEXICO. **Sonora:** Ciénega, Aug 1874, *J. Rothrock 560* (holotype: US; isotypes: GH!, NY).

Ruellia gooddingiana A. Nelson, Amer. J. Bot. 18:437. 1931. TYPE. — MEXICO. **Sonora:** La Ciénega, 18 Jul 1911, *L. Goodding 959* (holotype: RM!).

See Daniel (1995) for a complete listing of synonyms for this species.

Erect to ascending perennial herbs to 4.5 dm tall. Young stems quadrate to quadrate-sulcate, pubescent with an understory (sometimes sparse or absent) of retrorse eglandular trichomes 0.1–0.4 mm long and an overstory of flexuose eglandular trichomes 0.5–1 mm long. Leaves petiolate, petioles to 64 mm long, blades elliptic to ovate to broadly ovate, 70–200 mm long, 50–87 mm wide, 1.3–3.2 times longer than wide, rounded to subacute at apex, constricted-attenuate at base, surfaces pubescent with eglandular trichomes or becoming glabrate, margin undulate-crenate to sinuate. Inflorescence of pedunculate ascending or laterally spreading expanded dichasia from axils of proximal leaves and subsessile to pedunculate ± congested to ± expanded dichasia from axils of distal, usually reduced, leaves and bracts, the latter dichasia collectively forming a terminal leafy paniculiform thyrse, thyrse rachis pubescent with erect to flexuose glandular and eglandular trichomes 0.05–0.5 (–1.5) mm long (glandular pubescent); dichasia alternate or opposite, 3–many-flowered, 1 (–2) per axil, peduncles of proximal dichasia up to 85 mm long, subquadrate to quadrate, pubescent like stems (or sometimes glandular pubescent), peduncles of distal dichasia 1–45 mm long, glandular pubescent. Bracts sessile to petiolate, obovate to elliptic to narrowly elliptic to linear to subulate, 3–20 mm long, 0.7–8 mm wide, glandular pubescent, proximal (larger and more leaflike) bracts sometimes eglandular. Bracteoles sessile, lanceolate to lance-ovate to elliptic to oblanceolate, 2–10 mm, 0.5–5 mm wide, glandular pubescent (or those of proximal dichasia sometimes eglandular), secondary bracteoles similar to bracteoles except smaller. Flowers pedicellate, pedicels 1–18 mm long, glandular pubescent. Calyx 7.5–21 mm long, tube 1–3 mm long, lobes lance-subulate to subulate, 6.5–18 mm long, subequal to unequal in length, 4.3–9 times longer than tube, 0.4–1 mm wide, abaxially and marginally glandular pubescent. Corolla blue-purple, (25–) 31–60 mm long, externally glandular pubescent, tube 21–47 mm long, narrow proximal portion 8–27 mm long, ± abruptly expanded into throat, throat (9–) 11–25 mm long, longer than or ± equal to narrow proximal portion of tube, 4–12 mm in diameter near midpoint, limb 18–31 mm in diameter, lobes 7–17 mm long, 7–18 mm wide. Stamens included, longer pair 8–19 mm long, shorter pair 6–16 mm long, thecae 2.8–4 mm long. Style 15–47 mm long, pubescent with eglandular trichomes and sometimes glandular near base as well, stigma unequally 2-lobed, 1 lobe 1–2 mm long, other lobe 0.1–0.7 mm long. Capsule 11–21 mm long, externally glandular pubescent (eglandular trichomes becoming retrorse toward base of capsule and glandular trichomes sometimes sparse or restricted to apex), stipe 2–3.5 mm long, head linear-ellipsoid to obovoid. Seeds 8–12, 2.2–3.5 mm long, 2–3 mm wide, surfaces and margin covered with appressed hygroscopic trichomes. ($n = 17$, Daniel et al. 1990).

PHENOLOGY. — Fruiting: November–January. Elsewhere flowering and fruiting: February–October.

DISTRIBUTION AND HABITAT. — United States (Arizona, Louisiana, Texas), Mexico (Baja California Sur, Campeche, Chiapas, Chihuahua, Coahuila, Colima, Durango, Morelos, Nuevo León, Oaxaca, Quintana Roo, San Luis Potosí, Sinaloa, Sonora, Tabasco, Tamaulipas, Veracruz, Yucatán), Belize, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, and West Indies; in our region the species is known only by two collections from the Sonoran Desert (Central Gulf Coast and Magdalena subdivisions) of Baja California Sur (Fig. 36); plants occur on flats and along watercourses in desertscrub from 100–130 m elevation.

ADDITIONAL SPECIMENS EXAMINED. — MEXICO. **Baja California Sur:** Pradera, Ejido de Los Naranjos, 26°20′N, 111°53′W, *M. Domínguez L. 176* (HCIB); 4–5 mi SW of Rancho El Obispo, ca. 24°39′N, 111°10′W, *I. Wiggins 15576* (CAS, DS).

This species is reported from the peninsula of Baja California on the basis of two fruiting collections. Wiggins had identified his collection as *Ruellia nudiflora* var. *glabrata* but did not include the species in his *Flora of Baja California* (1980). The above description has been augmented with data from other Mexican collections. The dichasia which are usually evident in the axils of proximal leaves (and which presumably bear cleistogamous flowers) are not evident on *Wiggins 15576* but are present on *Domínguez L. 176*.

Ruellia nudiflora is an extremely variable and widely distributed species. This species along with *R. tuberosa* L., *R. intermedia*, *R. puberula* (Leonard) Tharp & F. A. Barkley, and several others that are sometimes recognized, comprise a complex that has not been fully resolved taxonomically. Additional notes on this species were provided by Daniel (1984, 1995).

TETRAMERIUM

Tetramerium Nees in Benth., Bot. voy. *Sulphur*, 147. 1846, nom. cons., non *Tetramerium* C.F. Gaertn. (1806). TYPE. — *Tetramerium* *polystachyum* Nees (= *Tetramerium nervosum* Nees).

Averia Leonard, J. Wash. Acad. Sci. 30:501. 1940. TYPE. —*Averia longipes* (Standl.) Leonard (≡ *Drejerella longipes* Standl.; = *Tetramerium nemorum* Brandegee).

Erect, ascending, or decumbent perennial herbs or shrubs with cystoliths. Older stems with epidermis exfoliating. Leaves opposite (elsewhere, rarely ternate), subsessile to petiolate (the distal leaves rarely sessile), margin entire to crenate, petioles detaching a short distance from their base leaving petiolar stubs at nodes. Inflorescence of terminal conspicuously and usually densely bracteate 4-sided unbranched dichasiate spikes; dichasia opposite, 1–3-flowered, sessile, subtended by a bract. Bracts opposite, green, margin entire to dentate. Bracteoles smaller than bracts. Flowers homostylous, subtended by 2 homomorphic bracteoles, sessile. Calyx deeply 4- or 5-lobed, lobes homomorphic or, if 5, one usually reduced in size. Corolla white, cream, yellow, blue, or red, often with maroon and purplish markings on upper lip, externally glabrous (in ours), tube subcylindric or gradually expanded distally, throat indistinct or distinct only near mouth, limb pseudopapilionaceous, upper lip entire to shallowly 2-lobed, lower lip 3-lobed, lower-central lobe (in ours) conduplicate and enclosing stamens and often style during anthesis, corolla lobes imbricate in bud. Stamens 2, inserted near base of lower-central lobe of limb, exserted from mouth of corolla, anthers 2-thecous, thecae equal to subequal in size, parallel to subsagittate, equally inserted, lacking basal appendages, dehiscing toward upper lip (i.e., flower stenotribal); pollen (Fig. 37) prolate, 3-colporate, 6-pseudocolpate, pseudocolpi 2 per mesocolpium, exine reticulate; staminodes 0. Style exserted from mouth of corolla, stigma 2-lobed, lobes triangular, equal. Capsule stipitate, head ellipsoid to obovoid, retinacula present, septae with attached retinacula separating from inner wall of mature capsule. Seeds 4 (or fewer by abortion), homomorphic, plano-convex (in ours, elsewhere also concavo-convex), lacking trichomes. ($x = 18$).

A genus of 28 species occurring from the southwestern United States southward throughout most of Mexico, Central America, and north-

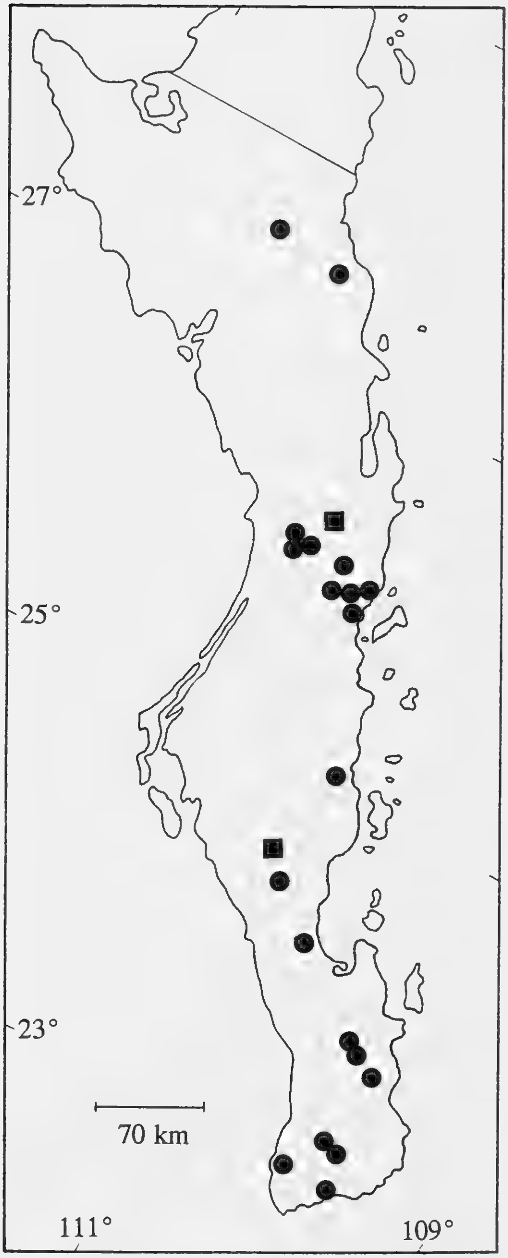


FIGURE 36. Distribution of *Ruellia nudiflora* (squares) and *Tetramerium fruticosum* (circles) in the peninsula of Baja California.

western South America to southeastern Bolivia. With 21 species, Mexico is the center of diversity of *Tetramerium*. A single species is known from the United States. Species occur primarily in regions of dry forest at relatively low elevations.

REFERENCES. — HAPP, G. B. 1937. Monograph of *Tetramerium* and *Henrya*. Ann. Missouri Bot. Gard. 24:501–583; DANIEL, T. F. 1986. Systematics of *Tetramerium* (Acanthaceae). Syst. Bot. Monogr. 12:1–134.

Key to Species of *Tetramerium*

1. Calyx 5-lobed; bracts with apical portion straight and erect, margin ciliate with trichomes up to 0.7 mm long; bracteoles linear to linear-lanceolate to linear-oblanceolate, 5–10 mm long; capsule glabrous .... *T. fruticosum*
1. Calyx 4-lobed; bracts with apical portion twisted and spreading, margin ciliate with at least some (usually most) trichomes longer than 0.7 mm; bracteoles subulate to lance-subulate, 2–5 mm long; capsule pubescent .... *T. nervosum*

1. Tetramerium fruticosum Brandegee, Zoe 5:171. 1903. TYPE. — MEXICO. **Baja California Sur**: San José del Cabo, Jan–Mar 1901, *C. Purpus 489* (holotype: UC!; isotypes: CAS!, GH!, MO!, NY!, US!).

Ascending to erect perennial herbs to 5 dm tall. Young stems subquadrate to terete, pubescent with an overstory (sometimes sparse or nearly absent) of flexuose to retrorse eglandular trichomes (0.05–) 0.1–0.5 (–0.8) mm long and often with an understory of inconspicuous glandular trichomes 0.05 mm (or less) long, trichomes concentrated in 2 lines, older stems becoming glabrate as epidermis exfoliates. Leaves petiolate; petioles to 20 (–35) mm long; blades ovate to broadly ovate, 16–62 mm long, 5–42 mm wide, 1.4–3.8 times longer than wide, acute to acuminate to subfalcate at apex, acute to truncate to subcordate at base, surfaces and margin pubescent (often sparsely so) like young stems or the trichomes mostly antrorse and eglandular, margin entire to subcrenate. Inflorescence of ± densely bracteate spikes to 60 mm long, 10–20 mm wide near midspike, rachis not or only partly visible, pubescent with an understory of inconspicuous glandular trichomes 0.05 mm long and usually with an overstory of longer scattered flexuose eglandular trichomes as well. Bracts erect, ovate to elliptic, 7–13 (–25) mm long, (4–) 5–9 (–15) mm wide, proximalmost bracts often petiolate and longer than the more distal subsessile bracts, acute to rounded to truncate and mucronate at apex, mucro 0.2–0.7 mm long, apical portion of bract straight and erect, major veins 3–5 (sometimes somewhat obscure), palmate to subpalmate, abaxial surface pubescent with cauline type trichomes, margin ciliate with antrorse or cauline type trichomes 0.05–0.7 mm long. Bractlets linear to linear-lanceolate to linear-oblanceolate, 5–10 mm long, 0.5–1.4 mm wide, abaxial surface pubescent like bracts. Calyx 5-lobed, 3–5.5 mm long, the tube 0.5–1 mm long, lobes subulate, 2.5–5 mm long, abaxially pubescent with an understory of glandular trichomes 0.05–0.1 mm long and an overstory of flexuose eglandular trichomes 0.2–0.5 mm long. Corolla cream with a maroon and purplish chevron (rarely absent) on the upper lip, 10–14 (–17.5) mm long, tube 4.5–6 (–7) mm long, upper lip obovate, 5.2–7.5 (–9) mm long, 3–4.5 mm wide, entire or emarginate at apex, lower lip 5.5–8.5 (–10.5) mm long, lateral lobes 5–7.5 (–9.5) mm long, 2–4.2 (–4.6) mm wide, lower-central lobe 4.2–6.3 (–7) mm long, 2.3–4 mm wide. Stamens 5.5–6.8 mm long, thecae 1–1.5 mm long. Style 6–13 mm long. Capsule 5–6.5 mm long, glabrous, stipe 1.5–2 mm long, head 3.5–4.5 mm long. Seeds 1.4–1.9 mm long, 1.2–1.7 mm wide, surfaces covered with conical papillae when young, these mostly becoming low and rounded on mature seeds. ($n = 18$, Daniel 1986, Daniel et al. 1984, 1990). Fig. 38.

PHENOLOGY. — Flowering and fruiting: October–April.

DISTRIBUTION AND HABITAT. — Northwestern Mexico (Baja California Sur and Sonora); in our region the species is known from nondesert portions of the Cape Region, the Sierra de la Giganta, and the Sonoran Desert (Central Gulf Coast, Vizcaíno, and Magdalena subdivisions) in Baja California Sur (Fig. 36); plants occur on slopes and along watercourses in desertscrub, thornscrub, and tropical deciduous forest from 100–950 m elevation.

ADDITIONAL SPECIMENS EXAMINED. — MEXICO. **Baja California Sur**: Cape Region, Cajoncito, *T. Brandegee s.n.* (UC); Purísima-Comondú, *T. Brande-*

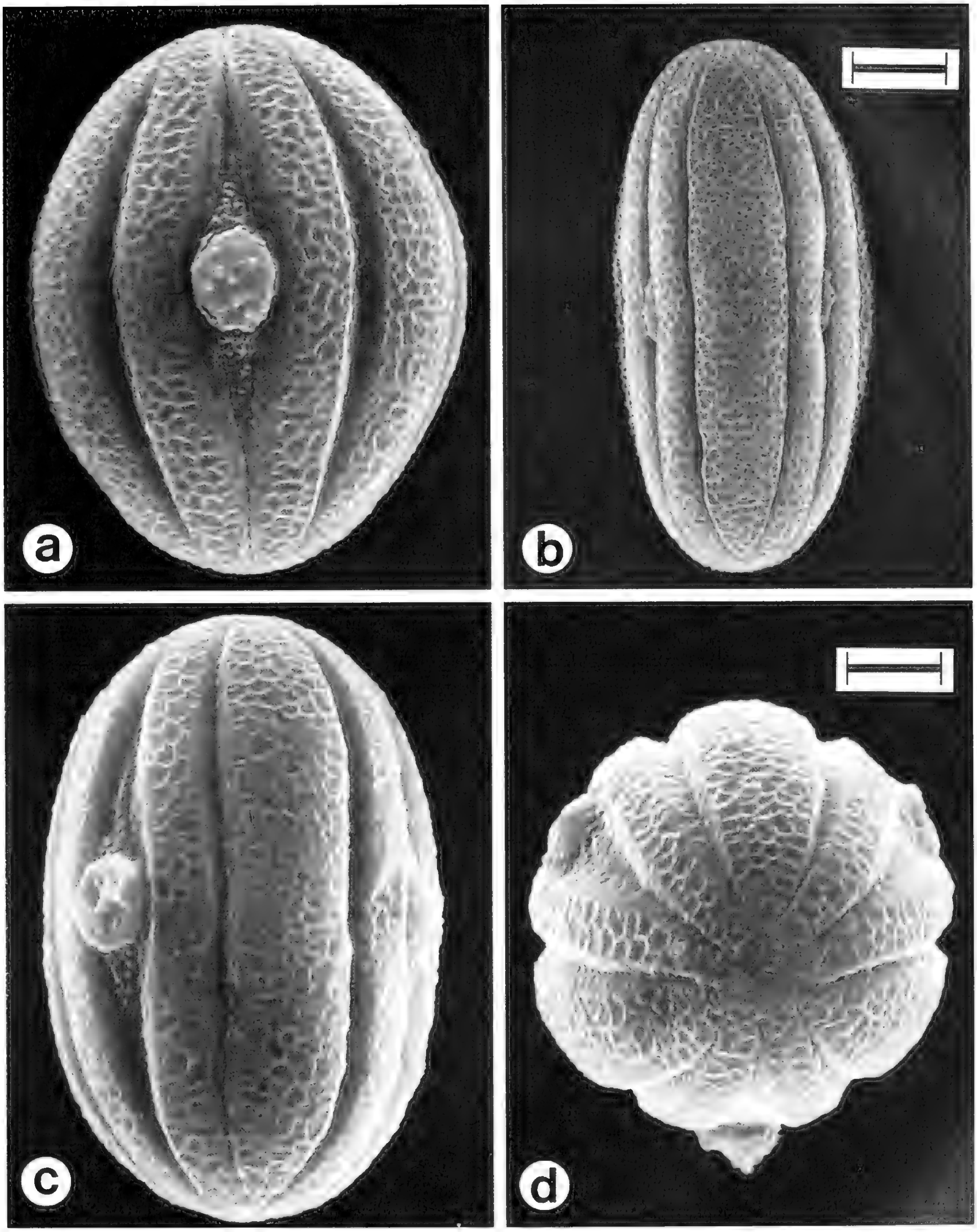


FIGURE 37. Pollen. a. *Tetramerium fruticosum* (*Daniel & Butterwick 6869*), colpal view; b. *T. fruticosum* (*Daniel & Butterwick 6869*), intercolpal view; c. *T. nervosum* (*Carter & Moran 5324*), intercolpal view; d. *T. nervosum* (*Carter & Moran 5324*), polar view. Scale for a, c, and d = 5 µm; scale for b = 7.5 µm.

gee 450 (NY, UC); Sierra de la Giganta, vic. Rancho Agua Escondido, ca. 90 km E of Villa Constitución, ca. 25°06′N, 111°W, *A. Carter 4748* (NY, TEX, UC); Sierra de la Giganta, Cañón de Teojo, W of Notrí, ca. 25°52′N, 111°22′W, *A. Carter 4913* (CAS, UC, US), *4914* (UC, US); Sierra de la Giganta, Arroyo Carrizal, E of Rancho El Horno (NE of San Xavier), ca. 25°53′N, 111°31′W, *A. Carter & R. Ferris 3832* (CAS, UC, US); Sierra de la Giganta, ridge S of La Victoria, ca. 25°52′N, 111°25′W, *A. Carter & R. Ferris 3899* (CAS, UC, US); Sierra de la Giganta, between La Victoria and portezuelo to the E, ca. 25°52′N, 111°25′W, *A. Carter & R. Ferris 3919* (MICH, UC); Sierra de la Giganta, Arroyo Gabilán, ca. 25°55′N, 111°23′W, *A. Carter & R. Ferris 4073* (MO, NY, SD, TEX, UC); Sierra de la Giganta, "El Pulpito" del Arroyo de las Parras, W of Loreto, 25°58′N, 111°27′W, *A. Carter & L. Kellogg 3157* (F, UC); Sierra de la Giganta, Arroyo Hondo, N side of Cerro Giganta, 26°08′N, 111°34′W, *A. Carter & M. Sousa S. 5168* (GH, MICH, SD, UC); along Hwy 1 between San Antonio and San Bartolo, ca. 4 km SE of San Antonio, ca. 23°48′N, 110°01′W, *T. Daniel & M. Butterwick 6869* (BR, CAS, HCIB, MEXU, MICH, MO, SBBG, US); along rd from Hwy 1 across Cape Region mts to Hwy 19, ca. 9–10 km W of Hwy 1, ca. 23°13′N, 109°50′W, *T. Daniel & M. Butterwick 6912* (CAS, HCIB, MEXU); along rd from Hwy 1 across Cape Region mts to Hwy 19, ca. 0.6 km W of San Pedro de la Soledad, ca. 23°14′N, 109°58′W, *T. Daniel & M. Butterwick 6949* (CAS); Hwy 1, 83.7 mi SE jct Hwy 22 in Cd. Constitución, *T. Daniel et al. 2438* (ASU, CAS, ENCB, MEXU); along Hwy 1, 4.4 mi NW of El Triunfo, *T. Daniel et al. 2490* (CAS, MICH, NY, SBBG); Hwy 1, SE of San Bartolo, 28.2 mi SE of El Triunfo, *T. Daniel et al. 2521* (ASU); 10 mi W of Comondú, *H. Gentry 4074* (ARIZ, DES, DS, RSA, UC); Comondú, *H. Gentry 4106* (ARIZ, DES, DS, GH, UC, US); San Antonio, *M. Jones 22505* (POM); above Primiera Agua near Loreto, *M. Jones 27390* (DS, MO, POM, UC); N base of Volcán las Tres Vírgenes, 27°29′N, 112°36′W, *R. Moran 20466* (ENCB, SD); Sierra San Francisco, Los Datiles, Arroyo Batequi, 27°35′N, 113°01′W, *R. Moran 23900* (SD); San Pablo, *C. Purpus 83* (DS, F, UC, US); central Baja California, *C. Purpus s.n.* (UC); 28.7 km N of Cabo San Lucas toward Todos Santos, ca. 23°05′N, 110°05′W, *A. Sanders et al. 3444* (UCR); near km 40 on hwy. between La Paz and Santo Domingo, *J. Thomas 8443* (CAS, DS, ENCB, GH, UC, US); N of Comondú, *I. Wiggins 5480* (DS).

Daniel (1986) discussed the unusual distribution pattern of this species, which is known from Baja California Sur and a single occurrence on the Mexican mainland. *Tetramerium fruticosum* was treated by Daniel (1986) in section *Tetramerium*. It superficially resembles *T. nervosum* which is undoubtedly a close relative.

2. Tetramerium nervosum Nees in Benth., Bot. voy. *Sulphur*, 148. 1846. TYPE. — ECUADOR. **Guayas:** Puna, 1836–1839, *A. Sinclair s.n.* (holotype: K!).

Tetramerium hispidum Nees in A. DC., Prodr. 11:468. 1847. TYPE. — MEXICO. State unknown: prope las Ajuntas ad flumen Montezuma, Jan, *C. Ehrenberg 1072* (lectotype, Ann. Missouri Bot. Gard. 24:529. 1937: B, destroyed; isolectotype: GH!).

Tetramerium nervosum var. *hispidum* Torr. in Emory, Rep. U. S. Mex. bound. 2(1):125. 1859. TYPE. — MEXICO. **Sonora:** Santa Cruz, Sep 1851, *G. Thurber 918* (lectotype, Syst. Bot. Monogr. 12:48. 1986: NY!; isolectotypes: F!, GH!, NY!).

Dianthera sonorae S. Watson, Proc. Amer. Acad. Arts 24:67. 1889. TYPE. — MEXICO. **Sonora:** vicinity of Guaymas, Sep 1887, *E. Palmer 240* (holotype: GH!; isotypes: K!, NY, US!).

Tetramerium scabrum Happ, Ann. Missouri Bot. Gard. 24:532. 1937. TYPE. — MEXICO. **Sonora:** Fronteras, Jun 1851, *G. Thurber 432* (holotype: NY!; isotypes: CAS!, GH!).

See Daniel (1995) for a complete listing of synonyms for this species.

Ascending to erect perennial herbs to 4 dm tall. Young stems subterete to subquadrate, bifariously pubescent with an understory of flexuose to retrorse eglandular trichomes 0.3–0.6 mm long and sometimes also ± evenly pubescent with an overstory of flexuose eglandular trichomes 0.7–1 mm long, older stems becoming glabrate as epidermis exfoliates. Leaves petiolate, petioles to 16 (–27) mm long, blades ovate to narrowly elliptic, 14–75 mm long, 4–38 mm wide, 2–4.6 times longer than wide, acute to acuminate at apex, rounded to acute to subattenuate at base, surfaces and margin pubescent with mostly antrorse eglandular trichomes, margin entire. Inflorescence of densely bracteate spikes to 50 mm long, 10–19 mm wide near midspike, rachis not visible, pubescent with antrorse eglandular trichomes 0.2–0.4 (–1) mm long and sometimes with inconspicuous sessile to stalked glandular trichomes 0.05–0.2 mm long (i.e., glandular pubescent) as well. Bracts erect to spreading, ovate

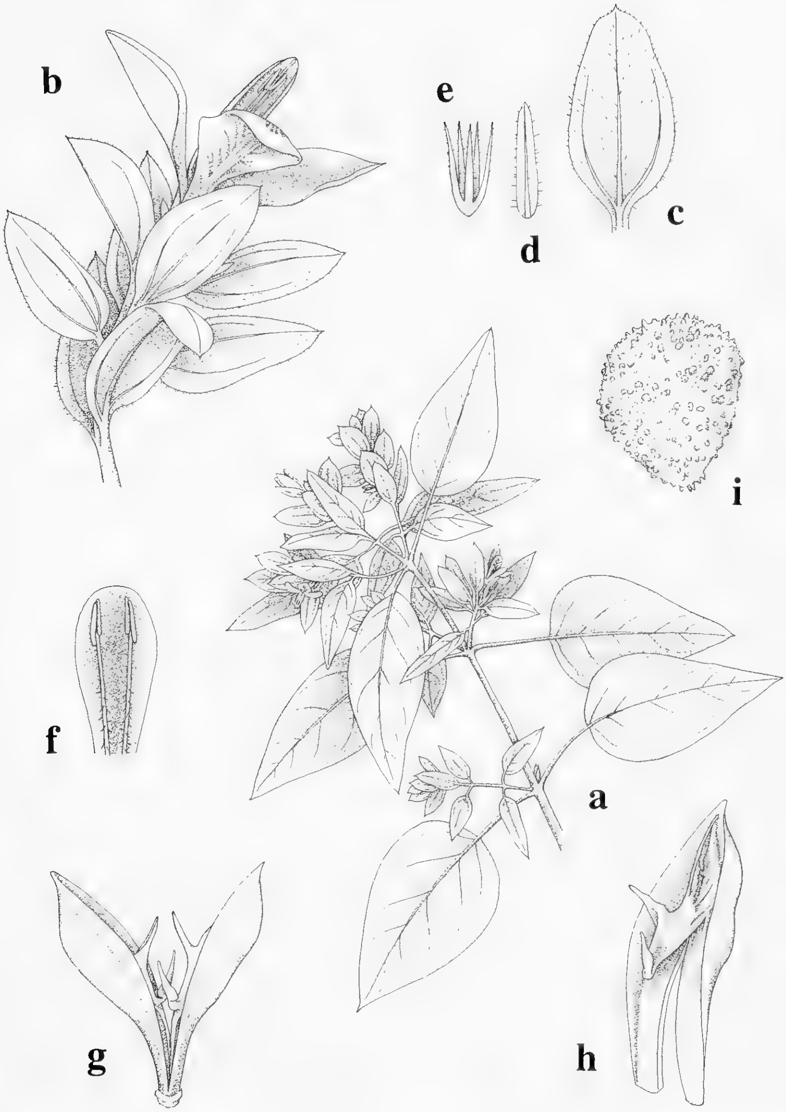


FIGURE 38. *Tetramerium fruticosum*. a. habit (*Carter 4913*), × 0.5; b. spike with flower (*Daniel et al. 2438*), × 2.7; c. bract (*Gentry 4074*), × 2.5; d. bracteole (*Thomas 8443*), × 2.5; e. calyx (*Thomas 8443*), × 2.5; f. lower lip of corolla with stamens (*Daniel & Butterwick 6869*), × 4; g. capsule (*Carter 4913*), × 5.5; h. capsule valve (*Gentry 4074*), × 7.5; i. seed (*Daniel et al. 2438*), × 15. Drawn by Jenny Speckels.

to elliptic to obovate, 9–14 mm long, (3–) 4.8–6 mm wide (proximalmost bracts sometimes larger and remote), rounded- to acute-mucronate at apex, mucro 0.4–0.8 mm long, apical portion of bract twisted and somewhat recurved-spreading, major veins 3–5, palmate, abaxial surface glandular pubescent and sparsely to densely pubescent with antrorse eglandular trichomes 0.2–1 mm long, the latter trichomes sometimes ± restricted to major veins, margin ciliate with antrorse eglandular trichomes 0.2–2.2 mm long (at least some trichomes > 1 mm long) and usually glandular pubescent as well. Bracteoles subulate to lance-subulate, (2.5–) 3–5 mm long, 0.5–0.6 mm wide, abaxial surface glandular pubescent and pubescent with eglandular trichomes to 0.6

mm long. Calyx 4-lobed, 3–5 mm long, tube 0.5–1 mm long, lobes subulate, 2.5–4 mm long, abaxially glandular pubescent. Corolla white to yellowish with purplish markings on upper lip, 12–16 mm long, tube 6–8 mm long, upper lip obovate, 5–7 mm long, 2 mm wide, entire at apex, lower lip 6–8 mm long, lateral lobes 4.5–7 mm long, 2.5 mm wide, lower-central lobe 4.5–7 mm long, 3–4.4 mm wide. Stamens 4.5–6 mm long, thecae 1–1.2 mm long. Style 6–9.5 mm long. Capsule 4.5–5.5 mm long, pubescent with erect to flexuose to retrorse eglandular trichomes 0.1–0.2 mm long, stipe 1–1.5 mm long, head 3.5–4 mm long. Seeds 1.3–1.6 mm long, 1–1.4 mm wide, surfaces covered with conical papillae bearing retrorse barbs. (*n* = 18, Daniel 1986, Daniel et al. 1984).

PHENOLOGY. — Flowering and fruiting: September–January, May.

DISTRIBUTION AND HABITAT. — Southwestern United States (Arizona, New Mexico, Texas), Mexico (Baja California Sur, Campeche, Chiapas, Chihuahua, Colima, Coahuila, Durango, Guanajuato, Guerrero, Hidalgo, Jalisco, México, Michoacán, Morelos, Nayarit, Nuevo León, Oaxaca, Puebla, Querétaro, San Luis Potosí, Sinaloa, Sonora, Tamaulipas, Veracruz, Yucatán, Zacatecas), Guatemala, Honduras, El Salvador, Nicaragua, Costa Rica, Panama, Colombia, Venezuela, Ecuador, and Peru; in our region the species is known from nondesert portions of the Cape Region, the Sierra de la Giganta, and the Sonoran Desert (Central Gulf Coast subdivision) of Baja California Sur (Fig. 34); plants occur along watercourses in thornscrub and tropical deciduous forest from 40–675 m elevation.

LOCAL NAME. — "Panalito" (*Domínguez C. 624*).

ADDITIONAL SPECIMENS EXAMINED. — MEXICO. **Baja California Sur**: Sierra de Laguna, *T. Brandegee s.n.* (NY, UC); Sierra de la Giganta, Valle de Los Encinos (S side of Cerro Giganta), ca. 26°04′N, 111°35′W, *A. Carter & R. Moran 5324* (BM, CAS, GH, MICH, SD, TEX, UC, US); along rd from Hwy 1 across Cape Region mts to Hwy 19, 16–20 km W of Hwy 1, ca. 23°14′N, 109°55′W, *T. Daniel & M. Butterwick 6939* (CAS, HCIB); Rancho La Burrera, W slope of Sierra de la Laguna, ca. 22 km NE of Todos Santos, ca. 23°31′N, 110°02′W, *T. Daniel et al. 6856* (CAS, MEXU); Cañón La Burrera, 25 km NE de Todos Santos, 23°32′N, 110°04′W, *R. Domínguez C. 624* (HCIB); desviación carretera al S a Todos Santos, 23°55′N, 110°15′W, *J. León de la Luz 3018* (HCIB); Cape Region, 11 km N of Santa Anita, ca. 23°15′N, 109°42′W, *R. Moran 6925* (CAS, DS, RSA, SD, TEX); Sierra de Guadalupe, San Sebastián, ca. 27°01′N, 112°24′W, *R. Moran 18773* (UC); 28.7 km N of Cabo San Lucas toward Todos Santos, ca. 23°05′N, 110°05′W, *A. Sanders et al. 3444* (CAS); between La Paz and San Pedro, *I. Wiggins 5595* (CAS, DS, GH, MICH, NY, POM, UC, US).

The distribution of and variation in *T. nervosum* was discussed at length by Daniel (1986). The above description is derived solely from plants from the peninsula of Baja California. Plants from our region all have four calyx lobes and are relatively homogeneous in other respects as well. Information on the reproductive biology and pollination ecology of this species was provided by Daniel (1986).

Tetramerium nervosum was included in section *Tetramerium* by Daniel (1986). Because of its phenotypic plasticity it greatly resembles, and is undoubtedly closely related to, many species of that section.

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SPECIES OF THE *HAZELAE* GROUP OF *PLATYMANTIS* (AMPHIBIA: RANIDAE) FROM THE PHILIPPINES, WITH DESCRIPTIONS OF TWO NEW SPECIES

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Three species Groups of Philippine anurans of the genus *Platymantis* are recognized. The Groups are diagnosed on the basis of combinations of digital characters. Species of the *hazelae* Group are revised. Eight species are placed in this Group, two of them (*reticulatus* and *panayensis*) previously undescribed. These small to moderate-sized (20–30 mm for males and 25–39 mm for females) frogs are forest species from mountain areas of islands in the Greater Negros and Greater Luzon island groups.

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The genus *Platymantis*, as it is currently diagnosed, has two centers of diversity, one in the Philippine Islands and one in the Bismarck-Solomon Islands. There are three small extensions beyond these archipelagos. New Guinea has three species, Fiji two species, and the Palau Islands one species. The relationships of the three Philippine Groups, recognized in this study, to each other and to the Groups that apparently exist in other parts of the range of the genus are unclear at this time. Phylogenetic studies of the Asiatic island ranids currently underway may provide some answers.

The latest revision of Philippine *Platymantis* is that of Inger (1954). He followed Taylor (1920) in assigning both the large-disked and small-disked species to one genus, whereas Boulenger (1918) and Noble (1931) had placed these assemblages in two genera (*Cornufer* and *Platymantis*). Inger (1954) regarded disk size as simply a measure of the degree of specialization of these structures representing a continuum.

Inger recognized seven Philippine species, five with broadly dilated finger disks and two without or with small finger disks. Since 1954, five more Philippine species have been described. Of these *ingeri*, *insulatus*, and *lawtoni* have large finger disks; *levigatus* and *spelaeus* have small to moderate disks.

When a combination of digital characters and size of finger disks are considered, it becomes evident that three species Groups are represented in the Philippine fauna. Species of the *hazelae* Group are the subject of this paper.

MATERIALS AND METHODS

Materials examined include: (1) all earlier reported specimens including types of previously described species and (2) all specimens of large-disked species in the recent samples of populations from the northern and central islands. These collections are in the California Academy of Sciences (CAS or CAS-SU), Cincinnati Museum of Natural History (CMNH), Field Museum of Natural History (FMNH), Museum of Comparative Zoology (MCZ), United States National Museum (USNM), and Philippine National Museum (PNM).

Morphometric characters, including snout-vent length (SVL), head length (HL), head breadth (HW), snout length (SnL), horizontal diameter of eye (ED), horizontal diameter of tympanum (TD), tibia length (TiL), third finger length from proximal edge of basal tubercle (3FL), diameter of third finger disk (3FD), and diameter of third toe disk (3ToD) were measured to the nearest 0.1 mm using a Helios dial caliper. The significance of differences between means (x) of various proportional measurements is based on Student's t tests. Only adult specimens were used on the assumption that growth is linear for this age class. Other non-metric, morphological characters include: webbing of fingers and toes, skin ornamentation, shape of snout, color pattern, vomerine teeth, structure of tubercles on hands and feet, shape of terminal phalanges, and shape and projection of snout. Useful characters such as vocalizations are still not available.

SYSTEMATIC SECTION

Although only the *hazelae* Group species are the subject of this study, preliminary diagnoses of the three Philippine Groups are provided.

The *hazelae* Group. — This Group is distinguished by the following combination of characters: (1) terminal phalanx a wide "T"; (2) disks of fingers, except first, broadly dilated; (3) first finger much shorter than second, not reaching beyond midpoint between subarticular tubercle and disk; (4) digits proximal to disks much broader than deep, the result of wide dermal flanges (Fig. 1a); (5) subarticular tubercles large, round, and only moderately protruding (Fig. 1a); (6) toe disks smaller than finger disks.

The *guentheri* Group. — This Group is distinguished by the following combination: (1) terminal phalanx a moderate to wide "T"; (2) disks of fingers, except first; moderately to broadly dilated; (3) first finger shorter than second, reaching as far as base of disk for some species; (4) digits proximal to disks about as deep as broad (Fig. 1b), the result of narrow, dermal flanges (Fig. 1b); (5) subarticular tubercles large and strongly protruding (Fig. 1b); (6) toe disks about as broad to half as broad as finger disks.

The *dorsalis* Group. — This Group is distinguished by the following combination of characters: (1) terminal phalanx bluntly rounded to pointed; (2) tips of fingers blunt, without disks, or with small to moderate disks (Fig. 1c); (3) first finger slightly shorter, about as long as, or longer than second; (4) digits proximal to disks about as deep as broad (Fig. 1c); (5) subarticular tubercles large, strongly protruding and frequently pointed (Fig. 1c); (6) finger disks smaller than to slightly larger than toe disks.

Four of the five large-disked species recognized by Inger (1954) are assigned to the *hazelae* Group. His sample for those four species was 22 specimens: *cornutus* (one), *subterrestris* (four), *polilloensis* (six), and *hazelae* (11). *Platymantis lawtoni* Brown and Alcala, 1974, was based on two specimens. Although the samples for some species are still small, field work during the past couple of decades by the junior authors and R. I. Crombie, L. R. Heaney, C. A. Ross, A. C. Diesmos and D. Balete has increased the sample size for the Luzon population of *montanus*, and added samples from previously unknown populations on several islands (Luzon, Masbate, Sibuyan, and Panay). It therefore is appropriate to reexamine the systematic status of these populations.

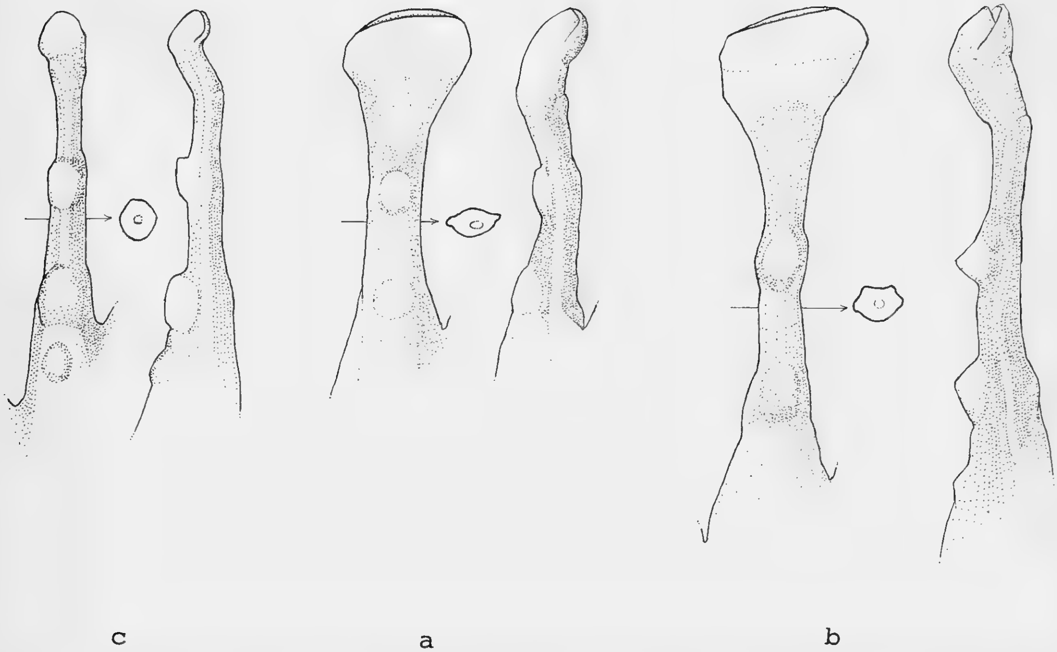

FIGURE 1. Ventral, cross-sectional, and lateral views of third finger, showing differences in disks, breadth proximal to disks, and subarticular tubercles for: a. *Platymantis hazelae* Group, b. *Platymantis guentheri* Group, and c. *Platymantis dorsalis* Group.

Key to *hazelae* Group Species

1a. No pale (yellow in life) and brown areolations in groin and on hind limbs; snout pointed to round-pointed; upper jaw moderately to strongly protruding 2

1b. Pale (yellow in life) and brown areolations in groin and on hind limbs present; snout rounded; upper jaw scarcely to moderately protruding 4

2a. Prominent, fleshy, triangular horn present on posterior upper eyelid . *cornutus* Taylor

2b. No such fleshy horn on upper eyelid . . . 3

3a. Snout pointed, short relative to head breadth (SnL/HW 35–43%, mean 39.0); tympanum large relative to eye (TD/ED 25–42%, mean 35.55); known from Negros and Masbate islands . . . . . *hazelae* Taylor

3b. Snout pointed, long relative to head breadth (SnL/HW 40–43%, mean 40.75); tympanum small relative to eye (TD/ED 19–40%, mean 29.0); known from Polillo Island . . . . *polilloensis* Taylor

4a. SVL 20–28 mm for males and 25–34 mm for females 5

4b. SVL greater than 28 mm for males and 35 mm for females. *lawtoni* Brown and Alcala

5a. Tympanum large, TD greater than 3FD and 42–52% of ED; finger disks moderately broad (3FD 19–31% of 3FL) . . . . *subterrestris* Taylor

5b. Tympanum small to moderate, TD less than 3FD and 23–50% of ED; finger disks very broad (3FD 31–48% of 3FL) 6

6a. Pale, brown-ringed areolations present on lower hind limbs, thighs and groin; frequent mottling of irregular brown lines on belly; known only from Mt. Isarog in southeastern Luzon . . . . *reticulatus* new species

6b. Pale and brown areolations rarely evident on lower hind limbs; no mottling of brown lines on belly 7

7a. TiL usually greater than 50% of SVL; ED usually greater than 30% of HW; known from Panay Island. *panayensis* new species

7b. TiL usually less than 50% of SVL; ED usually less than 30% of HW; known from mountains of southwestern Luzon Island . . . . *montanus* Taylor

Platymantis cornutus (Taylor)

Cornufer cornutus Taylor, 1922a:175 (Type loc.: Balabalan, Mountain Province, Luzon Island; holotype in CAS).

This species, described by Taylor on the basis of the unique holotype, is tentatively included in this Group. No further examples have been reported or are known to have been collected; and the condition of the type specimen does not permit x-raying for most skeletal characters that are critical for verification of the current generic assignment; although the omosternum is forked and the nasals appear to be large.

DESCRIPTION. — SVL 30.0 mm (in preserved state) for the unique type; HW 12.2 mm and HL 10.2 mm; snout rounded; SnL 4.2 mm; ED 3.5 mm; tympanum exposed; TD 1.3 mm; canthus rounded; lores moderately oblique, concave; fingers with very small webs but with flanges of skin; first finger only reaching distal edge of tubercle of second finger when adpressed; disks of fingers (except first) large and rather truncate; 3FD 2.0 mm and 3FL 5.8 mm; subarticular tubercles large, moderately protruding; one row of supernumerary tubercles; inner metacarpal tubercle moderate, middle one large, outer small; hind limbs long, TiL 14.7 mm; toes webbed to base of tubercle on inside of first and second toes, to middle of tubercle on third and fifth, short of basal tubercle on fourth; 3ToD 1.0 mm; subarticular tubercles moderately large; inner metatarsal tubercle low, elongate; outer round, pointed; no supernumerary tubercles; dorsum with only few scattered, low tubercles; prominent, triangular horn near posterior corner of eyelid; venter with some faint, flat granules posteriorly; more coarse granules on posterior thighs.

COLOR. — In life (after Taylor 1922a), "Blackish brown above with two putty-colored lines on side of back; small, scattered, greenish spots on back; spots on tympanum, loreal region, and top of head putty-colored; groin yellow; sides of body slightly yellow; upper part of femur yellowish green; throat and belly whitish; femur and tibia greenish yellow below. When preserved in alcohol the greenish spots appear dark. The spots on the tympanum, below the canthus rostralis, and on the upper lip are strongly pronounced."

In preservative, the black has faded to reddish brown and the green and yellow have faded completely.

REPRODUCTION.— No information is available for this species.

COMPARISONS.— In general appearance and the digital characters, this species is in agreement with others species of the *hazelae* Group; but the unique ornamentation, a prominent fleshy flap protruding from the upper eyelid distinguishes this species from other known species. Also the head would appear to be broader relative to its length than is characteristic of other species of this group.

ECOLOGICAL NOTE.— Taylor (1920) notes that the specimen was on a leaf of a shrub growing in a small mountain stream.

RANGE.— Known only from the type locality.

Platymantis hazelae (Taylor)

Philautus hazelae Taylor, 1920:298 (Type loc.: Mt. Canlaon, Negros; holotype in CAS).
?*Cornufer rivularis* Taylor, 1922b:270 (Type loc.: Balbalan, Mountain Prov., Luzon; holotype in CAS).

Taylor (1920) described *Philautus hazelae* from Mount Canlaon, Negros Island; (1922a) *Philautus polilloensis* from Polillo Island; and (1922b) *Cornufer rivularis* from northern Luzon Island. Inger (1954) concluded that all three species were based on populations of ranids belonging in the genus *Cornufer* (= *Platymantis*). He treated *hazelae* and *polilloensis* as valid species, based on the slightly longer, more pointed snout and possibly smaller size of the latter, but placed *rivularis* in the synonymy of *hazelae*. His samples were small: 11 specimens of *hazelae* from Negros, 3 of *rivularis* from Luzon, and 6 of *polilloensis* from Polillo. The samples of *rivularis* and *polilloensis* available at this time, are still limited to the specimens used by Inger, but that for *hazelae* is now large (100+), representing several areas on Negros and Masbate Islands.

Our analysis, using several proportional characters in addition to the characters cited by Inger, supports his view of probable relationships. We also treat *polilloensis* as a distinct species and *rivularis* as a possible synonym of *hazelae*, although with reservation. We need larger samples from northern Luzon and Polillo Islands. It is doubtful that this isolated montane population (*rivularis*) in the northern mountains of Luzon is conspecific with *hazelae* in the central islands.

DESCRIPTION. — SVL 21.6–28.1 mm for 20 males and 26.2–34.8 mm for 20 females; HW 104–111% of HL and 36–43% of SVL; snout pointed, sometimes terminating in a pointed knob, most evident in ventral view; upper jaw moderately to strongly protruding; SnL 35–44% of HL and 35–43% of HW; ED 75–94% of SnL and 26–37% of HW; tympanum distinct, TD 25–42% of ED; canthus sharply rounded; lores moderately oblique, concave; vomerine teeth faint, low, in small patches or absent; fingers without or with minute basal web; first finger shorter than second, reaching beyond tubercle or midpoint between tubercle and disk of second finger when adpressed; fingers (except first) with broad, somewhat truncate disks marked by a circummarginal groove; transverse, basal groove absent; 3FD 35–45% of 3FL and 142–225% of TD; subarticular tubercles large, rounded, moderately protruding; one row of supernumerary tubercles; inner metacarpal tubercle elongate, middle one large, oval, and outer small; hind limb long; TiL 46–52% of SVL and HW 72–86% of TiL; toes webbed to middle or distal edge of tubercle on first and second toes, to distal edge of basal tubercle on third, and about midway between tubercles on fifth; disks of toes smaller than those of fingers, rounded; 3ToD 54–78% of 3FD; subarticular tubercles rounded, low; plantar area with very small, scattered tubercles; inner metatarsal tubercle elongate, outer small, round or vague; dorsum nearly smooth or with a few scattered tubercles; belly and posterior thighs covered with coarse granules; throat nearly smooth or with finer granules.

COLOR. — In preservative, dorsal background color light to dark brown or reddish brown, nearly uniform or usually with some darker spots or blotches (25 of 36 specimens in sample); upper lateral surfaces of similar color or somewhat lighter; nearly always a distinct interorbital color-break (darker posteriorly and lighter anteriorly); dorsal and upper lateral surfaces more pinkish or creamy gray (five of 36 specimens); a broad, pale dorsum with upper lateral surfaces darker (five of 36 specimens); a pale vertebral stripe (one of 36 specimens); lips usually with vague dark bars; hind limbs usually with vague, transverse, dark bars; venter with brown flecks or spots, most dense anteriorly, rarely nearly uniform grayish cream.

In life, background color of dorsum highly variable, ranging from grayish tan through pale brown and reddish brown to blackish brown, usually with darker spots and blotches but also nearly uniform, sometimes with a narrow, vertebral streak or broad band extending from the tip of the snout to the posterior end of the body; hind limbs with vague or prominent, transverse dark markings; venter creamy, usually flecked or blotched with brown.

REPRODUCTION. — Clutches of eggs of this species have been found in arboreal ferns and leaf axils of *Pandanus*. The eggs are large, unpigmented, and the observed clutch size is five to nine. Developmental mode is direct and the developmental period is 49+ days (for details see Alcala, 1962).

COMPARISONS. — See *Platymantis cornutus* for comparison with that species. *Platymantis hazelae* differs from the remaining species other than *polilloensis* in the absence of brown and yellow areolations in the groin, on the thighs, and sometimes on the lower legs and on the venter. Since the small sample available for *rivularis* does not differ significantly from *hazelae* in any of the ratios tested, we continue to treat it, as did Inger, as possibly an isolated population of *hazelae*, although with reservations.

ECOLOGICAL NOTE. — *Platymantis hazelae* occupies primarily arboreal ferns and leaf axils of *Pandanus* in the submontane and montane forests above 1000 m in the mountains of Negros Island. There are a few records from gabi (Araceae) shrubs and even rocks in streams on Mount Canlaon. Also there are a few records from dipterocarp forest between 250 and 600 m on Cuernos de Negros or adjacent mountains (Brown and Alcala, 1961). In one project at Lake Balingsasayo, 65 specimens were taken from arboreal ferns, ranging from 2.5 to 24 m above the forest floor.

RANGE. — Recorded from Negros and Masbate islands.

Platymantis polilloensis (Taylor)

Philautus polilloensis Taylor, 1922a:171 (Type loc.: near town of Polillo, Polillo Island; holotype in CAS)

DESCRIPTION. — SVL 20.2–22.1 mm for two males and 25.5 mm for one female; HW 99–105% of HL and 38–41% of SVL; snout round pointed, upper jaw strongly protruding; SnL 42–43% of HL and 40–43% of HW; ED 76–86% of SnL and 31–34% of HW; tympanum distinct, TD 19–40% of ED; canthus sharply rounded; lores moderately oblique, concave; vomerine teeth in small, low patches; fingers without distinct webs; first finger reaching just beyond tubercle of second finger; disks of fingers (except first) broadly dilated, somewhat truncate; 3FD 33–40% of 3FL and 144–200% of TD; subarticular tubercles large, round, low; one row of supernumerary tubercles; inner metacarpal tubercle oval; middle and outer indistinct; hind limb long; TiL 52–53% of SVL and HW 71–79% of TiL; toes webbed to middle of tubercle on first and second fingers, just beyond basal tubercle on third, and midway between tubercles on fifth; 3ToD 50–62% of 3FD; subarticular tubercles rounded, low; plantar surface smooth; inner metatarsal tubercle elongate; outer vague; dorsum nearly smooth; belly and posterior thighs with flat granules.

COLOR. — In preservative, dorsal background color grayish tan with darker flecks and spots (greatly faded); venter grayish cream with a few dark flecks under head and throat.

In life, "Above creamy white to yellow, slightly pigmented with minute dots of cinnamon brown; a bar of cinnamon between eyes and dim spots about the dorsal tubercles; upper eyelids dark gray to blackish; spots on outer digits of all limbs; dim bars on tibia and femur; chin and throat yellow with very sparse peppering of brown; underside of hand and belly immaculate; underside of leg and foot strongly peppered with brown" (Taylor 1922a).

REPRODUCTION. — No information is available.

COMPARISONS. — For comparison with *P. cornutus* see that species. *Platymantis polilloensis* differs from *hazelae*, as indicated by Inger, in the possibly smaller size at maturity (Table 1), the difference in means for SnL/HW (*hazelae* mean = 39.00, SD = 2.285, n = 20; *polilloensis* mean = 42.33, SD = 0.577, n = 3; t = 2.466, df = 20, p = 0.023). It differs from the remaining species of the *hazelae* Group, as did *hazelae*, in the absence of yellow and brown areolations in the groin and on the hind limbs and venter.

ECOLOGICAL NOTE. — The specimens were found under and among the leaves of low growing plants along a forest trail (Taylor, 1922a).

RANGE. — Known only from Polillo Island.

Platymantis subterrestris

Cornufer subterrestris Taylor, 1922b:275 (Type loc.: Mountain Province, Luzon Island, Philippines)

Of the five species characterized by the yellow and brown areolations in the color, *Platymantis subterrestris* was the first one described, and this on the basis of a unique specimen. Only two additional specimens are known.

DESCRIPTION. — SVL 24.1 and 25.1 mm for two males, 27.6 mm for one female (two apparently immature specimens measure 19.9 and 22.1 mm); HW 110–114% of HL and 38–42% of SVL; snout broadly rounded; SnL 38–42% of HL and 32–35% of HW; ED 73–79% of SnL and 22–24% of HW; tympanum distinct, TD 42–52% of ED; canthus rounded; lores oblique, shallowly concave; fingers without webs or basal one between second and third and third and fourth; tips of fingers dilated into moderately large, slightly rounded disks, moderately broader than subtending phalange (except for first finger); 3FD 19–31% of 3FL and 80–89% of TD; subarticular tubercles large, rounded; row of supernumerary tubercles low and barely evident; inner metatarsal tubercle large, elongate; outer vaguely evident for one specimen; hind limbs moderately long; TiL 42–47% of SVL and HW 88–91% of TiL; toes webbed at base: to proximal edge or middle of tubercle on second, third, and fifth toes; disks of toes smaller than those of fingers; 3 ToD 56–75% of 3FD; subarticular tubercles moderate, low; plantar area smooth; inner metatarsal tubercle low, elongate; outer not clearly evident in present state of preservation; dorsum without distinct tubercles but with two or three narrow ridges of varying length (unless these result from preservation); belly region with vague, flattish granules.

COLOR. — In preservative, middorsal area and head brownish with some pale blotches; upper lateral surfaces grayish tan to brownish; lower lateral surfaces, especially in groin with pale areolations (yellow in life); thighs similarly marked; venter dusky, cream, or brownish under head and throat with a few brown spots or

TABLE 1. Snout-vent length (SVL) and color pattern for the *hazelae* Group species of Philippine *Platymantis* (N = number in sample, $\bar{X}$ = mean, F = female, M = male).

	SVL of Adults			
Species	N	Range	$\bar{X}$	Yellow and Brown Areolations Present
P. cornutus				
F	0			
M	1	30		
P. hazelae				
F	20	26.2–34.8	31.2	
M	21	21.6–28.8	26.0	
P. polilloensis				
F	1	25.5		
M	2	20.2–22.1		
P. lawtoni				
F	2	39.0–39.2		X
M	1	31.5		X
P. montanus				
F	5	26.0–28.5	27.6	X
M	8	23.9–27.7	26.1	X
P. panayensis				
F	7	28.4–32.2	29.9	X
M	7	25.4–28.0	27.5	X
P. reticulatus				
F	5	28.4–30.2	29.2	X
M	7	23.3–27.7	25.0	X
P. subterrestris				
F	1	27.6		X
M	2	24.1–25.1		X

blotches on belly. In life (after Taylor, 1922b), "Above purplish without markings on head; sides dark purplish brown with large rounding spots of cream to yellow, more prominent on groin and axilla; upper parts of limbs purplish; on sides and below with large, cream-yellow, irregular spots; throat dusky; belly dusky, reticulated with cream."

REPRODUCTION. — No information is available for this species.

COMPARISONS. — Differs from the other species included in this study primarily in the smaller finger disks and resulting proportional characters, (3FD 80–89% of TD and 19–31% of 3FL). Other species have third finger disks larger than the tympanum (3FD 118–220% of TD and 3FD 29–48% of 3FL). The eye is also smaller relative to head breadth (Table 2).

ECOLOGICAL NOTE. — The type specimen was collected on a mossy stream bank along a mountain trail in the forest.

RANGE. — Recorded only from the mountains of northern Luzon.

TABLE 2. Comparison of body proportions (in %) of four species of the *hazelae* Group that exhibit the yellow and brown areolations ($\overline{X}$ = mean, N = number in sample).

Species	TiL/SVL	ED/HW	3FD/3FL	3FD/TD
P. montanus				
Range	47–53	25–31	30–40	118–200
$\overline{X}$	51	28	35	154
N	13	13	12	13
P. panayensis				
Range	50–55	30–37	32–44	127–220
$\overline{X}$	52	34	37	165
N	14	14	13	12
P. reticulatus				
Range	47–53	27–33	32–42	125–180
$\overline{X}$	50	29	38	146
N	10	11	11	11
P. subterrestris				
Range	42–47	22–24	19–31	80–89
$\overline{X}$	45	23	26	84
N	3	3	3	3

Platymantis montanus (Taylor)
Fig. 2

Cornufer montanus Taylor, 1922b:272 (Type loc.: Mount Banahao, Laguna Prov., Luzon; holotype in CAS).

Inger (1954) placed *montanus* in the synonymy of *subterrestris*, having seen only four specimens: the type of *montanus* from Mt. Banahao in southwestern Luzon and the type of *subterrestris* along with two other specimens from the mountains of northern Luzon. He based his decision on general similarities: moderate to large digital disks, size at maturity, and pale and brown areolations in the groin and on the hind limbs. The availability of 13 more specimens from Mt. Banahao and three specimens from the Zambales mountains in western Luzon, that are in agreement with the type of *montanus* clearly differentiate this species from *subterrestris*. The finger disks are larger relative to 3FL or TP, and the eye is smaller relative to the head width (Table 2). Based on these differences, we resurrect *montanus* as a valid species.

DESCRIPTION. — SVL 23.9–27.7 mm for eight males and 26.0–28.5 mm for five females (two specimens measuring 21.9 and 22.9 mm are apparently immature); HW 105–121% of HL and 38–42% of SVL; snout broadly rounded, upper jaw scarcely protruding; SnL 33–42% of HL and 31–37% of HW; ED 76–94% of SnL and 25–31% of HW; tympanum distinct, TD 31–48% of ED; canthus rounded; lores oblique, concave; vomerine teeth in very low patches or absent; fingers without webs or occasionally as minute one at base; first finger much shorter than second, reaching just beyond tubercle; 3FD 30–40% of 3FL and 118–200% of TD; subarticular tubercles large, round, only moderately protruding; one row of prominent supernumerary tubercles; inner and middle metatarsal tubercles large, low, oval; outer small, low or scarcely evident; hind limbs moderately long, TiL 47–53% of SVL (only two examples below 50%) and HW 76–84% of TiL;

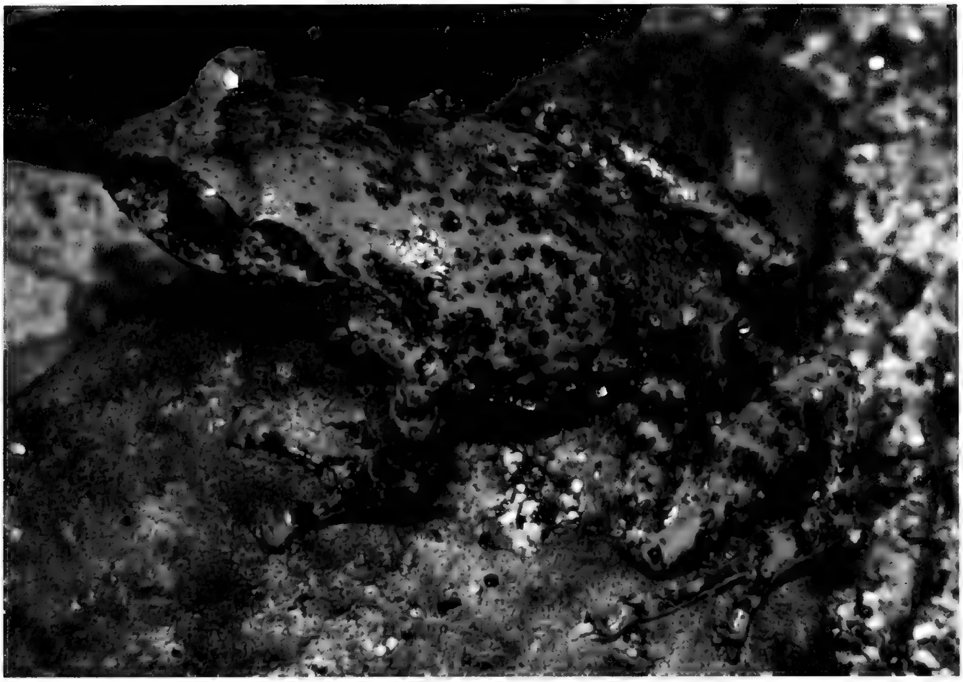

FIGURE 2. *Platymantis montanus* from Zambales Mountains, Luzon. Photo by D. Wechsler.

toes webbed: to middle of basal tubercle on inside of first and second fingers, distal edge of basal tubercle on third, and between tubercles on fifth; disks of toes smaller than those of fingers, 3ToD 42–73% of 3FD; subarticular tubercles moderately projecting; plantar surface smooth; inner metatarsal tubercle low, elongate; outer not evident; dorsum without tubercles or ridges; belly with vague, large, flat granules; smaller and more prominent granules on posterior surface of thighs.

COLOR. — In preservative, dorsal background color grayish, tannish with darker blotches; one specimen with a dark, mid-dorsal region, two with a narrow, pale, vertebral stripe; groin area with pale (yellow in life) areolations; anterior and posterior thighs usually similarly patterned; venter dusky white to creamy with brown spots and blotches, most prominent under head and throat.

In life, above gray-brown, variegated, with a broad median cream yellow stripe from tip of snout to anus; bars on legs dull cream to white; side and groin with large, bright, lemon yellow spots, separated by narrow lines of brown; belly and chin pinkish tan, mottled with brown; underside of limbs with large island like white or yellow spots; toes barred with cream; a narrow indistinct line from eye across tympanum and angle of mouth. Loreal region dark brown, mottled slightly with lighter.

REPRODUCTION. — One female had several unpigmented, nearly fully-developed eggs in each ovary.

COMPARISONS. — For comparisons with *cornutus*, *hazelae*, and *polilloensis* see those species. As noted in the introductory comments on this species, it differs from *subterrestris* primarily in its larger finger disks, as evidenced by the ratios of 3FD/3FL, 3FD/TD, and the larger eye relative to snout length or head width (Table 2). *Platymantis montanus* differs from *lawtoni* in its smaller size at maturity (Table 1).

ECOLOGICAL NOTE. — The type specimen is from a shrub on the face of a cliff at an elevation of about 1500 m on Mount Banahao (Taylor 1922b). The other specimens from Mt. Banahao are from shrubs, tree ferns, and *Pandanus*. Two of the three Zambales specimens were collected from the interior of a wet rotting log and one from beneath a rock in a dry stream bed on the forested slopes of Mount Apoy at elevations of about

1500 and 1600 m respectively. This mountain in the Zambales Range was heavily impacted by the Mount Pinatubo eruption in 1991 (Rafe Brown and Angel Alcala, pers. observ.), and, at the time of the collections (1993), the ground and much of the vegetation such as the arboreal ferns still had a covering of ashes 2–4 cm in thickness. These conditions may have been related to the unexpected microhabitat of these frogs (R. Brown et al., in press). One lizard species, *Sphenomorphus beyeri* also exhibits the same disjunct distributions (Brown, Ferner, and Sison, 1995).

RANGE. — Recorded only from Mount Banahao and Mount Apoy in southwestern Luzon.

Platymantis lawtoni Brown and Alcala

Platymantis lawtoni Brown and Alcala, 1974: 2; (Type loc.: Tablas Island, Philippines; holotype in CAS)

The following description is based on three adult specimens and five juveniles, except for proportions which are based on the adults.

DESCRIPTION. — SVL 31.2 mm for one male and 39.0–39.2 mm for two females (a female measuring 26.1 mm is immature); HW 107–116% of HL and 35–41% of SVL; snout rounded to round pointed; upper jaw usually moderately protruding; SnL 37–42% of HL and 36–39% of HW, ED 76–83% of SnL and 29–30% of HW; tympanum exposed, TD 28–38% of ED; canthus rounded; lores moderately oblique, concave; vomerine teeth in prominent, oblique patches; fingers not or only webbed at base; first finger much shorter than second; fingers (except first) with large, somewhat truncate disks; 3FD 35–45% of 3FL and 130–200% of TD; subarticular tubercles large and moderately protruding; one row of supernumerary tubercles; inner metacarpal tubercle elongate, outer rounded; hind limb long; TiL 48–55% of SVL and HW 72–86% of TiL; toes partially webbed: to midpoint or distal edge of subarticular tubercle on inside of first and second toes, to slightly beyond basal tubercle or midpoint between tubercles on third, and between tubercles on fifth; 3ToD 76–79% of 3FD; subarticular tubercles rounded, slightly protruding; plantar area smooth; inner metatarsal tubercle elongate; outer small, round; dorsal surfaces relatively smooth; belly with moderate flat granules; throat smooth.

COLOR. — In preservative, dorsum grayish tan to reddish brown with few to numerous dark brown spots and blotches or with middorsal brown band; groin area and posterior thighs with large, pale (yellowish in life) areolations; venter with dark flecks, especially on chin and throat; these flecks occasionally occur in clusters.

REPRODUCTION. — The large, unpigmented eggs (2.0 mm) are characteristic of other species of the genus and indicate a direct development mode.

COMPARISONS. — *Platymantis lawtoni* is the largest species of the *hazelae* Group with the possible exception of *P. cornutus* (Table 1). The SVL of 31.5 mm for the male and 39.0 and 39.2 mm for the two females is greater than the maximum for any of the other species.

ECOLOGICAL NOTE. — The holotype and paratype are from leaf axils of gabi (Araceae) plants at elevations 200–250 m in forest on Mount Progreso. The specimens from Sibuyan Island are from the forested slopes of Mt. Guitinsuitan.

RANGE. — Recorded from Tablas and Sibuyan islands.

Platymantis panayensis new species

This species shares with *lawtoni*, *reticulatus*, *montanus*, and *subterrestris* the pale (bright yellow in life) areolations in the groin and on the hind limbs. This feature of the color pattern is one of the characteristics that differentiates it from *hazelae*, the species that occupies the nearby island of Negros. This is the only large-disked species of either the *hazelae* or *guentheri* Groups thus far recorded from Panay Island and cannot be confused with any other species there.

Holotype.— PNM 2495, an adult female, northwest ridge approach to Mt. Madja-as (about 1410 m), Libacao, Aklan Prov., Panay Island, April 21, 1992, R. M. Brown and party.

Paratypes. — Aklan Prov., Nabas: CAS 137641–42, Mt. Madja-as: CMNH 4113–15, PNM 2314–16; Antique Prov., Culasi; Mt. Madja-as: CMNH 4116–18, 4120, PNM 2317–20.

Description of Holotype.— SVL 28.5 mm, HL 10.6 mm, HW 11.2 mm, SnL 3.8 mm, ED 2.4 mm, TD 1.15 mm, TiL 16.0 mm, 3FL 5.1 mm, 3FD 1.8 mm, 3ToD 1.2 mm. Dorsum grayish tan and dark brown, mottled pattern with the dark brown predominant; venter with prominent dark brown spots.

DIAGNOSIS. — Differs from other species of *Platymantis* in the following combination of characters: (1) bright yellow (in life) and brown areolations in the groin and on the anterior and posterior surfaces of the thighs; (2) size small, about 25–28 mm SVL for males and 28–32 mm for females; (3) HW 70–80% of TiL and TiL 50–56% of SVL; (4) ED 32–37% of HW; (5) toes with small webs: to proximal or distal edge of tubercle for first and second toes, to about distal edge of tubercle for third, and to nearly midpoint between tubercles for fifth toe.

DESCRIPTION. — SVL 25.4–28.0 mm for seven males and 28.4–32.2 mm for seven females; HW 103–111% of HL and 36–39% of SVL; snout rounded, not distinctly pointed; upper jaw slightly to moderately protruding; SnL 35–42% of HL and 32–40% of HW; eye large, ED 77–93% of SnL and 30–37% of HW; tympanum distinct, TD 23–40% of ED; canthus sharply rounded; lores moderately oblique, concave; vomerine teeth not evident except for low, oblique patches for a couple of specimens; fingers without or at most with a minute web at base; first finger much shorter than second, reaching slightly beyond tubercle to about midway between tubercle and disk of second finger; fingers, except first, with large, truncate disks; 3FD 32–44% of 3FL and 127–220% of TD; subarticular tubercles large rounded, low; inner metacarpal tubercle not clearly evident; outer usually distinct, low somewhat elongate; one row of moderately large, flatish supernumerary tubercles; hind limbs long; TiL 50–55% of SVL and HW 71–80% TiL; toes webbed: to middle or distal edge of subarticular tubercle on first finger to tubercle on inside of second, to distal edge on inside of third, short of basal tubercle on fourth, and midway between tubercles on fifth; diameter of 3ToD 50–74% of 3FD; subarticular tubercles large, rounded to slightly elongate, low; supernumerary and plantar tubercles not evident; inner metatarsal tubercle elongate; outer small and round or not evident; dorsal surfaces finely shagreened without tubercles or ridges except for small tubercle on eyelid for two specimens; belly with large, flat granules.

COLOR. — In preservative, dorsal background color grayish to grayish tan lightly to heavily mottled with reddish brown to dark brown, sometimes with a narrow or broad, pale vertebral stripe; hind limbs with vague to prominent light and dark transverse bands; pale, brown-bordered areolations in the groin and on the thighs; venter ivory cream, nearly uniform, or variably mottled with dark flecks and spots.

In life, dorsal ground color corn yellow to yellowish brown with dark brown to black spots, irregular bars, or occasionally a middorsal stripe; lateral surfaces with golden yellow or orangish yellow round spots, particularly in groin region; milky white to cream or sometimes pale blue on throat.

REPRODUCTION. — Two clutches of embryos (numbering three and six) were collected from leaf axils of a palm and a *Pandanus*, one accompanied by an adult frog. A third clutch of three embryos was found on the underside of a frond of an arboreal fern. Eggs are unpigmented and one measured 3.4 mm in diameter. The clutch from the *Pandanus* included three egg capsules containing froglets in an advanced stage of direct development. All digits on both fore and hind limbs are well-developed, and the tail ranges from nearly maximum length for one specimen to about two-thirds absorbed for another. These are nearly fully-developed (see Alcala, 1962).

ETYMOLOGY. — The name is derived from that of the island where the species occurs.

COMPARISONS. — *Platymantis panayensis* is one of five species exhibiting the pale (yellow in life), brown-bordered areolations in the groin and on the hind limbs, differing in this feature of the color pattern from *cornutus*, *hazelae*, and *polilloensis*. It also differs from *hazelae* in the longer tibia relative to SVL (*hazelae* mean = 49.579, SD = 2.341, n = 19; *panayensis* mean = 52.308, SD = 1.797, n = 13; t = 3.542, df = 30, p = 0.001).

For those species which share the color feature of brown and yellow areolations, *Platymantis panayensis* differs from *subterrestris* in the larger finger disks as evidenced in several ratios (Table 2). It differs from *lawtoni* in the smaller size at maturity and from *montanus* in the slightly larger size (Table 1), in the difference between the means for TiL/SVL (*panayensis* mean = 52.352, SD = 1.737, n = 14; *montanus* mean = 50.923, SD = 1.605, n = 13; t = 2.223, df = 25, p = 0.035), and in ED/HW (*panayensis* mean = 33.714, SD = 2.30, n = 14; *montanus* mean = 28.385, SD = 1.805, n = 13; t = 3.291, df = 13, p = 0.000).

ECOLOGICAL NOTE. — All of the specimens are from forests in mountain areas: Nabas 750 m elevation, Mt Madja-as area 1400–1450 m, and Culasi 1000–1050 m. As to microhabitat, five specimens are from leaf axils of *Pandanus*, three from arboreal ferns, one from a palm leaf, three on leaves of shrubs, and two on duff on the forest floor. While the advertisement call of the new species was not recorded, animals were observed (by RMB) calling from shrub-layer vegetation on Mt. Madja-as at 1400 m. The call is similar to the sound made by a small brass bell and is issued repetitively following rains or heavy fog coverage.

RANGE. — Known only from Aklan and Antique provinces on the western side of Panay Island.

Platymantis reticulatus new species
Fig. 3

The first examples of this species were three specimens collected by D. S. Rabor in 1961. At the time, they were identified as *Cornufer (=Platymantis) subterrestris*, based on the shared character, yellow and brown areolations on the groin and thighs and the similar size at maturity. The results of our study show that this Mt. Isarog population differs in several character states from the population in northern Luzon to which the name *subterrestris* applies.

Holotype. — CAS 197218, an adult male, Mt. Isarog (1200–1300 m), Camarines Peninsula, southeastern Luzon Island, collected Nov. 3–5, 1994, by Ely Alcala.

Paratypes. — CAS 21837; USNM 318277, 318300–06, FMNH 251633–40, from the same mountain as the holotype.

Description of Holotype. — SVL 23.5 mm; HL 8.2 mm; HW 9.2 mm; SnL 3.2 mm; ED 2.2 mm; TD 1.0 mm; TiL 12.2 mm; 3FL 4.1 mm; 3FD 1.3 mm; 3ToD 0.9 mm. Dorsal ground color is rather grayish with a dorsolateral row of blackish brown spots beginning at the posterior corner of the eye; a very narrow, pale, vertebral line, bordered by vague, irregular, slate-colored blotches and scattered dark spots. The groin, thighs and lower legs are covered with pale, brown-bordered areolations. The venter has a network pattern of brown lines.

DIAGNOSIS. — Differs from other species of *Platymantis* in the following combination of characters: (1) the usually more extensive yellow and brown areolations, extending onto the lower hind limbs as well as the groin area and thighs and the frequent reticulate pattern of brown lines on the venter; (2) SVL at maturity less than 28 mm for males and 31 mm for females; (3) the typical pattern of small, dark spots on the dorsum and usually a reticulum of brown lines on the venter; and (4) several proportional measurements that separate it from other individual species of this Group (see COMPARISONS).

DESCRIPTION. — SVL 23.3–27.7 mm for seven males and 28.4–30.2 mm for five females; HW 106–114% of HL and 37–43% of SVL; snout broadly rounded, upper jaw scarcely protruding; SnL 36–39% of HL and 32–37% of HW; ED 76–91% of SnL and 27–33% (only three of 13 examples above 29%) of HW; tympanum distinct, TD 35–52% of ED; canthus rounded; lores strongly oblique, concave; vomerine teeth rarely present or sometimes in a low patch; fingers without webs; first finger much shorter than second, reaching only slightly beyond the tubercle of the second when adpressed; 3FD 32–42% of 3FL and 125–180% of TD; subarticular tubercles large, rounded, only moderately projecting; one row of supernumerary tubercles or indistinct; inner metacarpal tubercle low, somewhat elongate; outer rarely evident; hind limbs moderately long, TiL 47–53% of SVL (rarely greater than 50%) and HW 75–86% of TiL; toes webbed: to midpoint or distal edge of tubercle on inside of first, second and third toes and midway between tubercles on fifth; disks of toes smaller than those of fingers, 3ToD 50–88% of 3FD (only two immature specimens above 70); subarticular tubercles large, round, moderately protruding; no supernumerary tubercles; inner metacarpal tubercle elongate; outer small, round, or not evident; projecting tubercle at distal end of tibia; dorsum without prominent tubercles or ridges; lateral surfaces with some tubercles; belly with large, flat granules; throat relatively smooth or with small granules.

COLOR. — In preservative, dorsum grayish tan to tan, mottled with dark (usually brown), small spots and sometimes larger blotches; groin area and usually both thighs and lower legs with pale, brown-bordered areolations; venter pale cream, with a reticulum of brown lines or scattered brown spots.

FIGURE 3. *Platymantis reticulatus* from Mt. Isorog, Luzon: a. dorsal view and b. ventral view.

In life, dorsal background color grayish to orange brown, marked with varied darker spots and blotches; a pale vertebral line, beginning on snout for some specimens; dark transverse bars on hind limbs; yellowish, brown-ringed areolations in groin, on thighs, and frequently the lower legs; venter with brown spots or reticulations.

REPRODUCTION. — Eggs of gravid females are large and unpigmented, five in one ovary of one female. Deposition sites and development remain unknown.

ETYMOLOGY. — The name refers to the netlike pattern resulting from the brown lines on the belly for some specimens and the areolations on the hind limbs.

COMPARISONS. — *Platymantis reticulatus* differs from *cornutus*, *hazelae*, and *polilloensis* in the pale, brown-bordered areolations present in the groin and on the hind limbs and the brown reticulum on the venter.

For those species that share the brown and yellow areolations, *Platymantis reticulatus* differs in their expansion on the lower legs and reticulate ventral pattern. It also differs from *subterrestris* in its larger finger disks and the resultant proportional differences (Table 2); from *lawtoni* in its smaller size at maturity (Table 1); and from *montanus* in the color pattern; and from *panayensis* in the means for ED/HW (*reticulatus* mean = 29.091, SD = 1.921, n = 11; *panayensis* mean = 33.714, SD = 2.301, n = 14; t = 6.660, df = 25, p 0.001); and TiL/SVL (*reticulatus* mean = 50.200, SD = 1.687, n = 10; *panayensis* mean = 52.352, SD = 1.737, n = 14; t = 3.035, df = 22, p = 0.006).

ECOLOGICAL NOTE. — Specimens were collected in submontane and montane forest on Mount Isarog at elevations of about 1100–1500 m. Two specimens were from birdnest ferns, three on branches and trunks of trees, and one on the forest floor.

RANGE. — Known only from Mount Isarog in southeastern Luzon Island.

DISCUSSION

The eight species included here are, with the exception of *hazelae*, poorly known. *Platymantis panayensis* is known from 17 specimens, *reticulatus* from 18, *montanus* from 15, *lawtoni* from five, *subterrestris* from three, *polilloensis* from three, and *cornutus* from one. They are, however, assumed to be a natural assemblage, with the probable exception of *Platymantis cornutus*. The remaining seven species share not only the primary digital characters that are diagnostic of the group, but also are small to moderate in size with modest sexual dimorphism (Table 1). Five of the seven share a particular color feature, variable yellow and brown-bordered areolations in the groin, on the thighs, and sometimes the lower legs. These five species differ in combinations of other character states: (1) small, but relatively consistent differences in various features of the color pattern, (2) some differences in size at maturity, (3) shape of snout, (4) size of eye, tympanum, or digital disks, (5) length of hind limbs, as measured by tibia length, (6) various proportional measurements (Table 2).

Known populations are restricted to forest habitats, primarily montane and submontane. *Platymantis hazelae*, for example, is abundant in forests above 1000 m but rare at lower elevations on Cuernos de Negros and Mt. Canlaon, both on Negros Island. Other species from several mountain areas of Luzon and the mountains in western Panay are also recorded at elevations ranging from about 900 to 1700 m. *Platymantis lawtoni* is recorded from Mt. Progreso on Tablas Island at an elevation of 200–250 m, but this mountain is only about 1000 m high. Most specimens have been found in arboreal ferns, leaf axils of *Pandanus*, or similar microhabitats, and rarely on low shrubs or the surface stratum. This Group of species is also limited to islands of the Greater Negros and Greater Luzon regions (Fig. 4). Thus far no species of this Group has been recorded from Mindoro Island, although *Platymantis lawtoni* occurs on the nearby island of Tablas.

Two different isolating mechanisms have operated in producing the differentiation evidenced by the populations. The populations on Negros, Panay, Sibuyan, and Tablas have been isolated from each other, as well as from those on Luzon, by marine barriers for varying periods of time. A land connection between Negros and Panay presumably existed as recently as 18,000–20,000 years BP during the lowered sea level of that period; but possible land connections involving Luzon and/or Sibuyan and Tablas would have necessitated even lower sea levels. Such conditions may have occurred at times earlier, mid-Pleistocene about 100,000 to 500,000 years BP (Morley and Flenley, 1987). The isolating

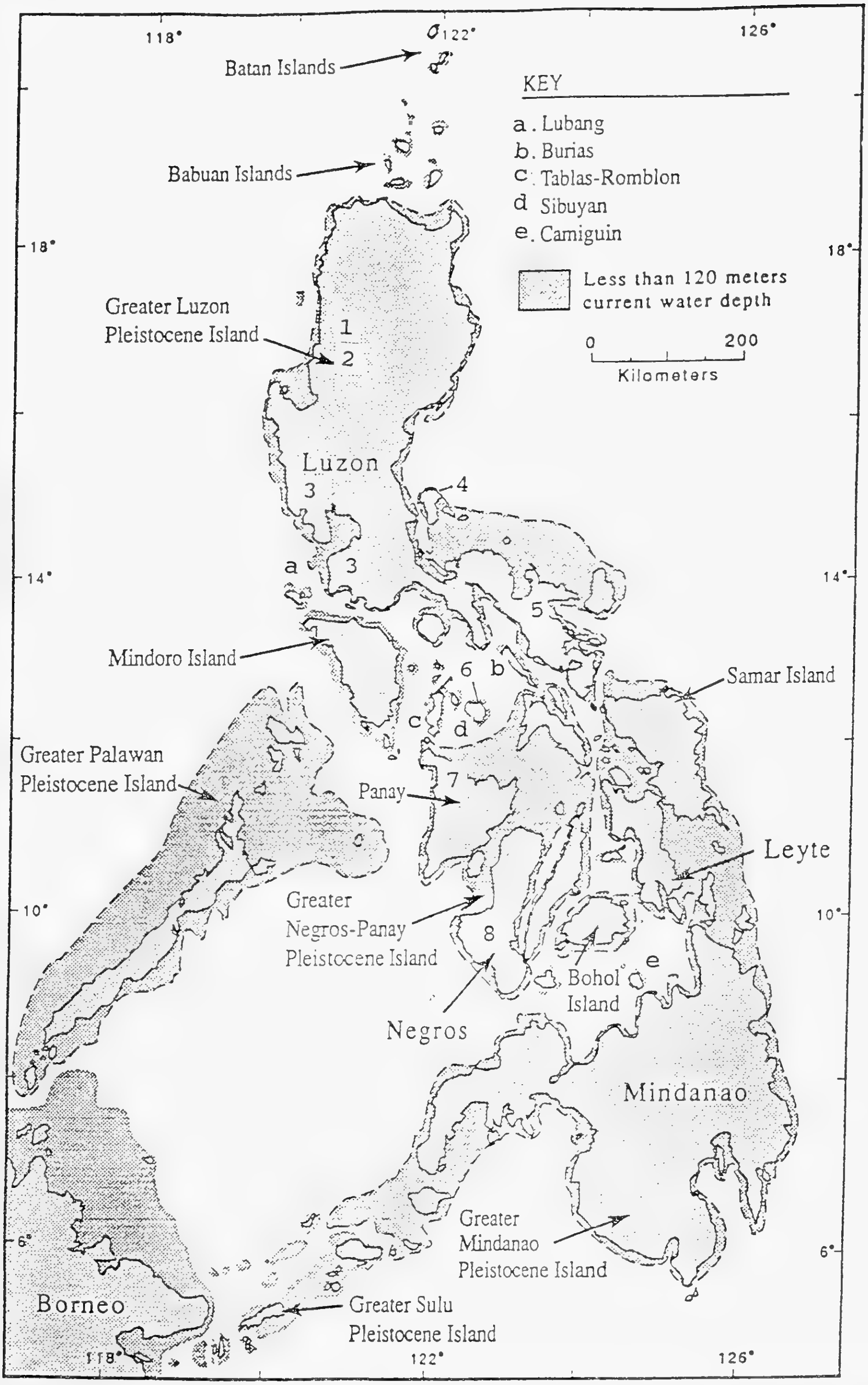

FIGURE 4. Distribution of *hazelae* Group species in central and northern Philippine Islands: (1) *Platymantis subterrestris*, (2) *Platymantis cornutus*, (3) *Platymantis montanus*, (4) *Platymantis polilloensis*, (5) *Platymantis reticulatus*, (6) *Platymantis lawtoni*, (7) *Platymantis panayensis*, (8) *Platymantis hazelae*.

mechanism operating for the Luzon populations is the montane habitat preference of the frogs on isolated mountain or volcanoes (Mount Isarog). These are separated by lowland forest or manmade habitats.

These montane, tropical forest refugia were maintained throughout the alternating sea-level fluctuations, since there is no evidence of dramatic changes in local climates such as occurred in temperate mountains. It is estimated that sea and lowland surface temperatures in such tropical areas as Sunda, New Guinea, and the Philippine Islands were no more than two to three degrees centigrade below its present level (Walker, 1981). Tropical forests were narrower in terms of its north-south limits, and the width of the lowland, submontane, and montane zones on the mountains was reduced in breadth (Whitmore, 1981). It is also assumed that rainfall was reduced in some areas.

Similar patterns of montane endemism are known not only for amphibians but also reptiles, mammals, and even birds on other large islands in the Philippines, Borneo, New Guinea, Solomon Islands, and Fiji. For some examples see Brown (1991, 1995), Brown and Gibbons (1986), Diamond (1985), Inger and Stuebing (1992), Leviton and Brown (1959), Heaney and Rickart (1990), Rickart, Heaney, and Utzurrum (1991).

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APPENDIX A
Specimens Examined

For brevity, only general locality, island names, and museum numbers are provided. Precise locality and other data are available from museum catalogs.

Platymantis cornutus. — Luzon I., Mountain Province: CAS 61476 (holotype).

Platymantis hazelae. — Negros I., Mt. Canlaon area: CAS-SU 16615–28, 23458–63, 2346, 23470, 23526, 23538-59, 23560–627, 63712–17, 23723–31, 23736–37, 23741–79, CAS 139264–73, 185870–76; southern Negros I.: CAS-SU 16615–28, 18157, 18436–38, 18440–43, 18446–48, 18488–92, 18494–95, 13619–24, 18528, 18717–26, 19010, 19442, 19461, 19497, 19499, 19838–40, CAS 89806–07, 128916–18, 128920, 133912–14, 133946–54, 134231–34, 137429–495, 138197–98, 139262–63, 145225–43, 145893–94, 147292–94, 185445–49, 185827, 185844–69, 185870–76, 185939–48; Luzon I.: CAS 61477 (holotype of *Cornufer rivularis*), CAS 61478 and MCZ 14386 (paratypes of *C. rivularis*).

Platymantis polilloensis. — Polillo I.: CAS 62250 (holotype), CAS 62251-52 and MCZ 14469-72 (paratypes).

Platymantis lawtoni. — Tablas I.: CAS 135732 (holotype), CAS 135733 (paratype); Sibuyan I.: FMNH 236092, 236096, 236142, 236146, 249701.

Platymantis montanus. — Luzon I., Mt. Banahao: CAS 61179 (holotype), CAS 200998–201002, 201204, 201213–14, 201222–29, 201504–35, 202529, 202536–37, 202542–43, 202545; Zambales Prov.: CMNH 4112, PNM 2314-15.

Platymantis panayensis. — See holotype and paratypes for this species.

Platymantis reticulatus. — See holotype and paratypes for this species.

Platymantis subterrestris. — Luzon I., Mountain Prov.: CAS 61518 (holotype); MCZ 14387–88, FMNH 172392, 173165.

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A NEW GENUS AND SPECIES OF NEPHTHEID SOFT CORAL (OCTOCORALLIA: ALCYONACEA) FROM THE WESTERN PACIFIC OCEAN, AND A DISCUSSION OF CONVERGENCE WITH SEVERAL DEEP-SEA BENTHIC ORGANISMS

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A remarkable new genus and species of soft coral, recently discovered by SCUBA, is described from Okinawa. The new taxon is assignable to the family Nephtheidae on the basis of having a distinct stalk, multiply-branched polyparium, monomorphic polyps without calyces, and densely-spiculated stalk, and it shows some resemblances to species of two nephtheid genera—*Umbellulifera* and *Coronephthya*. It differs from all previously described nephtheid taxa by the presence of a very slender and elongate stalk together with a relatively small and sparsely branched divaricate polyparium in which the primary branches share a common point of origin, relatively few polyps sparsely distributed and not grouped into catkins, and the dense occurrence of only spindles and needles in the stalk. The unusual growth form appears to show convergence with deep-sea pennatulacean octocorals of the genus *Umbellula*, as well as species of the bryozoan genus *Kinetoskias* and the crinoid genus *Bathycrinus*.

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Several specimens of a newly discovered soft coral, representing a new genus and species, have recently been collected by biologist Robert Bolland at approximately 60 meters in depth off Okinawa, Ryukyu Islands, Japan. The new taxon exhibits a convergence in general growth form to species of the pennatulacean genus *Umbellula* (Cuvier, 1798), the bryozoan genus *Kinetoskias* Danielssen, 1868, and the crinoid genus *Bathycrinus* Thomson, 1872. The new soft coral is here allocated to the family Nephtheidae and shows some similarities to the nephtheid genera *Umbellulifera* Thomson and Dean, 1936, and *Coronephthya* Utinomi, 1966.

Imahara (1991) reported on the Octocorallia of the Ryukyu Islands, which included 47 species.

SYSTEMATIC ACCOUNT

Family **Nephtheidae** Gray, 1862

Mostly bushy or arborescent soft corals, upright, with a distinct stalk. Polyparium usually multiply-branched. Polyps monomorphic, well spaced or more often arranged in clusters or catkins, along the surface of branches and/or at the tips of ultimate branches. Sclerites are often densely distributed, mainly spindles, clubs, and radiates. A family of approximately eighteen genera of worldwide distribution; currently in need of revision.

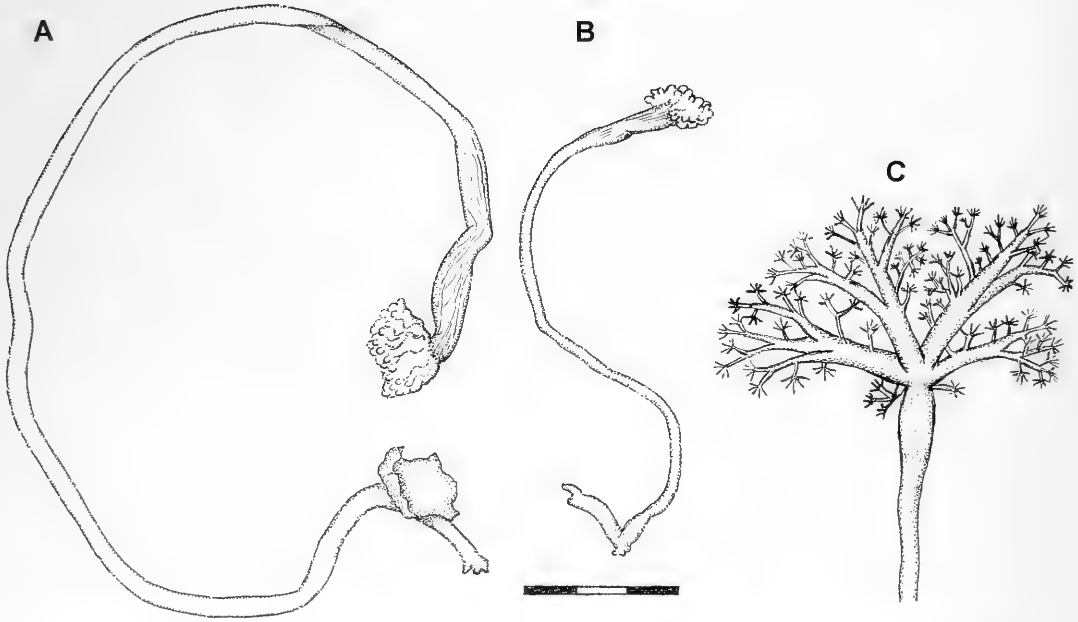

FIGURE 1. *Pacifiphyton bollandi* gen. and sp. nov. A. Holotype. B. Paratype (*CASIZ* #106206). C. Branching pattern of a fully extended polyparium from specimen photographed at 54.8 m depth by R. F. Bolland. Scale bar for A, B, and C = 30 mm.

Genus **Pacifiphyton** gen. nov.

DIAGNOSIS. — Soft corals with divaricate polyparium arising from elongated stalk. Several primary branches arise from a common point of origin, each with only few secondary and tertiary branches. Polyps monomorphic, sparsely distributed on branches of polyparium, without calyces, but with weak and variable armature of sclerites, sometimes approaching weakly constructed crown and points. Stalk densely spiculated with more or less longitudinally disposed spindles. Sclerites of stalk, polyparium, and polyp walls are spindles with highly variable tuberculation.

TYPE SPECIES. — *Pacifiphtyon bollandi* sp. nov.

ETYMOLOGY. — The new generic name is derived from 'Pacific' (Pacific Ocean) and the Greek 'phyton' (a creature, either plant or animal).

Pacifiphyton bollandi sp. nov.
Figs. 1–10

Nephtheid sp. (Slender-Stalked Soft Coral): Gosliner, Behrens, and Williams, 1996:44, pl. 113.

HOLOTYPE. — *CASIZ #106205*; RFB #3357-B; one whole specimen; collected by Robert Bolland; 12 February 1995; Seragaki, Okinawa, Japan; 68.6 m in depth.

PARATYPES. — *CASIZ #106206*; one whole specimen; same data as holotype. *CASIZ #106207*; four specimens in several pieces, attached to coral rubble; same data as holotype.

OTHER MATERIAL EXAMINED. — *CASIZ #106208*; RFB #3406-D; two specimens in three pieces; collected by Robert Bolland; 6 May 1995; Seragaki, Okinawa, Japan; 62.5 m in depth. *CASIZ #106209*; RFB #3426-H; three specimens in four pieces, attached to coral rubble; collected by Robert Bolland; 28 May 1995; Seragaki, Okinawa, Japan; 62.5 m in depth. *CASIZ #102890*; RFB #3331-A; one partial specimen; collected by Robert Bolland; 10 December 1994; Seragaki, Okinawa, Japan; 57.9 m in depth. *CASIZ #102891*; RFB #3330-B; two specimens in three pieces; collected by Robert Bolland; 9 December 1994; Seragaki, Okinawa, Japan; 57.9 m in depth. *CASIZ #102892*; RFB #3332; one whole specimen attached to coral rubble; collected by Robert Bolland; 11 December 1994; Seragaki, Okinawa, Japan; 62.5 m in depth. *CASIZ #102893*; RFB #3336; two whole specimens attached to coral rubble; collected by Robert Bolland; 18 December 1994; Seragaki, Okinawa, Japan; 57.9 m in depth. *CASIZ #102894*; RFB

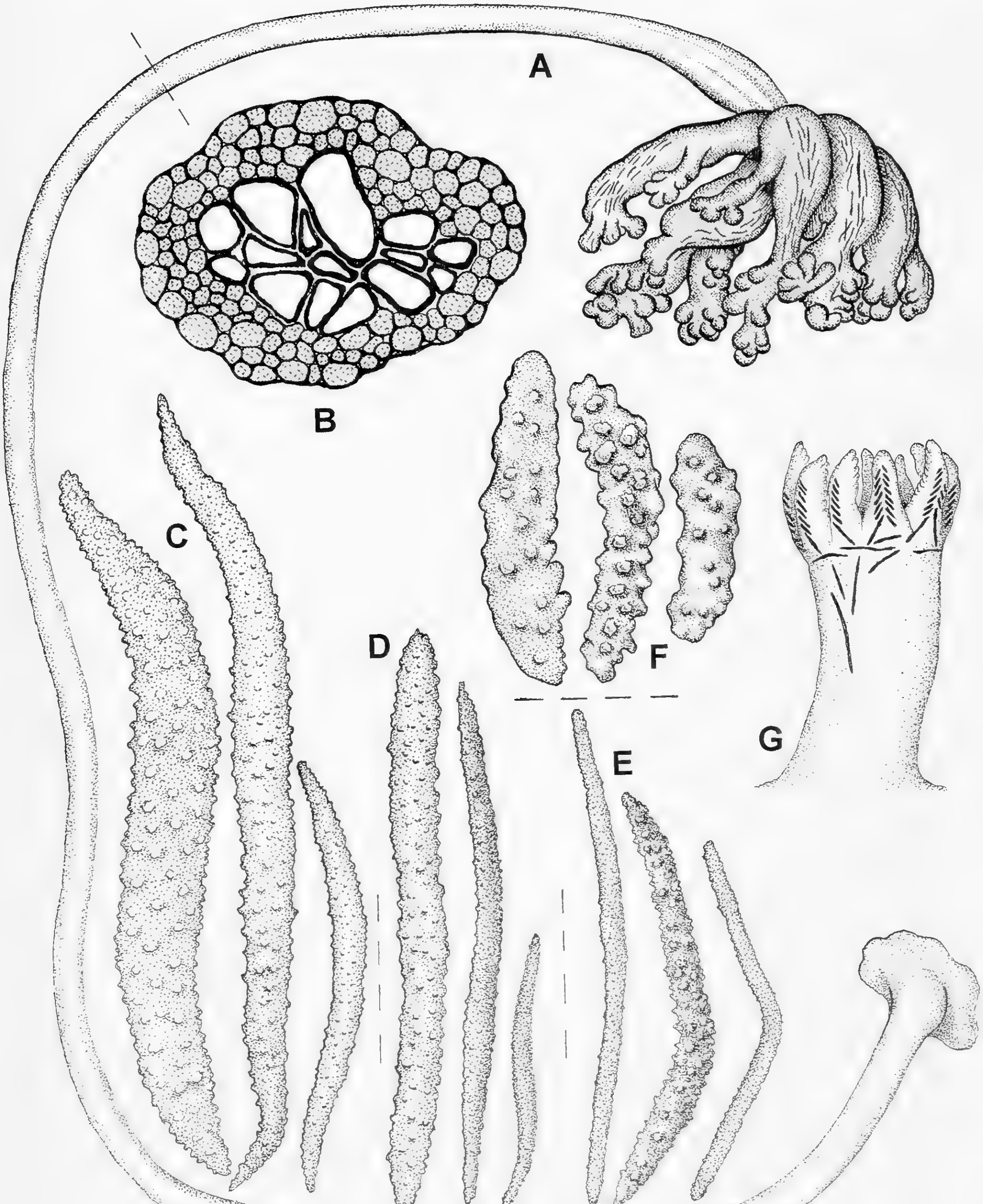

FIGURE 2. *Pacifiphyton bollandi* gen. and sp. nov. General morphology of preserved specimen *CASIZ #102894*. A. Entire specimen; total length = 305 mm. B. Transverse section at level of dashed line in A, showing central canals surrounded by densely-set sclerites; diameter of section = 3 mm. C. Sclerites from the stalk; left, 2.2 mm, center 1.65 mm, right 0.9 mm. D. Sclerites from the branches of the polyparium; left 3.5 mm, center 2.5 mm, right 1.3 mm. E. Sclerites of the polyp body wall; left 1.01 mm, center 0.57 mm, right 0.50 mm. F. Tentacle sclerites; left 0.18 mm, center 0.16 mm, right 0.11 mm. G. A single polyp, 3.2 mm in height, showing arrangement of polyp sclerites.

#3326, one specimen in two pieces; collected by Robert Bolland, 29 November 1994; Seragaki, Okinawa, Japan; 59.4 m in depth. *CASIZ #102895*; RFB #3326, two specimens in five pieces; collected by Robert Bolland; 27 November 1994; Seragaki, Okinawa, Japan; 59.4 m in depth.

In addition, twenty-nine color transparencies taken by Dr. Bolland of living specimens are cataloged in the CASIZG photo collection. Of these, ten are in situ photographs.

DIAGNOSIS. — Stalk slender and elongated. Polyparium divaricate with several primary branches emanating from a common point of origin, which is represented by the distal terminus of the stalk. Secondary and tertiary branching sparse. Polyp calyces absent. Polyps sparsely distributed on branches of polyparium, not forming catkins. Individual polyps with weakly developed armature, sometimes approaching crown and points; supporting bundles absent. Sclerites of tentacles rod-like, arranged *en chevron* along longitudinal axis of each tentacle. Branches of polyparium with or without needle-like spindles. Stalk densely spiculated with more or less longitudinally disposed needles in the swollen distal portion, and randomly disposed robust spindles in the rest of the stalk. Sclerites are tuberculate spindles throughout, some of which are needle-like.

DESCRIPTION OF THE HOLOTYPE (Figs. 1A, 4E, 6, 9).—*Stalk:* The stalk of the holotype is 306 mm in length. The spreading holdfast is ovoid in shape, 15 mm at its widest and 22 mm at its longest. The stalk varies in width from 3–4 mm (throughout most of its length) to 6–8 mm in the swollen portion just below the polyparium (Fig. 1A). The swollen portion is approximately 35 mm in length. In preservation, the entire stalk is relatively stiff and brittle.

Polyparium: The contracted polyparium is 15 mm in length by 20 mm in width, and consists of a divaricately branched arrangement at the distal end of the long, narrow stalk. The polyparium is comprised of five main branches radiating outward from the center. The main branches ramify distally to form two or three secondary branches.

Polyps: The polyps are contractile but not retractile. Calyces are absent. The polyps do not form distinct groups, clusters or catkins, but are sparsely and individually disposed on the branches. Polyps are more densely distributed in the distal portions of the polyparium and are absent from the proximal portions.

Sclerites: The sclerites from the proximal and middle portions of the stalk are predominantly robust spindles, mostly 1–2 mm in length and up to 0.3 mm in width (Fig. 6A–K), which are for the most part not disposed parallel to the axis of the stalk but are rather arranged at all angles. In contrast to this, the sclerites from the swollen distal-most region of the stalk are elongate needles, mostly 2–3.5 mm in length by 0.1 mm in width (Fig. 6L). These are arranged parallel to the axis of the stalk. Many of these needles are very narrow and sinuous with gradually tapering ends.

Sclerites of the branches of the polyparium in the holotype are apparently absent altogether.

The sclerites of the polyps are of two kinds: needles and spindles of the body wall, and rods of the tentacles. Sclerites that are mostly needle-like spindles form a relatively weak crown and points in a majority of the polyps. In addition, one or more needle-like spindles may be longitudinally disposed on the polyp wall (Fig. 4E).

The outer surface of the tentacles is densely spiculated. The sclerites are arranged *en chevron* along most of the length of the tentacles. These sclerites are relatively robust rods with somewhat coarse tuberculation (Fig. 9A–H). They vary in length from 0.05 to 0.18 mm.

Color: The preserved holotype is cream to light tan in color, while the contracted polyps are white due to the white sclerites of the tentacles.

PHENOTYPIC VARIABILITY. — The twenty wet-preserved specimens examined range in

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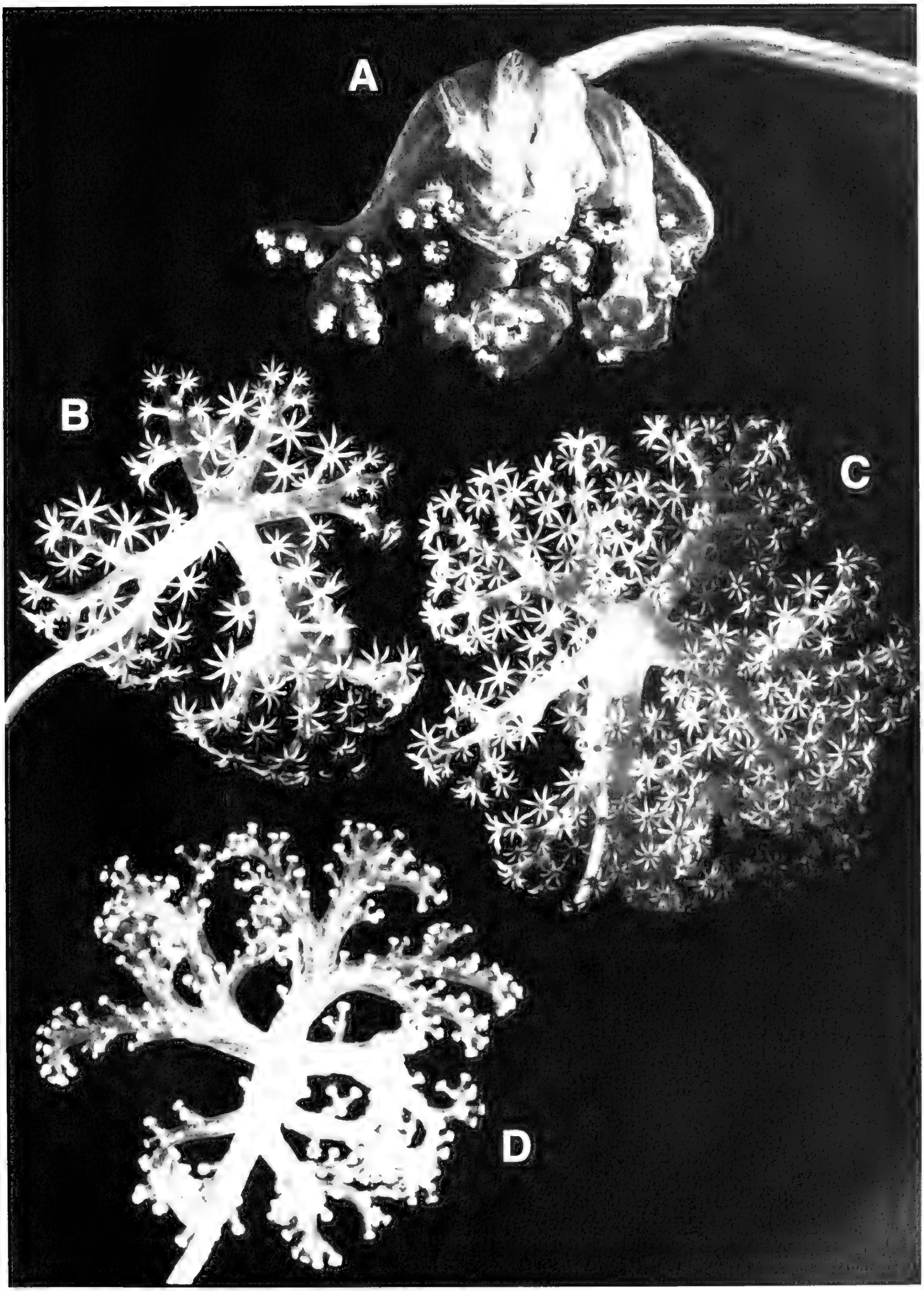
FIGURE 3. *Pacifiphyton bollandi* gen. and sp. nov. Photographs of living specimens by R. F. Bolland. A. Contracted polyparium of *CASIZ #102895*, photograph taken in aquarium; maximum dimension of polyparium shown is 44 mm. B. Photograph of a specimen with expanded polyparium and polyps taken in situ at 59 m in depth. C. Expanded polyps and polyparium of another specimen photographed in situ at 59 m in depth. D. Polyparium of a specimen with contracted polyps photographed in aquarium; maximum diameter of polyparium = 66 mm.


A
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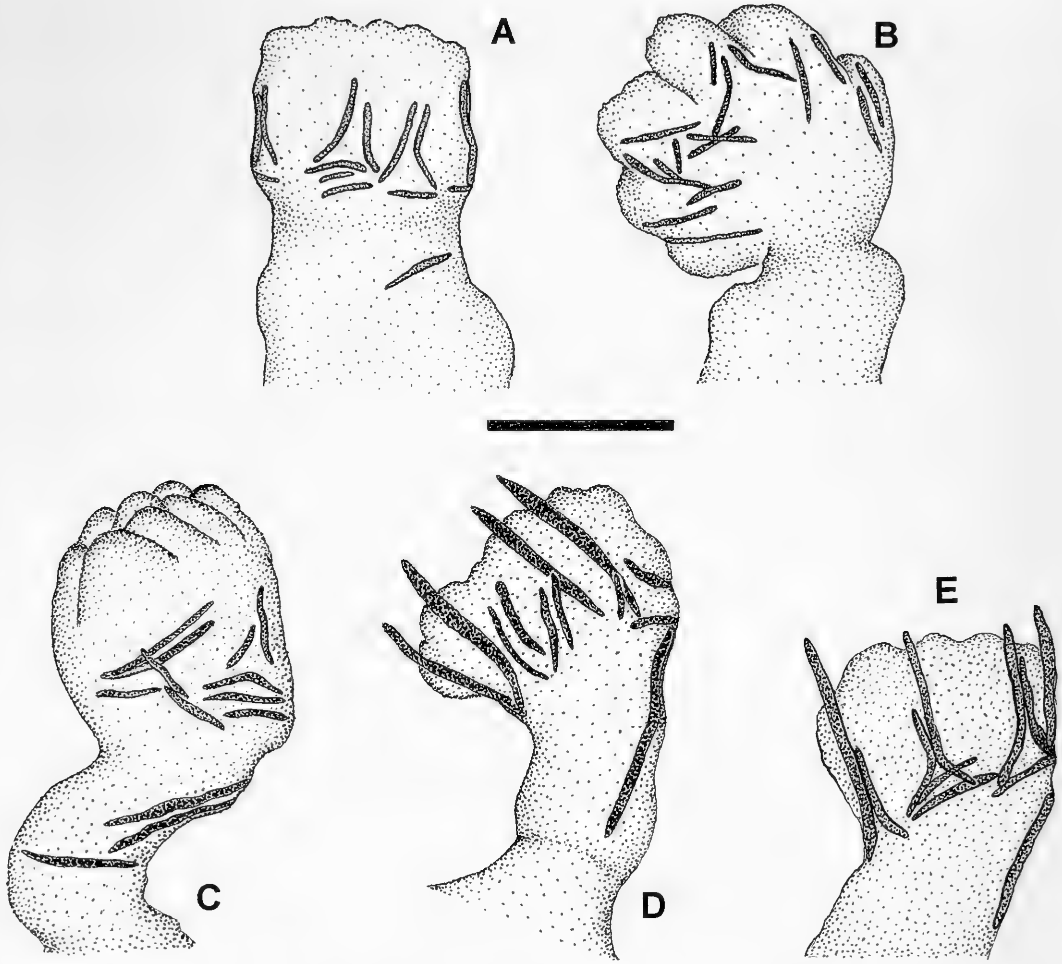

FIGURE 4. *Pacifiphyton bollandi* gen. and sp. nov. Variation in polyp armature. A. Polyp with weak crown and points arrangement. B. Polyp with scattered arrangement of sclerites at the bases of the tentacles. C. Polyp with sparse more-or-less transverse arrangement of sclerites in the polyp wall. D. Polyp with elongated needles protruding from the apex. E. Polyp from the holotype with weak crown and points. Scale bar = 1 mm.

length from 65–321 mm. The holotype is 321 mm long (Fig. 1A), and paratype (*CASIZ #106206*) 142 mm long (Fig. 1B). In both the holotype and this paratype, as well as in some of the other specimens, the holdfasts are attached to hard coral rubble.

The interior of the stalk consists of seven to fifteen large, hollow canals surrounded by an outer region of densely-set sclerites (Fig. 2B). This spiculiferous outer portion varies in thickness and in the number of layers of sclerites, depending on the portion of the stalk from which transverse sections are made. Sclerites are for the most part absent from the canal walls of the interior of the stalk, or if present, they are only very sparsely distributed.

The distal-most portion of the stalk is relatively swollen compared to the rest of the stalk (Figs. 1C, 2A, 5). The surface of this inflated portion is relatively densely-set with longitudinally disposed sclerites, which are spindles, mostly needle-like, varying from 1.5 to 4.0 mm in length (Fig. 5B, 6L). The surface of the rest of the stalk is also densely-set with spindles, but these are usually more robust than those of the distal inflated portion of the stalk, and vary in

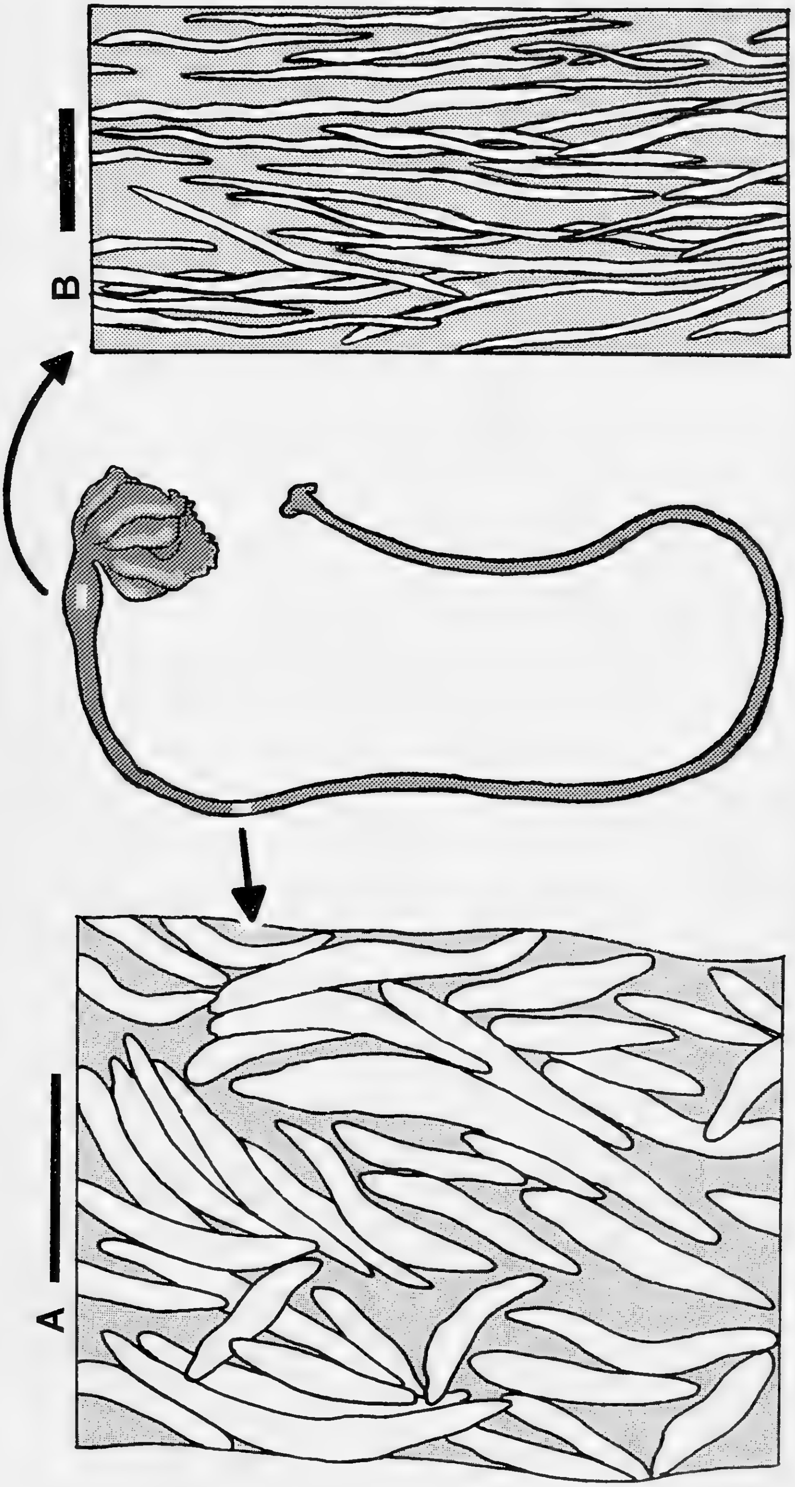

FIGURE 5. *Pacifiphyton bollandi* gen. and sp. nov. Arrangement of sclerites in the surface of the stalk from a 300 mm long specimen. A. Middle of stalk. B. Distal swollen portion of stalk. Scale bars = 1 mm.

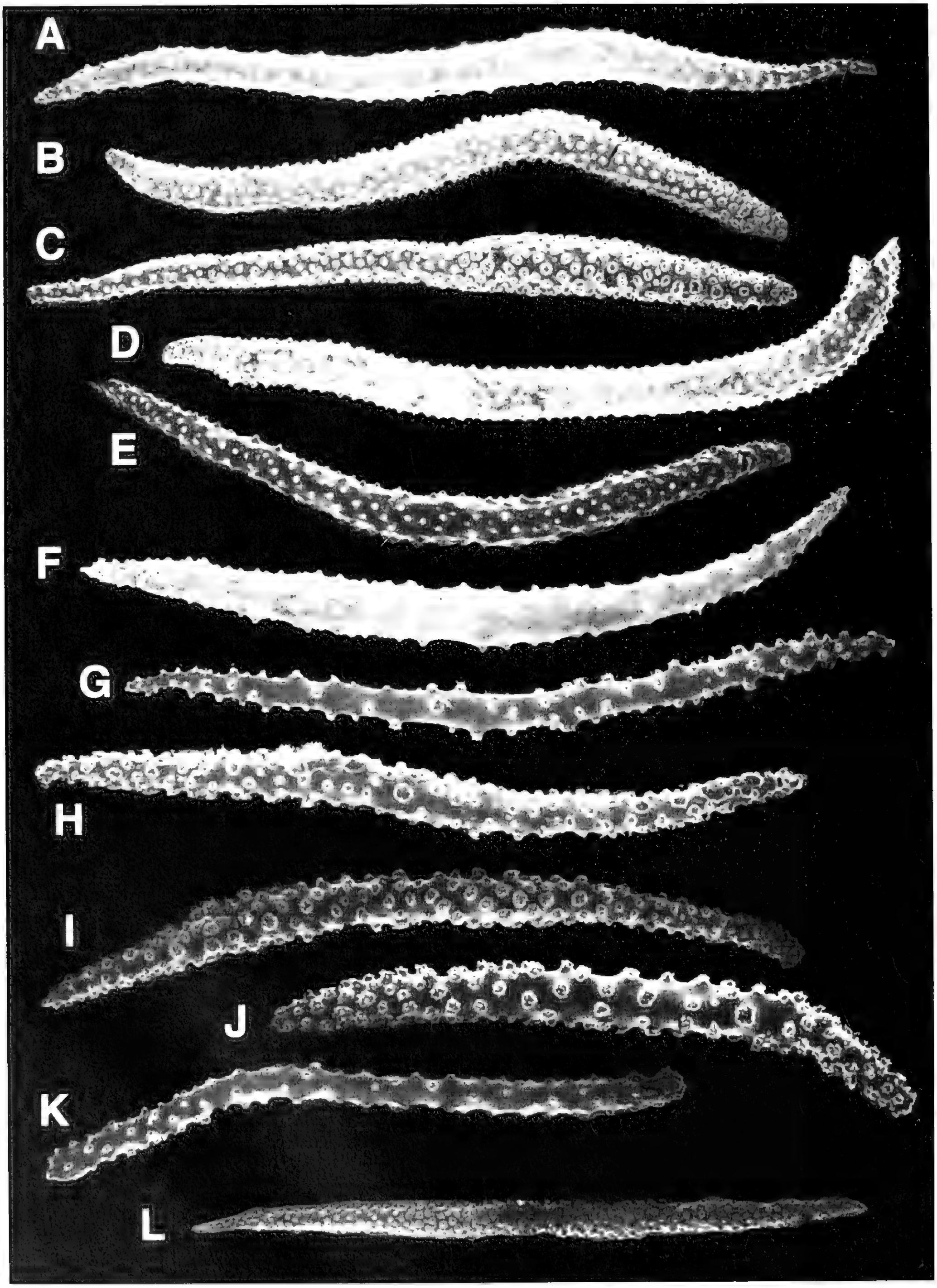

FIGURE 6. *Pacifiphyton bollandi* gen. and sp. nov. Scanning electron micrographs of stalk sclerites from the holotype. A. 1.8 mm. B. 2.1 mm. C. 2.3 mm. D. 2.3 mm. E. 1.5 mm. F. 1.0 mm. G. 0.8 mm. H. 0.9 mm. I. 1.6 mm. J. 0.6 mm. K. 0.6 mm. L. 2.6 mm.

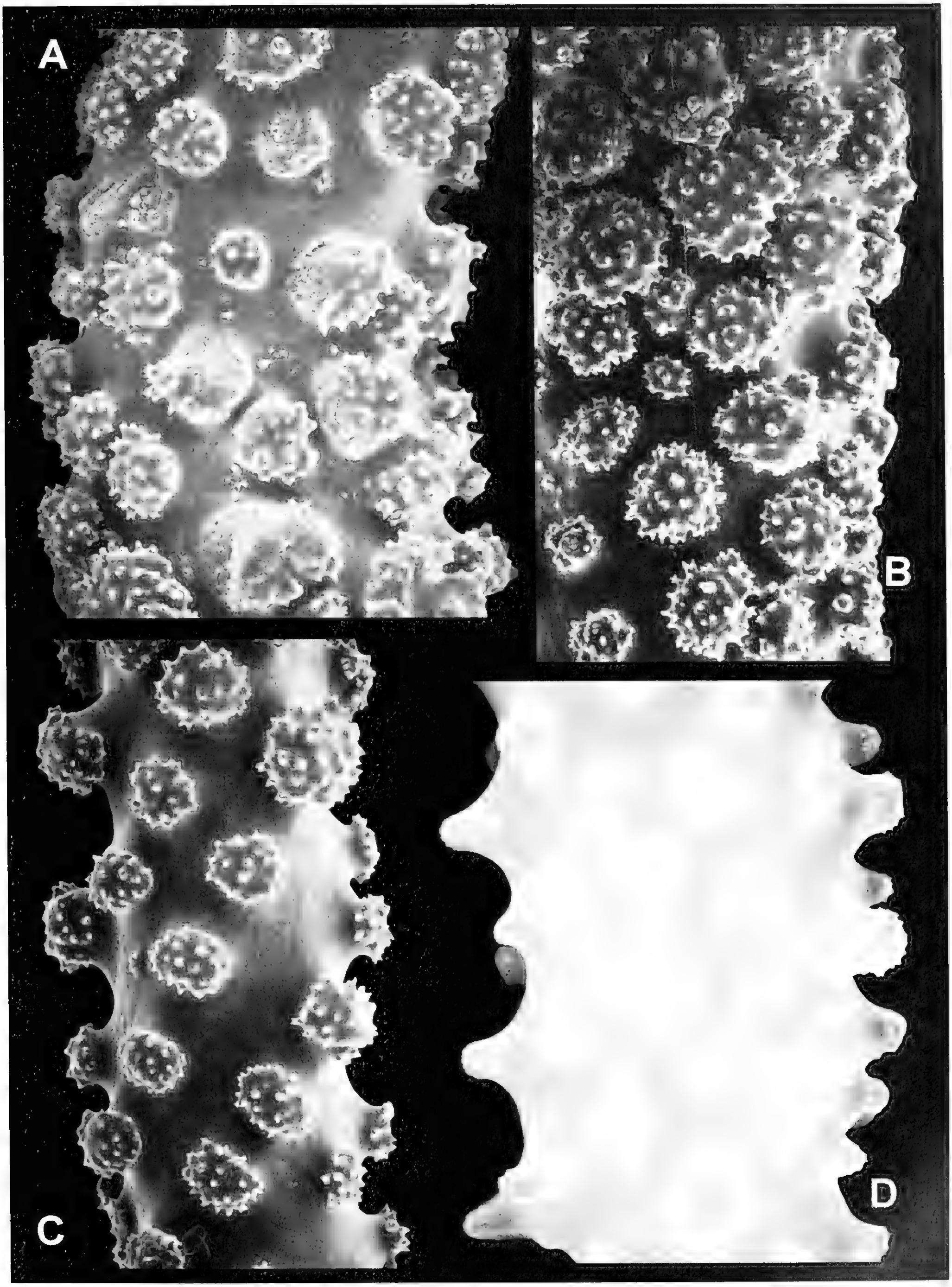

FIGURE 7. ***Pacifiphyton bollandi*** gen. and sp. nov. Scanning electron micrographs showing details of stalk sclerites. A. Length of portion shown = 0.19 mm. B. Length of portion shown = 0.21 mm. C. Length of portion shown = 0.26 mm. D. Length of portion shown = 0.24 mm.

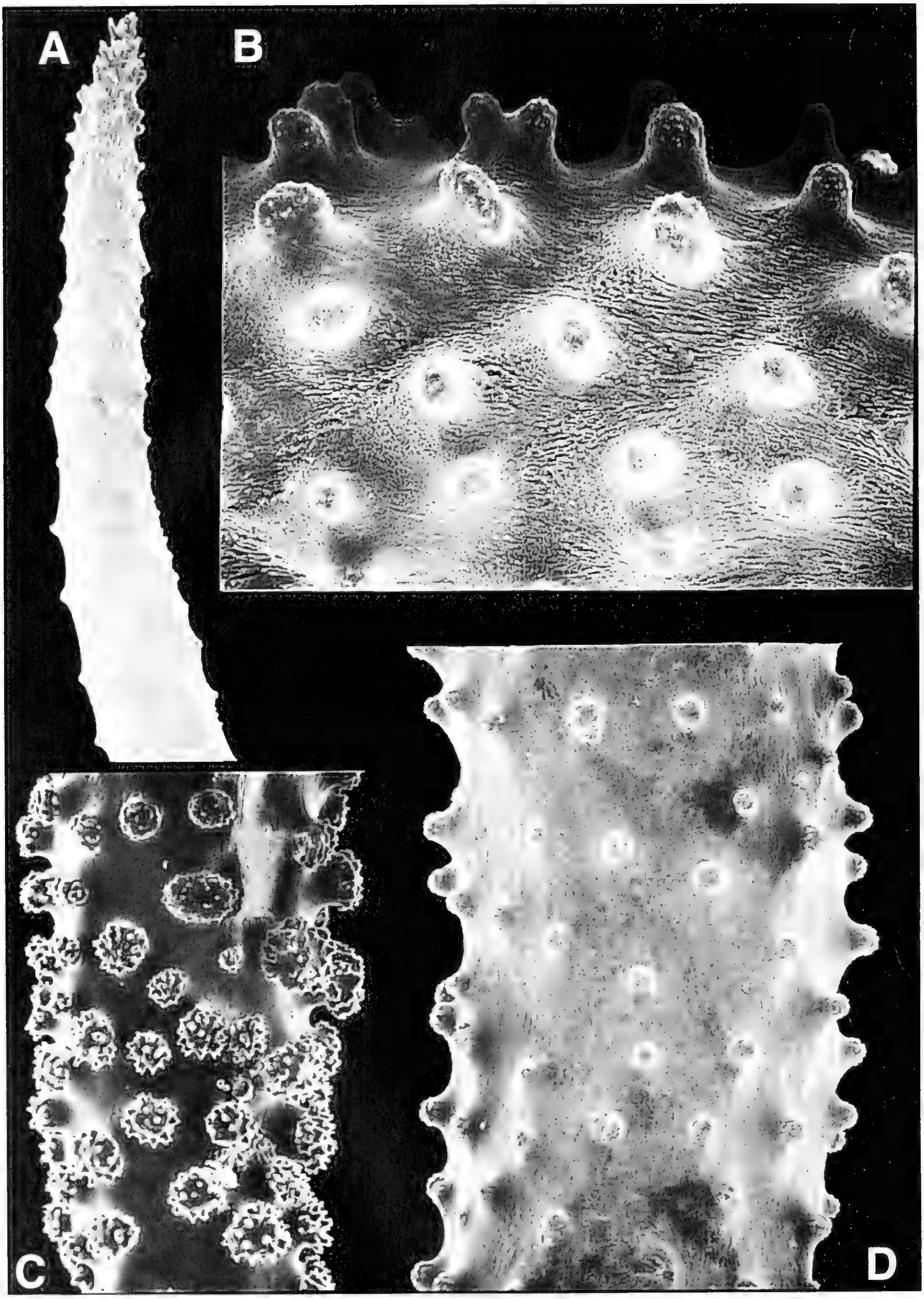

FIGURE 8. *Pacifiphyton bollandi* gen. and sp. nov. Scanning electron micrographs showing tubercle variation of stalk sclerites. A. Length of portion shown = 0.38 mm. B. Length of portion shown = 0.21 mm. C. Length of portion shown = 0.26 mm. D. Length of portion shown = 0.24 mm.

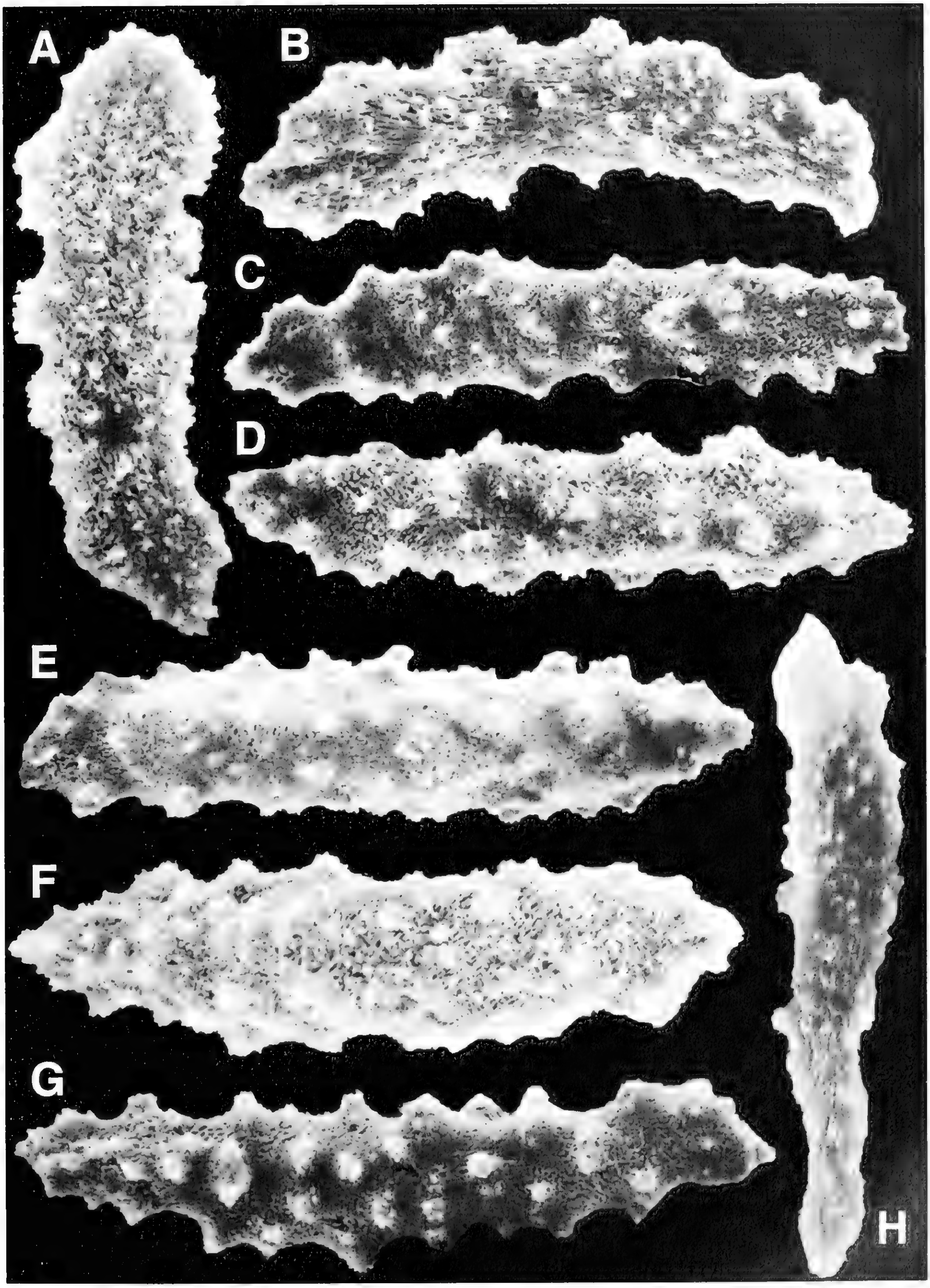

FIGURE 9. *Pacifiphyton bollandi* gen. and sp. nov. Scanning electron micrographs of tentacle sclerites from the holotype. A. 0.063 mm. B. 0.064 mm. C. 0.105 mm. D. 0.104 mm. E. 0.161 mm. F. 0.112 mm. G. 0.116 mm. H. 0.051 mm.

length from 0.6 to 2.5 mm in length (Fig. 6A–K). Many of these spindles are arranged more or less longitudinally, but many are disposed obliquely to the longitudinal axis of the stalk, at various angles. Some of these sclerites appear to be clumped together (Fig. 5A).

The tubercles of the stalk sclerites show considerable variability regarding degree of ornamentation. These may vary from simple, relatively smooth protuberances to coarsely spiny spheroid structures (Figs. 7, 8).

The polyparium may have four or five main branches emanating from the center, which represents the point of insertion of the naked stalk. The distal half of each main branch further ramifies into two to four secondary branches (Figs. 1C, 3B–D). Two or three polyps may arise from the short tertiary branches (Figs. 1C, 3D). Polyps are sparsely distributed and arise singly along the secondary and tertiary branches. Some polyps may be scattered upon the main branches as well. The tertiary branches do not form conspicuous catkins, as the polyps are nowhere distinctly clustered or grouped together. A single main branch together with its associated secondary and tertiary branches may contain 9 to approximately 90 polyps (Fig. 1C, 3).

Spiculation of the divaricate polyparium is highly variable. The polyparium, excluding the polyps, may be totally devoid of sclerites (as in the holotype), or the main branches and secondary branches may be sparsely to relatively densely spiculated with needle-like spindles. These sclerites are mostly long, narrow and sinuous and range in length from approximately 1.0 to at least 3.5 mm. They resemble sclerites from the swollen distal-most portion of the stalk that immediately subtends the polyparium. In life, most of these sclerites are aligned more-or-less parallel to the longitudinal axes of the branches, but in preserved and contracted material, they seem to be scattered about near the surface of the branches with no particular orientation or alignment (Figs. 2A, D; 3A).

The arrangement of sclerites in the polyps varies considerably, including the degree of development of the crown and points (Figs. 2G, 4A–E).

In life, the stalk is tan, light rose, or flesh colored, while the branches of the polyparium vary from colorless to light orange or yellow, sometimes with a bright green or yellow-green iridescence. The polyp walls are colorless, while the pharynxes and mesenterial filaments are apricot orange and the tentacles are white (due to the presence of densely-set sclerites) (Gosliner, Behrens, and Williams, 1996:44, pl. 113). Specimens preserved in ethanol are uniformly cream colored.

ETYMOLOGY. — This species is named for its discoverer, Dr. Robert Bolland, University of Maryland biologist.

DISTRIBUTION. — The new taxon is at present known only from the type locality—Seragaki, Okinawa, Ryukyu Islands, Japan, western Pacific; 58–69 m in depth.

DISCUSSION

COMPARISON WITH OTHER TAXA.— *Pacifiphyton bollandi* gen. and sp. nov. exhibits superficial resemblances to two nephtheid genera: *Umbellulifera* Thomson and Dean, 1936 and *Coronephthya* Utinomi, 1966. The three taxa all have congested polyparies atop elongate stalks. However, the new taxon is easily distinguished from species of these genera.

Both *Pacifiphyton* and *Umbellulifera* have long narrow stalks terminated with a branched polyparium. However, in *Umbellulifera*, the stalk contains many small six-radiate capstans, mostly less than 0.2 mm in length, and the polyps are numerous and densely distributed on a copiously branched umbellate polyparium. In addition, the armature of the polyps include a weak to well-developed supporting bundle and eight well-developed points of chevroned sclerites, but no transverse collaret or crown formation is present. In contrast, *Pacifiphyton* contains only robust spindles or elongate needles in the stalk, 0.6–4.0 mm in length, and the polyps are relatively sparsely distributed on the sparsely branched divaricate polyparium. The points of the polyps are often only weakly developed (if at all) and some polyps have crowns or transverse collarets below the points as well.

Both *Pacifiphyton bollandi* and *Coronephthya macrospiculata* (Thomson and MacKinnon, 1910) have similar sclerites of mostly robust spindles in both the polyparium and the stalk. However, in *Coronephthya*, the polyparium is unbranched, as the large polyps emanate directly from the conical distal tip of the stalk. In addition, each polyp is subtended by a conspicuous sup-

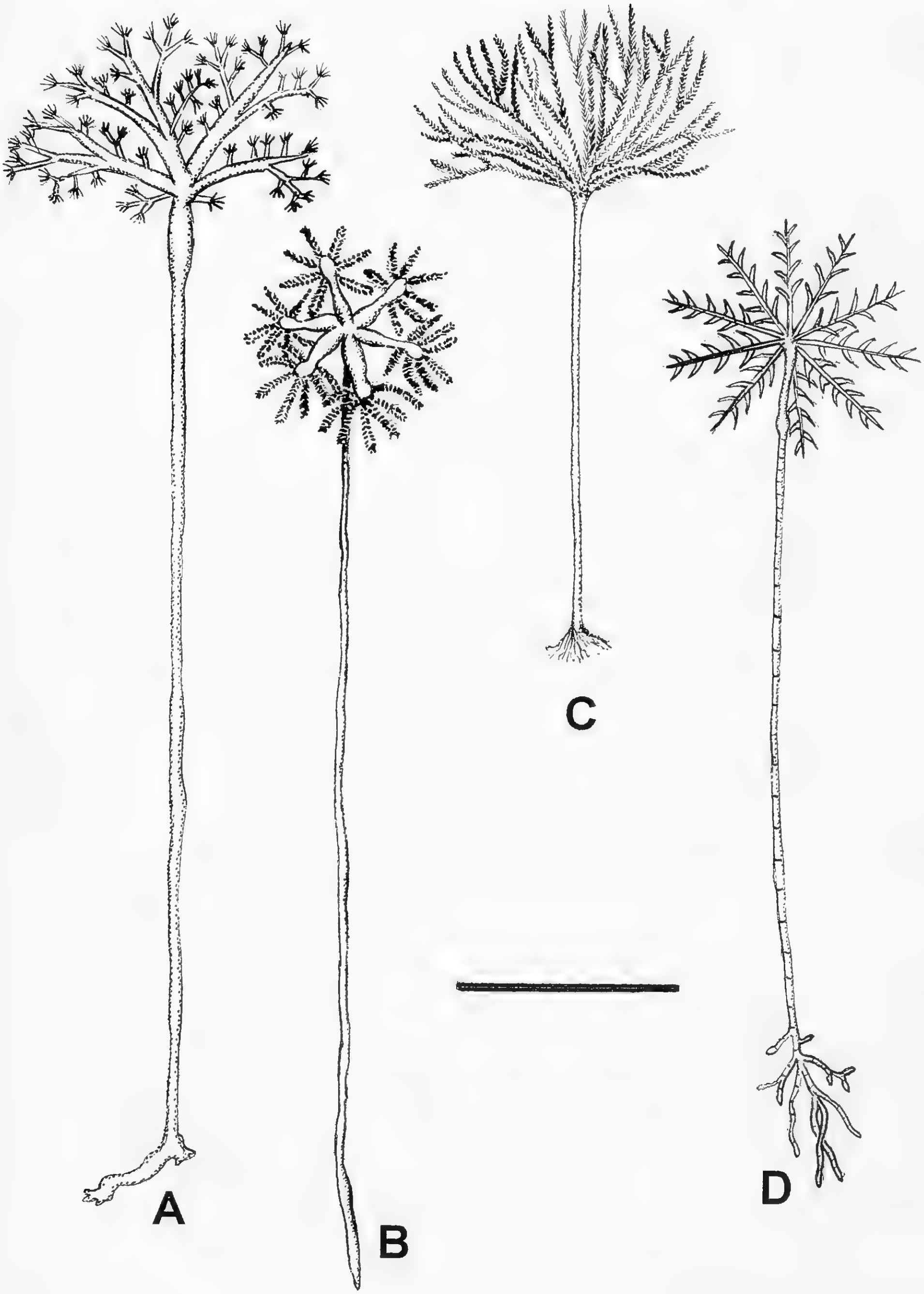

FIGURE 10. Convergence of body form in four deeper-water benthic organisms. A. The soft coral *Pacifiphyton bollandi* gen. and sp. nov. B. The pennatulacean *Umbellula* sp. (adapted from Heezen and Hollister, 1971:41, fig. 2.21). C. The bryozoan *Kinetoskias cyathus* (adapted from Marshall, 1979:168, fig. 68). D. The crinoid *Bathycrinus gracilis* (adapted from Gage and Tyler, 1991:104, fig. 4.45). Scale bar = 30 mm.

porting bundle of large spindles (Utinomi, 1966: 212, fig. 3; 215). On the other hand, in *Pacifiphyton*, the polyparium is multiply-branched and divaricate, and the polyps do not have supporting bundles of sclerites.

Chironephthya dipsacea Wright and Studer, 1889 (p. 231; pl. 37, fig. 1) also shows some resemblance to the new taxon, but as in other members of the soft coral family Nidaliidae, has permanent, strongly spiculated calyces into which the polyps retract. Calyces are absent in *Pacifiphyton bollandi*.

STALK MECHANICS.—A remarkable character of the new taxon is the differential appearance and form of spiculation between the swollen distal portion of the stalk and the rest of the stalk (Fig. 5). The swollen portion contains slender needles aligned parallel to the axis of the stalk. Between this distal portion and the basal region, the sclerites are mostly robust spindles and are more or less longitudinally disposed but many are also aligned at oblique angles. In the basal region of the stalk, many sclerites have an alignment approaching perpendicular to the longitudinal axis.

This differentiation of sclerite alignment and composition throughout the length of the stalk no doubt results in maximum rigidity toward the base and maximum flexibility just below the polypary. This morphological differentiation perhaps reflects the amount of movement the various portions of the stalk receive in strong bottom currents. The flexible and inflatable distal portion may act as a swivel and may be capable of at least some amount of back and forth rotation, giving the expanded polyparium maximum flexibility in strong currents.

Conceivably, this capability would keep the inflated polypary aligned to slight or marked changes in direction of the bottom current, somewhat like the pivoting of a wind vane with changing wind direction.

CONVERGENCE. — *Pacifiphyton* is remarkable in the similarity of its palm-like growth form to several unrelated deep-sea benthic animals (Fig. 10). They are all similar in having a congested, divaricate (Fig. 10A, C, D) or umbellate (Fig. 10B) feeding assemblage at the end of a very long and narrow stalk. These taxa include species of the pennatulacean octocoral genus *Umbellula* (see Williams, 1995:116, fig. 4E), the bryozoan genus *Kinetoskias*, and the crinoid echinoderm genus *Bathycrinus*. The resemblance between *Umbellula* and stalked crinoids has been noted by several authors including Gage and Tyler (1991:99). Marshall (1979:183) stated, "*Umbellula* is one of the classic animal types of the deep-sea floor, and so are the stalked sea-lilies (crinoids), both converging in their palm-like forms — forms that look well designed for passive suspension feeding. Bent over by currents, they look like palms in a breeze. . . ."

The often large and long-stalked suspension feeders, such as the four above-mentioned taxa, are rheophiles (current-lovers) and are most abundant in areas with prevailing currents as opposed to quieter regions of the sea floor (Marshall, 1979:295). The palm-like growth form is presumably advantageous to maximize feeding efficiency in similar benthic habitats.

Cowen (1981:332) described the mechanics of food gathering in stalked crinoids and described a resemblance to the ideal layout for harvesting roads on a banana plantation. In the stalked crinoids, food is harvested in an evenly distributed micro-particulate resource area, and is delivered to a central processing point (thus the analogy to a banana plantation). The harvested food material is transferred down the pinnules, and via the arms to the central mouth along a series of ciliated food grooves. In *Umbellula*, *Kinetoskias*, and *Pacifiphyton*, because of the modular nature of these organisms, harvesting and processing takes place on numerous distinct sites throughout the feeding structure and food is not delivered to a single central location for processing.

In stalked crinoids such as *Bathycrinus* and *Rhizocrinus*, the arms and stalk typically form a parabolic filtration fan with the stem tilted downstream in the bottom current (Gage and Tyler, 1991:105). Five, ten, or more arms radiate outward from a central mouth region. Each arm has numerous articulated pinnules. Both the pinnules and arms have a central ciliated groove. Each pinnule has several tube feet, which capture suspended particles and bring them into the central groove. In these crinoids, the entire body structure represents a single individual with a central mouth.

In contrast to this, *Pacifiphyton*, *Umbellula*, and *Kinetoskias* are modular organisms with many individual zooids or polyps, each with a separate mouth, and each similar in size and appearance. Modularity in a variety of benthic organisms has been discussed by Hughes (1983). In *Umbellula* large tubular polyps radiate from a central point. Each polyp has eight tentacles with many pinnules in two longitudinal rows. The pinnules capture suspended food particles, then each tentacle is subsequently brought over the mouth of the respective polyp, where the food material is removed by the mouth and transferred to the pharynx. In *Pacifiphyton*, many small polyps are evenly distributed on the branches of the polyparium (Fig. 1C). In shallower habitats such as that of *Pacifiphyton*, micropredation is probably a more important source of nutrition than is suspension feeding. In *Kinetoskias*, each of the numerous minute zooids arranged along the branches of the bushy distal region of the colony gathers food with a circular tentaculated feeding structure (the lophophore).

All of these unrelated palm-like organisms inhabit unconsolidated soft ooze or mud deposits (*Umbellula*, *Bathycrinus*, and *Kinetoskias*), or areas of sand and coral/stone rubble (*Pacifiphyton*). Many stalked sea lilies such as *Bathycrinus* and *Rhizocrinus* have root-like projections at the base of the stalk (known as terminal rootlets) that root the animal in the substratum (Fig. 10D). In *Kinetoskias*, colonies are rooted into the substratum by rhizoids at the base of a long stem formed by the fusion of reduced and modified individuals known as kenozooids (Fig. 10C) (Marshall, 1979:169). *Pacifiphyton* has a holdfast which may adhere to one or several fragments of stone or coral rubble (Fig. 1B, 10A). *Umbellula* has a long muscular peduncle, which penetrates into the soft sediment (Fig. 10B).

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I am grateful to Dr. Frederick Bayer (National Museum of Natural History, Washington, D. C.), Dr. Phil Alderslade (Museum and Art Gallery of the Northern Territory, Darwin, Australia), and Leen van Ofwegen (Nationaal Natuurhistorisch Museum, Leiden, The Netherlands) for their insights concerning various aspects of nephtheid systematics, and to Dr. Rich Mooi (California Academy of Sciences) for discussions regarding crinoid feeding mechanisms.

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A NEW SPECIES OF TREEFROG FROM THE SERENGETI NATIONAL PARK, TANZANIA (ANURA: HYPEROLIIDAE: *HYPEROLIUS*)

By

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A remarkable new rough-skinned, rock-dwelling species of the genus *Hyperolius* (Hyperoliidae) is described from Serengeti National Park, Tanzania. The new species is not related to the other rough-skinned *Hyperolius tuberculatus* of West Africa, nor to the sympatric *Hyperolius viridiflavus goetzi*.

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The Hyperoliidae is the dominant treefrog family of Africa. Members of this monophyletic family (Drewes, 1984), consisting of 226 species in 20 genera, also occur on Madagascar and in the Seychelles Islands.

The sedge frogs, genus *Hyperolius* Rapp, with over 100 species are the most numerous of the hyperoliids (Duellman, 1993). They are found throughout the Afrotropical Region in all suitable habitats except true desert. Schiøtz (1971) stated that the genus *Hyperolius* "seems to be in the process of rapid evolution with a vast number of morphologically very similar species, many of which show much variation and tendency to geographical splitting up," and Drewes (1984) characterized the genus as in a "state of evolutionary flux." In two major works on African treefrogs, Schiøtz (1967, 1975) treated the West and East African species known at the time. He provided descriptions, photographs, sonograms, distribution maps and natural history information available at the time. South African members of the genus were treated separately in a monograph on South African frogs by J. C. Poynton (1964) and central African species recently by Poynton and Broadley (1987).

Diversity within the genus *Hyperolius* is partly illustrated by proposed taxonomic changes within the past few decades. For instance, *H. thomensis* Bocage, 1886 has been moved in and out of the genus *Hyperolius* for a number of years (Perret, 1976, 1988; Drewes, 1984). In 1988, Perret removed three other species from the genus *Hyperolius* and placed them in three new genera. Recent unpublished morphological work by L. Henwood, California Academy of Sciences (CAS) added additional support to Schiøtz's contention (1975) that *Hyperolius parkeri* Loveridge does not fall within the currently recognized definition of the genus.

During the course of a 1992 photographic safari in Serengeti National Park, Tanzania a single adult female *Hyperolius* of strikingly cryptic appearance was discovered on Gong Rock, a famous boulder on an isolated inselberg known as Moru Kopjes in the southern sector of Serengeti National Park. Permission was granted by Tanzanian wildlife authorities for a subsequent visit to Serengeti in May of 1993 during the rainy season. At that time, an additional four juveniles were collected; of these, two were deep-frozen for work in progress on the *Hyperolius viridiflavus* complex and two were preserved as voucher specimens. No additional adults have been collected thus far; the male advertizement call remains unknown.

DESCRIPTION

Hyperolius orkarkarri n. sp.
(Plate 1A, B; Fig. 1)

HOLOTYPE.— CAS 186087 female; TANZANIA: Mara Region: Serengeti Dist: Serengeti National Park: Moru Kopjes, on Gong Rock. 02° 43.05′S; 34°47.6′E at an elevation of 1585 m. Collected by R. C. Drewes and C. M. Burnette, 24 July 1992 at approximately 1200 hrs.

PARATOPOTYPES.—CAS 191486–7 (juveniles); same locality as holotype. Collected by R. C. Drewes, M. T. Mendonca, E. Blankenship, B. C. Drewes and A. Fetter, 13 May 1993, 1525–1625 hrs.

DIAGNOSIS. — Differs from all other members of the genus *Hyperolius* by the extreme verrucosity of the dorsal and lateral surfaces of the body and limbs, and differences in size of the eye, finger and toe pads and amount of webbing between the toes.

ETYMOLOGY. — This species is named in honor of the Maasai, nomadic pastoralists who inhabited the Serengeti before it was gazetted a national park, and who used Gong Rock for ceremonial purposes. *Orkarkarr* is the *Maa* word for "gong."

DESCRIPTION OF THE HOLOTYPE. — Female, 21.1 mm snout-vent length; habitus squat; snout blunt; eye small, not protruding, its diameter less than distance to tip of snout and less than width of interorbital space; tips of fingers and toes dilated, truncated anteriorly, forming a flattened horizontal oval shape; third fingertip less than 1.5 times the diameter of eye; webbing of fingers reduced to a fringe except between third and fourth finger which is 1/3 webbed; toes fully webbed, web extending to or beyond distal subarticular tubercle except between first and second toes.

All dorsal and lateral surfaces of body, including the supraocular region, and exposed surfaces of limbs densely beset with warts of various sizes, so that nowhere is the skin smooth; the largest warts are isolated in the sacral region at approximately the level of the lateral extent of the sacral diapophyses, those on the left side nearly 1/2 diameter of the eye, those on the right side slightly smaller; the next largest are in roughly longitudinal dorsolateral rows extending from behind the eyes to the sacrum, followed by somewhat smaller tubercles arranged in two nearly parallel paravertebral rows extending from the snout to the anus; warts extend laterally onto the eyelids and superciliary region and ventrally to the canthal regions (Fig. 1).

Dorsal light pattern in the form of a broad band extending from tip of snout to above tip of urostyle, interrupted by a darker triangle on the head, the apices of the base extending laterally to the edges of the eyelids, the posterior extent of the apex to a distance roughly equal to equal the diameter of the eye. Three pairs of lateral extensions of the dorsal light pattern present, the anterior-most projecting diagonally forward from the scapular region to above the eyes, a large mediodorsal saddle extending laterally, then posteriorly on the flanks, and a posterior pair extending laterally from the area above the pelvic region onto the flanks. An elongated mid-dorsal smudge of darker pigment present; the flanks and remaining lateral surfaces darker (Fig. 1).

Forelimbs with a light oval spot extending from wrist halfway up the forearm; hind limb with a large light oval extending from heel halfway up the tibiofibula; a light patch on the dorsal surface of the foot above the approximate origin of the metatarsals. The light oval on the tibiofibula is confluent with the posterior portion of the light dorsal pattern when frog is at rest.

Ventrum semitranslucent medially; all areas of the belly beset with verrucae hydrophilicae (Drewes et al., 1977); a transverse gular fold present.

Color in life (Plate 1A). Iris silver; dorsal pattern white on ground color of silver-grey. Finger tips, toe tips, fingers, toes and ventral surface of hind limbs dark orange; throat and ventrum white.

Color in preservative. Light dorsal and limb patterns fade to beige, ground color to medium

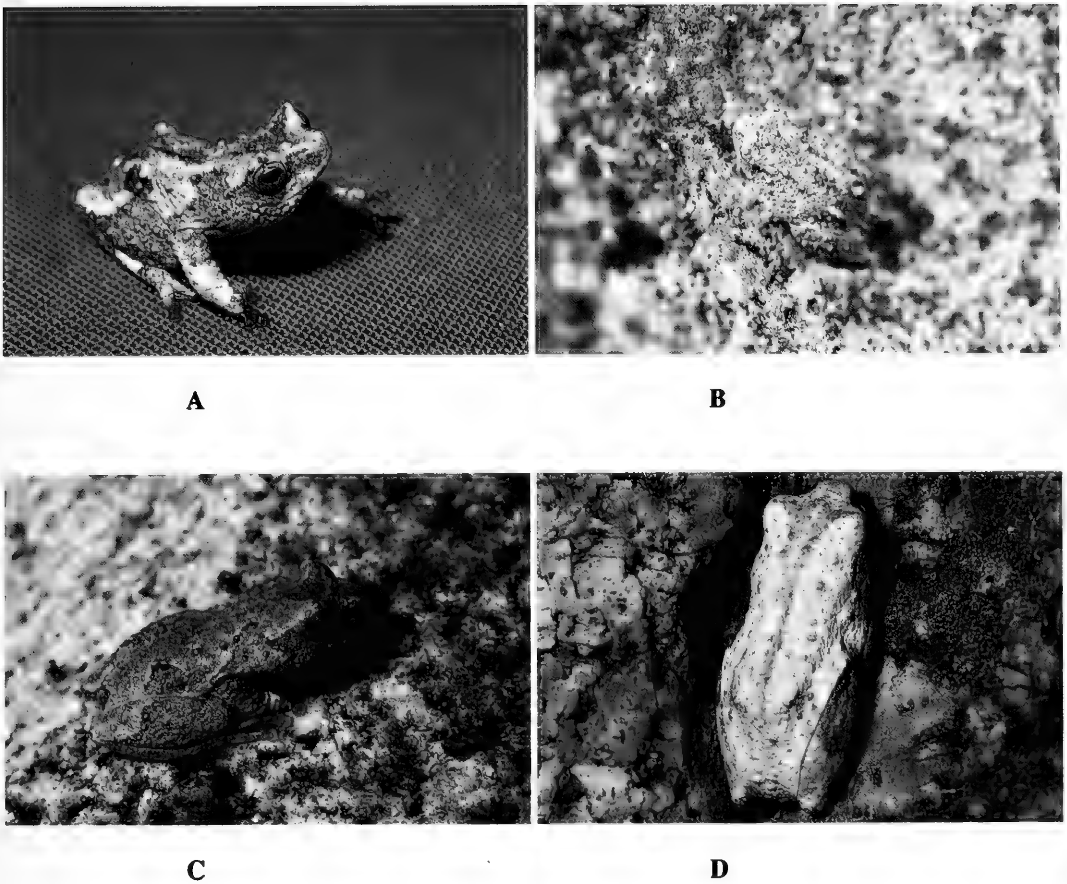

PLATE 1. A. Type: *Hyperolius orkarkarri*, CAS 186087 female, in life.
B. Type *in situ* on north face of Gong Rock just prior to collection.
C. Paratype, CAS 191486, just prior to collection.
D. Paratype, CAS 191487, just prior to collection.

brown; dark orange coloration of extremities fades to white.

VARIATION IN PARATYPES. — CAS 191486-87, 18.7 and 20.3 mm. snout-vent length respectively, are both juveniles and agree well with the description of the holotype. In the former, the color pattern and distribution of warts are nearly identical to the holotype; although the two large warts in the sacral region appear smaller than in the holotype, they are still the largest relative to all other warts in dorsal aspect (Plate 1C). In CAS 191487 the warts are somewhat smaller than in the type and other paratype but still obvious and distinct from all other *Hyperolius* material examined. Moreover, the dorsal color pattern (Fig. 1) differs in that the posterior apex of the dark triangle on the head narrows and extends posteriorly to the sacral region, giving the specimen a striped appearance (Plate 1D).

One additional specimen exists in the collection of the Serengeti Research Institute at Seronera that is probably referable to *Hyperolius orkarkarri*. The unnumbered specimen was collected by D. Kreulen at Galen's Drift, Serengeti and briefly examined by the author. As no curator nor other individual in a position of authority was present during the author's visit (12 May 1993), the specimen was unavailable for loan.

COMPARISONS. — The type material of *H. orkarkarri* was compared with all of Schiøtz' (1975) material referable to *Hyperolius viridiflavus goetzi* Ahl with which *H. orkarkarri* is apparently sympatric and seemingly syntopic. In 1993, the nearest population of calling *H. v. goetzi* was located 1.9 km west of Gong Rock, and a single juvenile *H. v. goetzi* (CAS 191488) was collected on Gong Rock along with the paratypes of *H. orkarkarri*. Additionally, although the possession of heterogeneous dorsal warts is unique to this species, the dorsal color pattern of *H. orkarkarri* is somewhat similar in shape to one of the juvenile color phases (Ph J) exhibited in some subspecies of *H. viridiflavus* (Schiøtz, 1971).

Hyperolius viridiflavus goetzi differs from *H. orkarkarri* in its generally smooth dorsal and lateral skin, absence of a dorsal pattern, absence of dark orange coloration on the extremities and presence of dark spotting or marbling on the flanks (diagnostic of this taxon). In *H. v. goetzi*, the eye is larger than in *H. orkarkarri*, being roughly equal in diameter to the interorbital distance and the distance from the anterior margin of the eye to the tip of the snout. In *H. orkarkarri*, the diameter is less in both dimensions. In both species, the horizontal oval configuration and size of the finger and toe pad expansions are similar.

Hyperolius orkarkarri was also compared with series of *Hyperolius tuberculatus* (Mocquard) (including the type) and *H. t. nimbae* Laurent. A West African form, *H. tuberculatus* is the only other *Hyperolius* species whose type description includes tubercles and verrucose dorsal skin (Mocquard, 1897). Moreover, examination of West African material was deemed necessary because J.-L. Perret (MHNG) sent the author a photocopy of a photograph taken by A. Schiøtz (ZMUC) of a treefrog from Ivory Coast identified as *H. t. nimbae*, whose skin is remarkably similar to that of *H. orkarkarri*, including verrucosity on the limbs (although significant differences such as size of finger and toe pads are also apparent in the photo). The origin and identity of this specimen is in doubt, as it cannot be located with certainty in the ZMUC collection (J. B. Rasmussen, pers. comm.). Perret also sent a photo by J.-L. Amiet of a treefrog from Pont de So, Cameroon; evidently a much larger species but equally verrucose, this specimen remains unidentified and its whereabouts unknown.

Hyperolius tuberculatus (including *H. t. nimbae*) is a much smoother species than *H. orkarkarri*, although in many specimens there are scattered low warts, usually a few on the dorsum in the occipital region and on the posterior portions of the flanks. These are generally of uniform size unlike *H. orkarkarri*, and none approach the largest in the latter species in size. In none of the material examined are there verrucosities on the supraocular regions nor on the exposed surfaces of the limbs as in *H. orkarkarri*. *H. tuberculatus* and *H. t. nimbae* differ from both *H. orkarkarri* and *H. v. goetzi* in possession of much larger digital tips that are rounded, not truncated anteriorly; the width of the third finger tip is more than 1.5 times the diameter of the eye; the hands are extensively webbed (nearly half webbed between 2nd and 3rd fingers). The diameter of the eye is greater than its distance to the tip of the snout, and the interobital distance. Many specimens have a conspicuous white spot on the upper jaw below the eye, not present in *H. orkarkarri* nor *H. v. goetzi*.

DISCUSSION

Much of Serengeti National Park is classified as "edaphic grassland on volcanic soils" and lies within the more widely distributed *Acacia-Commiphora* bushland vegetation zone (White, 1983). Annual rainfall is variable in the park, but 20 year data from Ikoma, near the northern margins, indicate a mean annual rainfall of 862 mm and mean annual temperature of 19.1°C. (Wernstedt, 1972). For the five year period January 1988 to January 1993, rainfall at Moru Kopjes averaged 64.5 mm per month (K. Campbell, pers. comm.).

The Gong, from which this inselberg within Moru Kopjes takes its name, is a large lemon-wedge shaped boulder which lies on its rounded surface on top of the main massif (Plate 2 A). The thin edge of the Gong is aligned in an east-west attitude. This large boulder is famous for its resonance when struck with a small rock and was evidently used in the past to signal the beginning of Maasai ceremonies—it's north and south-

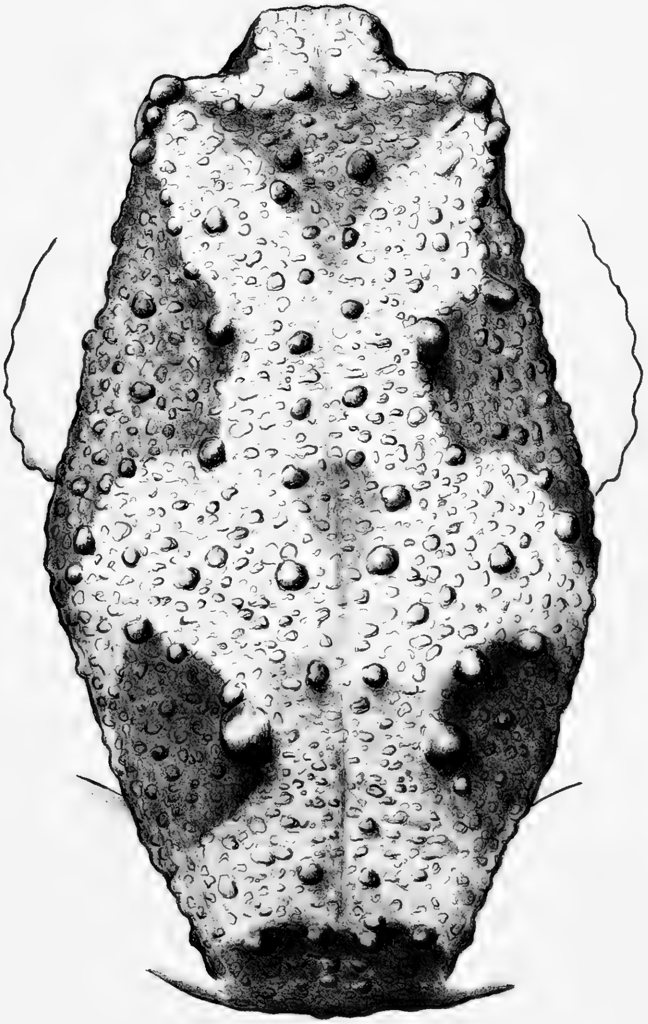

FIGURE 1. Dorsal pattern and distribution of warts in holotype.

facing surfaces are beset with linear rows of uniform, man-made, cup-shaped depressions. Larger boulders of the inselberg are decorated with recent pictographs. The type of *H. orkarkarri* was discovered in full sunlight in one of the depressions in the top row on the north face of the Gong. The following year, the first paratype, CAS 191486 (Plate 1C), was also found on the Gong itself, but in a depression on its south face (Plate 2B); CAS 191487 was taken from a vertical crevice in a nearby boulder about 1.5 m above the ground. The color pattern and texture of the skin very closely approximate the general aspect of the rock on which the specimens were collected (Plate 1B, C, D). Two additional specimens, presently frozen, were found in vertical crevices above wet seepage areas at the west base of the main massif, at grass level. The specimens were found in association with several *Chiromantis*, possibly *C. petersii* Boulenger, numerous *Agama*, and one example of *Hyperolius v. goetzi*.

Although most treefrogs are thought to seek shelter from desiccation during the daylight hours, the fact that the type specimen was discovered at rest in full sunlight is not too surprising. The South African Arum frog, *Hyperolius horstocki*, has long been known to rest in exposed positions (Wager, 1965), and recent work by Withers et al. (1982, 1984) and others has shown that all members of the genus *Hyperolius* tested so far exhibit much lower rates of evaporative water loss than would be predicted for treefrogs of their size. A dermal mechanism that might account for these observations has yet to be discovered.

The systematic relationships of *Hyperolius orkarkarri* are unclear, and will not be determined until a comprehensive phylogeny of *Hyperolius* is produced. *Hyperolius orkarkarri* shares a few of the characteristics diagnostic of the "*Hyperolius viridiflavus* group," such as the shape of the snout, shape of the dorsal pattern, and the presence of a gular fold. Moreover, it is in apparent sympatry with one of the group's purported members, *H. viridiflavus goetzi*. The morphological and behavioral characters that unite the *viridiflavus* complex are listed by Schiøtz (1971): snout brief ("pug-nosed"), digital webbing extensive, vocal sac and gular gland very large relative to snout-vent length, and females often with a transverse gular fold. In addition, eggs are deposited in water (unlike most other *Hyperolius*), post-metamorphs are exceptionally large relative to adult size, and the group has a distinctive call. None of these characters has been demonstrated to be apomorphic, and much of the taxonomic work on this complex at the population (subspecies) level has been based on dorsal color-pattern analysis.

Although there are many taxonomic problems within *Hyperolius*, with its 112 recognized species, the *viridiflavus* complex is most important because of its great geographical range, the ubiquitousness and size of its populations, and its confused taxonomic history. There are four reasons for more than a century of taxonomic confusion, resulting in the publication of more than 100 nominal subspecies as of 1971 (Schiøtz): (1) the members of this complex are widespread in tropical savannas; (2) where present, populations are large and usually a conspicuous component of any breeding anuran aggregations; and (3) though members of the group share a number of morphological and behavioral characters, (4) they are highly variable in dorsal color pattern, both within populations and between them.

The fact that a new species of treefrog can exist, undiscovered, on a famous rock in the middle of the Serengeti National Park—possibly the most intensively studied ecosystem in tropical Africa—is far less surprising than it is regrettable. The overlooked existence of *Hyperolius orkarkarri* in Serengeti reflects the fact that for years the great majority of effort, support and funding for species-level biological work has been applied toward ecological and behavioral studies, and these are usually of mega-vertebrates such as bovids, carnivores and primates. Meanwhile, the arthropod and smaller vertebrate faunas have been almost totally neglected, and while these are just as ecologically important (if not more so) as the large mammal and bird faunas, they remain very poorly understood. The past funding trend reflects the profound misunderstanding that these habitats and their species are already fully documented and well-understood. This is far from the case. In truth, the behavior and ecology of the Serengeti megafauna is available for study **only** because these conspicuous species have already been described by systematists and their evolutionary relationships clarified to some degree.

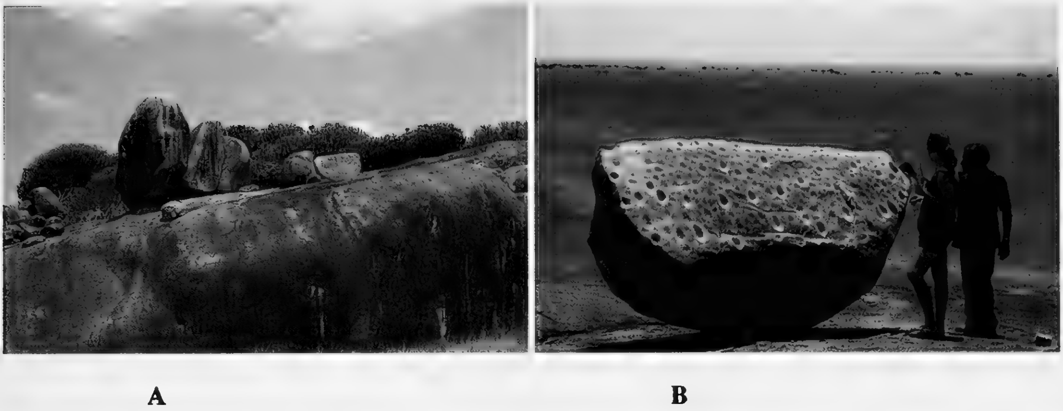
A B

PLATE 2. A. Gong Rock on Moru Kopje. The Gong is the lighter colored structure on the right
B. Southern aspect of Gong Rock; paratype CAS 191486 was collected on this face.

It is true that as awareness of environmental problems has grown on a world-wide scale, African governments have begun to pay more attention to habitat issues, especially those that directly affect economies and attract significant monies from non-governmental organizations. There has been much global media attention to "vanishing habitats," and perhaps as a result, we are beginning to meet African students who see careers in biology as viable options. Most unfortunately, opportunities to train in systematic biology, the foundation for all other biological disciplines, are almost nonexistent, and most of the students we know have trained in ecology or ethology. Like the rest of the world, Africa needs more systematists.

MATERIAL EXAMINED

Museum acronyms follow Leviton et al. (1985).

Hyperolius viridiflavus goetzi: Tanzania: CAS 191482–5 near Moru Kopjes, CAS 191488 Gong Rock; ZMUC RO 76959–63 Seronera; ZMUC RO 79440–4 Dabaga; ZMUC RO 79064–70 15 m. E. Sao Hill; ZMUC RO 78885–7, 78889–904 E. Singida.

Hyperolius tuberculatus tuberculatus: Gabon: Type — MNHN 1896.570 Lambarene; Topotypes — MNHN 1901.576–7; Cameroon: MNHN 1994.5748; BMNH 1937.12.1.29–30 Lomi Dist; BMNH 1908.5.30.67–69, 1909.12.3.17, 1913.10.29.26, Bitye; BMNH 1907.5.22.94 5 mi. inland from Kribi; BMNH 1906.5.28.115–118 Zima Country; BMNH 1904.2.29.12 Efulen. Zaire: CAS 145286–7 Gembe; BMNH 97.9.30.6–10 Stanley Falls; MNHN 1988.1307–31 Maniema, Kalima; MNHN 1988.1246–94 Kamituga; BMNH 1952.1.5.77 Kamituga. Nigeria: BMNH 1938.1.11.4–8 Uyo. Equatorial Guinea: BMNH 1977.2132–41, 2142–4, 2156–60 Fernando Po, Largo de Biao.

Hyperolius tuberculatus nimbae: Ivory Coast: ZMUC RO 75461, 66, 70, 74, 79 between Zeale and Denane.

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THE TAXONOMY OF THE SOUTHERN AFRICAN LEAF-TOED GECKOS (SQUAMATA: GEKKONIDAE), WITH A REVIEW OF OLD WORLD "*PHYLLODACTYLUS*" AND THE DESCRIPTION OF FIVE NEW GENERA

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Despite the removal of several monophyletic groups of leaf-toed geckos, the gekkonid genus *Phyllodactylus* remains polyphyletic. An evaluation of morphological features and allozymes suggest that Old World species assigned to the genus *Phyllodactylus* are not closely related to New World taxa, to which this generic name applies. Further, Old World species as a unit do not form a demonstrably monophyletic group. Osteological and external characters are used to describe and diagnose five new genera of leaf-toed geckos, each corresponding to a clade supported by apomorphic characters: *Dixonius* (two species, southeast Asia), *Haemodracon* (two species, Socotra Island, Yemen), *Cryptactites* (monoptypic, South Africa), *Goggia* (eight species, southern Africa), and *Afrogecko* (three species, southern Africa). In addition, the genus *Euleptes* Fitzinger 1843 is resurrected for a single species endemic to the Mediterranean region. Redescriptions and diagnoses are provided for two other currently recognized genera of leaf-toed geckos, *Christinus* from Australia and *Ebenavia* from Madagascar. *Phyllodactylus* is restricted to New World species only (although the monophyly of this group is not strongly established), with the Madagascan species *P. brevipes* remaining *incertae sedis*.

The recognition of monophyletic units of leaf-toed gekkonids is a necessary step towards the reconstruction of phylogeny, but available higher order analyses do not suggest appropriate outgroups. Regardless of whether other African gekkonids or other leaf-toed gekkonids are chosen as the outgroup, character analysis supports a partially resolved pattern of relationship within the southern African genus *Goggia*. The preferred phylogeny for this genus is: (*G. microlepidotus* (*G. gemmulus* (*G. lineatus* (*G. braacki*, *G. essexi*, *G. hewitti*, *G. hexaporus*, *G. rupicolus*)))). Speciation events associated with the evolution of taxa in the unresolved portion of the phylogeny were probably simultaneous and related to Late Tertiary climatic changes in temperate southern Africa. If this is true, the lack of resolution in the phylogeny is real (representative of the synchronous loss of continuity between several populations) rather than artifactual. Genetic distances beween species pairs in this group reflect both isolation by geographic distance prior to speciation and post-speciation divergence.

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The genus *Phyllodactylus,* as presently construed, is a speciose and geographically widespread assemblage of small to moderate sized geckos, with representatives on five continents. All of the geckos assigned to this genus possess a terminal pair of enlarged "leaf-like" scansors on each digit, reflecting the traditional reliance of gekkonid systematists on digital morphology as the primary, and often sole, indicator of generic allocation (e.g., Boulenger 1885; Loveridge 1947). Digital structure, however, is notoriously prone to parallel evolution in this group of lizards (Russell 1979; Carillo de Espinoza et al. 1990) and there is no a priori reason to assume that digital similarity reflects phylogenetic affinity any more accurately than other characters. Although the digital similarities shared by members of some gekkonid genera have been corroborated by other characters (Russell 1972; Bauer 1990; Kluge and Nussbaum 1995), this is not the case in *Phyllodactylus.* Indeed, Kluge (1983) could find no features that served to unite all of the species then assigned to the genus into a diagnosable whole.

Although the distribution of *Phyllodactylus* was regarded as possibly relictual by some authors (Schmidt 1923; Russell 1972; King and Horner 1993), nearly all modern workers have recognized the probable polyphyly of the group (Dixon 1964; Dixon and Anderson 1973; Russell 1972; Rieppel and Schneider 1981; Cogger et al. 1983; King 1987; King and Horner 1993). Dixon (1964) stated the "studies of the osteology of Old and New World members of the genus reveals [sic] constant differences in such features as phalangeal formulae, scapulocoracoid element, shape of the prefrontals, number of presacral vertebrae, fusion of nasals, neoteny in union of parietals, all of which suggests that the Old and New World groups belong to separate genera." Russell (1972) indicated that differences between some Old World groups were as great as those between Old and New World taxa and believed that the Old World members of the group did not form "a coherent entity," and this has subsequently been echoed by other authors (e.g., Dixon and Kroll 1974; Kluge 1983; Haacke 1996).

Certain putatively monophyletic groups have been recognized within *Phyllodactylus* (*sensu lato*) and have been accorded generic status. Dixon (1964) reviewed the systematics of the North and Central American members of the group, and Dixon and Huey (1970) reviewed the South American forms. Dixon and Anderson (1973) diagnosed and separated the southwest Asian taxa now referred to *Asaccus*, and Dixon and Kluge (1964) separated *Crenadactylus*, now referred to the family Diplodactylidae. Dixon and Kroll (1974) resurrected the older name *Paroedura* for the casque-headed Madagascan forms. Kluge (1983) regarded the remaining *Phyllodactylus* as polyphyletic and indicated that Dixon held similar views. Kluge (1983) further erected the genus *Urocotyledon* for those African and Seychellian forms exhibiting the derived conditions of the loss of the second ceratobranchial arch and the presence of caudal scansors. Most recently, Wells and Wellington (1984) erected the genus *Christinus* for the Australian geckos formerly assigned to *Phyllodactylus*, although their evidence for its diagnosis was unconvincing.

Even after the removal of these units, there is still no convincing evidence for the monophyly of *Phyllodactylus*. Kluge (1993) recognized 56 *Phyllodactylus* species. An additional five species have since been described and two others have been resurrected from synonymy, all from South Africa. Species currently retained in *Phyllodactylus* are chiefly distributed in the New World, with the greatest diversity in the arid regions of the Pacific coast of Mexico and South America, and in Venezuela. The remaining Old World *Phyllodactylus* include two species in Thailand, one in the Mediterranean region, two on the island of Socotra, one in Madagascar, and 13 (one undescribed) in southern Africa (Figs. 1, 2). This scattered distribution is difficult to explain and further suggests that the members of the genus do not form a single evolutionary unit. In this paper we present further evidence against the monophyly of *Phyllodactylus*, provide additional evidence for the monophyly of several of the Old World leaf-toed genera that have not been rigorously diagnosed (*Christinus* and *Ebenavia*), and provide evidence for the recognition of six additional monophyletic groups of Old World "*Phyllodactylus*."

Although higher order patterns of relationship within the Gekkonoidea are generally well established (Kluge 1987), relationships at the intergeneric level within the Gekkonidae remain obscure (Russell 1972; Bastinck 1981; Bauer

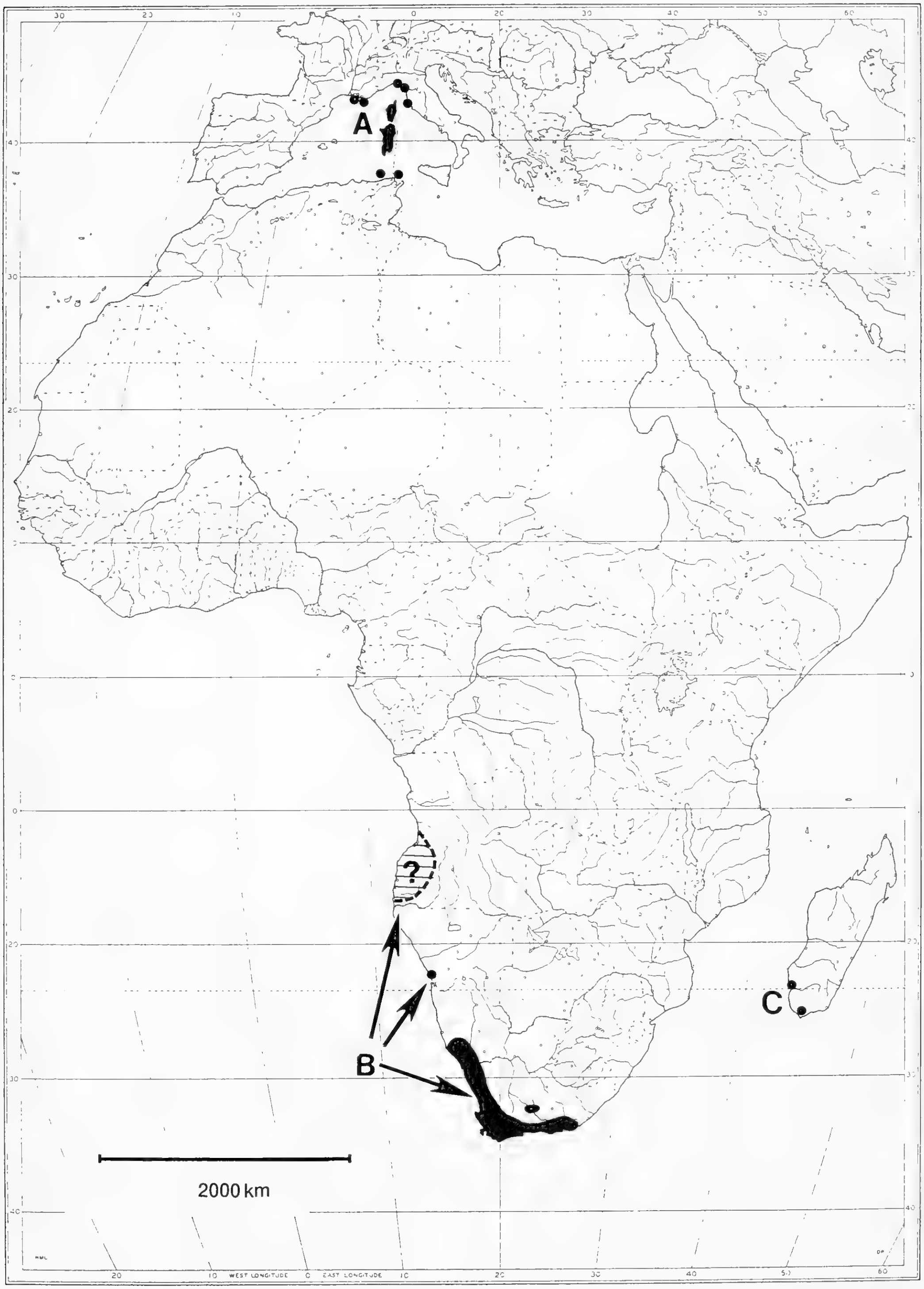


FIGURE 1. Distribution of *Phyllodactylus europaeus* in and around the central Mediterranean (A), the 12 species of southern African *Phyllodactylus* (B), and *P. brevipes* in Madagascar (C, after Glaw and Vences 1994).

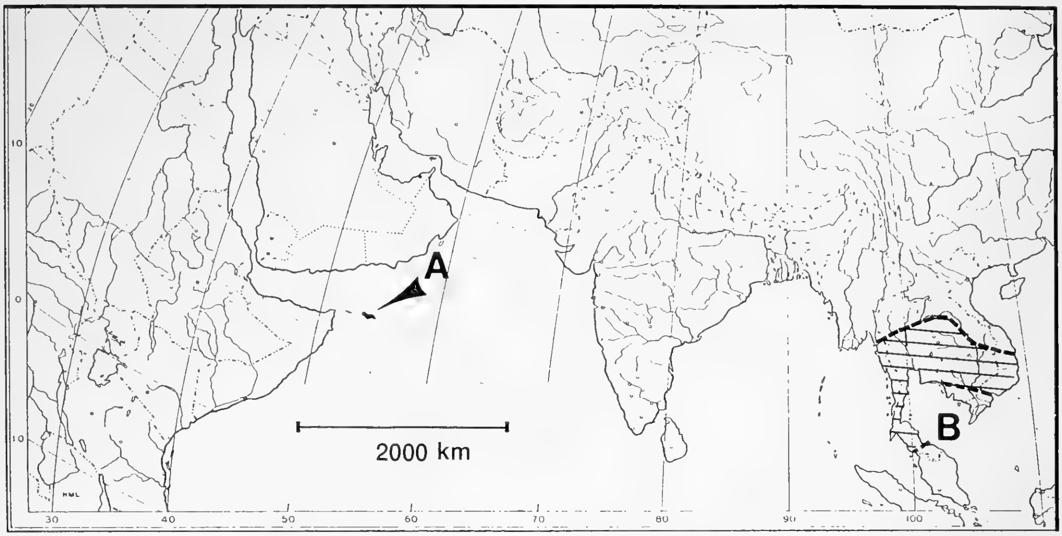


FIGURE 2. Distribution of *Phyllodactylus riebeckii and P. trachyrhinus* on Socotra Island, Yemen (A), and *P. siamensis and P. melanostictus* in Southeast Asia (B).

1990; Kluge 1983, 1987, 1995; Kluge and Nussbaum 1995). Phylogenetic analyses of single genera are thus hampered by a lack of knowledge of possible outgroup taxa, or outgroups must be defined so broadly as to make polarity assignments virtually impossible. Although we are unable to present a phylogenetic hypothesis for relationships among the various clades up to now included within *Phyllodactylus*, the recognition of such monophyletic subunits and their removal from the polyphyletic assemblage to which they are now assigned is a necessary step toward this goal. The new and resurrected genera recognized herein may be treated as monophyletic operational units in any subsequent attempts to reconstruct the phylogeny of gekkonids as a whole.

Relationships within each of the newly recognized clades of leaf-toed geckos are generally non-problematic, as most of these clades correspond to a single geographic region and all but one of these regions contains only one or two species. In the case of the *Phyllodactylus* of southern Africa, however, there are twelve recognized species in three apparently very distantly related clades (genera). Several hypotheses of higher order relationship exist for southern African gekkonids, but these are poorly resolved and partially conflicting. Nonetheless, there are sufficient data for us to present some phylogenetic and biogeographic analysis of the most speciose of these clades.

MATERIALS AND METHODS

Specimens were examined externally using a binocular dissecting microscope or hand lens. Specimens of all Old World *Phyllodactylus* species (except *P. brevipes)* were examined, as were representative New World species and species referred to other leaf-toed gekkonid genera. The species lists of Kluge (1983, 1991, 1993, 1996) served as a guide to the recognized taxa. We follow Kluge (1987) for the naming of higher taxonomic units of gekkonids. The following species were examined externally: *Asaccus elisae, A. gallagheri, A. griseonotus, Christinus guentheri, C. marmoratus, Ebenavia inunguis, Phyllodactylus angelensis, P. angustidigitatus, P. ansorgii, P. bauri, P. braacki, P. bugastrolepis, P. clinatus, P. darwini, P. davisi, P. delcampi, P. dixoni, P. duellmani, P. essexi, P. europaeus, P. galapagensis, P. gemmulus, P. gerrhopygus, P. gilberti, P. heterurus, P. hewitti, P. hexaporus, P. homolepidurus, P. inaequalis, P. insularis, P. interandinus, P. julieni, P. lanei, P. leei, P. lepidopygus, P. lineatus, P. martini, P. melanostictus, P. microlepidotus, P. microphyllus, P. muralis, P. palmeus, P. partidus, P. pau-*

cituberculatus, P. peringueyi, P. porphyreus, P. pulcher, P. pumilus, P. reissii, P. riebeckii, P. rupicolus, P. santacruzensis, P. sentosus, P. siamensis, P. swartbergensis, P. tinklei, P. trachyrhinus, P. tuberculosus, P. unctus, P. ventralis, P. wirshingi, P. xanti, Paroedura androyensis, P. bastardi, P. gracilis, P. guibeae, P. pictus, P. stumpffi, Urocotyledon inexpectata, and U. wolterstorffi. Specimens were examined in or borrowed from the following collections: California Academy of Sciences (CAS), British Museum (Natural History) (BMNH), University of Kansas Museum of Natural History (KU), Academy of Natural Sciences of Philadelphia (ANSP), Louisiana State University Museum of Natural Sciences (LSUMZ), United States National Museum (USNM), Field Museum of Natural History (FMNH), Museum für Naturkunde der Humboldt Universität zu Berlin (ZMB), Port Elizabeth Museum (PEM and PEM-AM), American Museum of Natural History (AMNH), John Ellerman Museum, University of Stellenbosch (JEM), Transvaal Museum (TM), National Museum, Bloemfontein (NMB), Museo Zoologico de la Specola, Universita di Firenze (MZUF), Zoologisches Forschungsinstitut und Museum A. Koenig (ZFMK), and the South African Museum (SAM). In addition, several specimens in the collection of the senior author (AMB) were also consulted. These specimens will be deposited in the CAS collection. Specimens of the following species were not examined, but were compared on the basis of published descriptions: *Phyllodactylus bordai, P. brevipes, P. rutteni, P. transversalis, Paroedura homolorhinus, P. masobe, P. oviceps*, and *Urocotyledon weileri*. For some of the taxa, represented by small samples in our study, observations were supplemented by literature information. These include *Christinus guentheri* (Cogger 1971; Cogger et al. 1983), *C. marmoratus* (Stephenson 1960), *Phyllodactylus ansorgii* (Boulenger 1907), *P. europaeus* (Wiedersheim 1876; Fürbringer 1922; Rieppel and Schneider 1981), and the Socotran *Phyllodactylus* (Loveridge 1947).

Osteological comparisons were made using cleared-and-stained specimens [prepared following the methods of Wassersug (1976) and Bauer (1986)], dry skeletal material, and radiographs prepared from intact museum specimens. Radiographs were prepared using a Faxitron cabinet x-ray unit at 20–40 kV for 20–45 seconds. Images were exposed onto Polaroid type 55 positive/negative film and observations made with a Micron 775 microfiche reader. A complete list of osteological specimens and radiographic material is presented in Appendix A. As only representative New World species were examined in detail, we here rely on Dixon (1964; in litt.) for the generality of certain statements regarding the osteology of these taxa.

Protein electrophoresis was also used to examine phenetic and phylogenetic relationships among representative leaf-toed gekkonid taxa. Tissues from all southern African *Phyllodactylus* (except *P. ansorgii*), as well as from representative "leaf-toed" geckos from other regions (see Appendix B) were compared at 24 allozyme loci (Table 1). Most tissues were obtained by the authors in the field and have been deposited in the frozen tissue collection at the Museum of Natural Science, Louisiana State University (LSUMZ H-series). Additional material was obtained from the frozen tissue collections of the Museum of Vertebrate Zoology, University of California, Berkeley (MVZ-FC) and Dr. S. Blair Hedges, Pennsylvania State University (SBH). Samples of liver tissue dissected from freshly killed specimens or obtained from frozen tissue collections were homogenized in deionized water, stored in liquid nitrogen or in an ultracold freezer, and subjected to horizontal starch gel electrophoresis using standard techniques (Selander et al. 1971; Harris and Hopkinson 1976; Hillis et al. 1996). In the phylogenetic analysis (applied only to African *Phyllodactylus*) loci were considered to be characters and alleles character states (Buth 1984). Polymorphisms were treated as recommended by Murphy (1993) and Mabee and Humphries (1993) and data were analyzed using PAUP 3.0 (Swofford 1990). In the phenetic analysis Nei (1978) genetic distances were calculated using the BIOSYS computer package (Swofford and Selander 1981).

RELATIONSHIPS AMONG LEAF-TOED GECKOS

The relationships of *Phyllodactylus* to other gekkonine genera have never been adequately reconstructed. This has been due, in part, to the fact that, aside from the leaf-like scansors of the toes, most *Phyllodactylus* are relatively conservative in morphology, retaining many plesio-

TABLE 1. Buffer systems and loci scored in the analysis of the Old World leaf-toed geckos.

Enzyme	Enzyme Commission No.	Locus	Buffer System
Aspartate aminotransferase (2 loci)	2.6.1.1	Aat-1,2	B
Aconitase (2 loci)	4.2.1.3	Acon-1,2	C
Adenylate kinase	2.7.4.3	Ak	A
Creatine kinase	2.7.3.2	Ck	A
Fumarase	4.2.1.2	Fum	A
Glucose dehydrogenase	1.1.1.47	Gdh	B
Glucose phosphate isomerase (2 loci)	5.3.1.9	Gpi-1,2	B
Isocitrate dehydrogenase (2 loci)	1.1.1.42	Icdh-1,2	C
L-lactate dehydrogenase (2 loci)	1.1.1.27	Ldh-1,2	B
Malate dehydrogenase (2 loci)	1.1.1.37	Mdh-1,2	B
Malic enzyme	1.1.1.40	Me	C
Dipeptidase (2 loci)	3.4.13.11	Pep-1,2	A
Tripeptide aminopeptidase	3.4.11.4	Pep-3	A
Phosphogluconate dehydrogenase	1.1.1.44	Pgdh	C
Phosphoglucomutase (2 loci)	5.4.2.2	Pgm-1,2	B
Pyruvate kinase	2.7.1.40	Pk	A

morphic character states relative to other gekkonid taxa (Hamilton 1960; Kluge 1983).

Few authors have suggested explicit pattens of relationship among the various geographically delimited groups of "*Phyllodactylus*." Russell (1972) recognized a number of groups of gekkonid geckos on the basis of similarities in digital structure. He specified, however, that these represented morphological groupings only, rather than explicitly evolutionarily cohesive units. Russell's *Phyllodactylus* group included *Phyllodactylus, Ebenavia, Ptyodactylus* and *Uroplatus*, and the taxa now allocated to *Paroedura, Urocotyledon, Asaccus*, and *Christinus*. Although he did not initially regard these as necessarily forming a natural unit, Russell (1976) subsequently suggested that similarities between *Uroplatus*, *Ptyodactylus*, and *Phyllodactylus* might have phylogenetic significance. Nonetheless, he proposed no explicit hypothesis of relationship among these forms. Kluge (1983) subsequently presented evidence from hyoid morphology to argue for the non-monophyly of Russell's *Phyllodactylus* group.

In analyzing relationships within *Asaccus*, Arnold and Gardner (1994) used a range of leaf-toed geckos as the outgroup (*Paroedura stumffi*, *Phyllodactylus europaeus*, *P. galapagensis*, *P. riebeckii, P. siamensis, P. trachyrhinus*). They regarded *Paroedura* as "apparently related" to other *Phyllodactylus* and by implication they accepted at least some level of close relationship among the remaining leaf-toed geckos in their outgroup. However, no explicit support for this assumption was provided.

The only hypothesis explicitly suggesting affinities between geographically separated groups of *Phyllodactylus* is that of Greer (1990). He suggested that the Australian leaf-toed geckos (genus *Christinus)* might have evolved from African *Phyllodactylus* stock, citing for his support the shared derived conditions of *Christinus* spp. and *Phyllodactylus porphyreus*. The fusion of the nasal bones is, however, the only derived feature mentioned by Greer that is shared by this pair of taxa (and several other leaf-toed gekkonids).

Thus, little or no evidence from morphology exists to corroborate *Phyllodactylus* monophyly. Likewise in our study we uncovered no putative synapomorphies for this genus as presently construed. Although it cannot be used to demonstrate monophyly, nor to falsify phylogenetic hypotheses, we used genetic distance data to examine the issue of similarity among leaf-toed geckos. The distribution of alleles among the 24 loci is presented in Table 2. A total of 185 alleles was observed among the loci surveyed. Alleles per locus ranged from three in Gpi-2, Mdh-1, and Mdh-2 to 14 in Pep-3. The average number of alleles per locus was 7.7. Numbers of fixed allozyme differences and Nei (1978) genetic distances (D_N) were calculated among sixteen species of leaf-toed geckos (Table 3), including all southern African species (except *Phyllodactylus ansorgii*) as well as *Christinus marmoratus* (Australia), *Paroedura pictus* (Madagascar), *Phyllodactylus xanti* (western North America), *P. wirshingi* (Puerto Rico), and *P. siamensis* (southeast Asia). *Afroedura loveridgei* (Mozambique), a representative of a genus that may be among a cluster of African geckos forming the outgroup to southern African *Phyllodactylus* was also included. Pairwise differences between *Phyllodactylus* species and the other genera are large (Nei distances 1.10–2.08, mean 1.62; fixed allozyme differences 16–21, mean 19), and many approach or exceed the limit of resolution of allozyme electrophoresis. For example, any similarity between two taxa showing 21 fixed differences out of 24 loci (see Table 3) is more likely to be due to chance than to common ancestry.

Similarly high levels of differentiation exist between sets of *Phyllodactylus* species inhabiting different geographic regions (Table 4; Fig. 3). Indeed, some of the differences within "*Phyllodactylus*" are even greater than those between "*Phyllodactylus*" and the other leaf-toed genera. For example, there are 23 fixed differences between *Phyllodactylus porphyreus* and *P. siamensis, P. xanti,* and *P. wirshingi* ($D_N = 3.18$).

Even within geographic regions, huge genetic distances exist. *Phyllodactylus xanti* and *P. wirshingi*, both members of the *P. tuberculosus* group (Dixon 1960, 1964), are as distinct from one another (18 fixed differences, $D_N = 1.39$) as are many of the species on different continents. The same is true of some of the comparisons among southern African species. *Phyllodactylus peringueyi* is particularly distinct (20–22 fixed differences [$D_N = 1.79$–2.49] from any other *Phyllodactylus* species, including the others in southern Africa). *Phyllodactylus porphyreus* and *P. swartbergensis* are slightly less distinct from the remaining African forms, but still very different (15–18 fixed differences from other species [$D_N = 0.98$–1.38], 17 [$D_N = 1.23$] from each other). *Phyllodactylus microlepidotus* shows 13–15 fixed differences ($D_N = 0.78$–0.98) from the *lineatus* group species, and within the *lineatus* group, fixed differences range from three to 11 ($D_N = 0.16$–0.61).

Maximum recorded intrageneric Nei (1978) genetic distances in geckos are 1.19 for *Phelsuma* (Good and Bauer 1995), 1.04 for *Rhoptropus* (Bauer and Good 1996), 0.87 for *Pachydactylus* (Branch et al. 1996), and 0.68 for *Rhacodactylus* (Good et al. 1997). Most of the distances among *Phyllodactylus* species far exceed those levels, and in fact are equivalent to distances among the genera *Hemidactylus*, *Lygodactylus*, *Phelsuma*, *Rhoptropus*, *Pachydactylus*, *Palmatogecko*, and *Tarentola* (D_N = 1.25–3.14; Good and Bauer unpubl.). The only distances in the present analysis that are consistently less than these intergeneric distances are within the *lineatus* complex of southern African *Phyllodactylus* and between this complex and *P. microlepidotus* (Fig. 3).

We use the evidence from this analysis, along with the absence of morphological characters supporting *Phyllodactylus* monophyly to justify the assumption that the genus consists of several unrelated, or distantly related clades that have been artificially grouped. This necessitates the further analysis of characters within "*Phyllodactylus*" in order to delineate putatively monophyletic subunits.

PREVIOUSLY RECOGNIZED MONOPHYLETIC GROUPS OF LEAF-TOED GECKOS

New World *Phyllodactylus*

In the New World *Phyllodactylus* occurs from Riverside County, California south along the west coast of North America to northwestern Panama, and in South America from southern Ecuador to northern Chile. It is also present along the coast of Colombia and Venezuela, on Barbados and Puerto Rico, in Belize and adjacent offshore islands, and in the Galapagos (Dixon 1962, 1964, 1968; Dixon and Huey 1970). Most authors have accepted the monophyly of New World *Phyllodactylus* as a whole (e.g. Dixon 1964; Vanzolini 1968; Carillo de Espinoza et al. 1990) although this has not been rigorously demonstrated. Dixon (1964) provided a diagnosis for the Neotropical (including North American) spe-

TABLE 2. Overall allele frequencies of African and other selected leaf-toed gekkonids. Abbreviations: BRA = *Phyllodactylus braacki*, ESS = *P. essexi*, GEM = *P. gemmulus*, HEW = *P. hewitti*, HEX = *P. hexaporus*, LIN = *P. lineatus*, MIC = *P. microlepidotus*, RUP = *P. rupicolus*, POR = *P. porphyreus*, SWA = *P. swartbergensis*, PER = *P. peringueyi*, SIA = *P. siamensis*, XAN = *P. xanti*, WIR = *P. wirshingi*, AFR = *Afroedura loveridgei*, CRI = *Christinus marmoratus*, PAR = *Paroedura pictus*. *Afroedura loveridgei* has been included as a representative of the African gekkonid radiation. Lower case letters represent different allelic states of each locus. Unless multiple alleles and their frequencies are listed it may be assumed that all of the specimens examined for a given species (see Appendix B) are homozygous for the indicated allele.

Locus	Taxa/Alleles																
	BRA	ESS	GEM	HEW	HEX	LIN	MIC	RUP	POR	SWA	PER	SIA	XAN	WIR	AFR	CRI	PAR
Aat-1	b	b	b	b	b	b	b	b	b	a	c	d	e	f	c	g	h
Aat-2	a	a	a	a	a	a	a	a	a	a	b	c	c	d	b	b	b
Acon-1	b(0.25) c(0.75)	b	e	b	b(0.85) d(0.15)	e(0.95) f(0.05)	g	b	g	a	h	i	j	j	h	h	b
Acon-2	b	b	b	b	b	b	c	b	b	a	d	e	f	g	h	i	j
Ak	a	a	a	a	a	a	b	a	b	a	c	d	e	f	g	h	i
Ck	b	b	c	b	b	c	e	c	d	a	f	g	h	i	j	k	l
Fum	b	b	b	b	b	b	b	b	c	a	c	d	e	d	f	g	h
Gdh	a	a	a	a	a	a	a	a	b	a	c	a	a	a	d	e	f
Gpi-1	c	b	e	c	c	d	f	c	a	a	g	d	h	i	j	k	c
Gpi-2	a(0.95) b(0.05)	a	c	a	a	a	a	a	c	a	a	a	a	a	a	a	c
Icdh-1	b	b	c	b	b	b(0.85) c(0.15)	d	b	a	a	a	e	g	g	h	i	j
Icdh-2	b	b	b	b	b	b	a	b	c	a	a	d	e	f	a	a	g
Ldh-1	b	b	b	c	b	b	b	b	c	a	d	e	f	g	c	h	h
Ldh-2	a	a	a	a	a	a	a	a	b	a	a	a	a	c	d	a	a
Mdh-1	b	b	b	b	b	b	b	b	c	a	b	b	b	b	b	b	b
Mdh-2	a	a	a	a	a	a	a	a	a	a	b	c	c	a	a	a	a
Me	a	b	a	a	a	a	a	a	b	a	c	a	a	d	a	a	e
Pep-1	d	b	c	c	c	c	e	c	c	a	f	g	h	i	j	j	k
Pep-2	b	b	a	b	b	a	c	a	a	a	d	a	a	e	a	a	a
Pep-3	c	a	g	b	d	e	i	f	h	a	j	k	l	m	n	a	m
Pgdh	b	b	b	b	b	b(0.95) c(0.05)	e	b	d	a	f	g	h	h	e	b	i
Pgm-1	b	b	d	b	b	c	e	b	b	a	f	g	h	i	j	k	k
Pgm-2	b	b	b	b	c	b	a	b	a	a	d	b	b	e	f	f	g
Pk	a	a	b	a	a	a	a	a	a	a	c	d	e	e	f	a	a

TABLE 3. Fixed differences (above diagonal) and Nei (1978) genetic distances (below diagonal) between species pairs of leaf-toed geckos. Abbreviations as for Table 2.

	BRA	ESS	GEM	HEW	HEX	LIN	MIC	RUP	POR	SWA	PER	SIA	XAN	WIR	AFR	CRI	PAR
BRA	—	4	10	3	3	7	13	4	18	16	21	18	18	20	20	17	18
ESS	0.213	—	11	5	5	8	14	6	17	16	21	19	19	20	21	17	19
GEM	1.232	0.613	—	10	10	5	15	7	17	17	22	18	18	21	20	18	19
HEW	0.162	0.234	0.539	—	3	7	14	4	16	16	21	18	18	20	19	17	18
HEX	0.158	0.235	0.553	0.135	—	7	13	4	17	16	21	19	19	20	20	17	18
LIN	0.339	0.408	0.275	0.347	0.341	—	13	4	17	15	21	16	17	20	19	16	19
MIC	0.775	0.875	0.981	0.875	0.775	0.771	—	13	17	15	20	19	19	20	20	18	17
RUP	0.213	0.288	0.405	0.182	0.184	0.183	0.780	—	16	15	21	17	17	20	19	16	17
POR	1.376	1.232	1.232	1.099	1.227	1.223	1.232	1.099	—	17	22	23	23	23	21	21	20
SWA	1.095	1.099	1.232	1.099	1.093	0.981	0.981	0.981	1.232	—	20	19	19	21	19	16	20
PER	2.086	2.079	2.485	2.079	2.074	2.070	1.792	2.079	2.485	1.792	—	20	21	21	22	18	18
SIA	1.385	1.569	1.386	1.386	1.563	1.089	1.569	1.232	3.178	1.569	2.079	—	15	20	20	19	21
XAN	1.385	1.569	1.386	1.386	1.563	1.223	1.569	1.232	3.178	1.569	2.079	0.981	—	18	20	19	21
WIR	1.794	1.792	2.079	1.792	1.786	1.782	1.792	1.792	3.178	2.079	2.485	1.792	1.386	—	21	21	21
AFR	1.794	2.079	1.792	1.569	1.786	1.559	1.386	1.569	2.079	1.569	1.386	1.792	1.792	2.079	—	14	20
CRI	1.229	1.232	1.386	1.232	1.227	1.096	1.386	1.099	2.079	1.099	1.386	1.569	1.569	2.079	0.875	—	16
PAR	1.510	1.569	1.569	1.386	1.406	1.559	2.079	1.232	1.792	1.792	2.079	2.079	2.079	2.079	1.792	1.099	—

TABLE 4. Mean Nei genetic distances (below diagonal) and fixed alleles differences (above diagonal) of leaf-toed geckos by geographic region.

	Southern Africa	Southeast Asia	New World
Southern Africa	–	18.7	19.7
Southeast Asia	1.64	–	17.5
New World	1.84	1.39	–

cies of *Phyllodactylus*, which he assumed were monophyletic. These taxa were characterized by the absence of femoral or preanal pores, the presence of cloacal bones, phalangeal formulae of manus and pes 2-3-4-5-3, cruciform interclavicle, 26 presacral vertebrae, five pairs of sternal ribs, fused premaxillary bones, paired nasals, vomers, and parietals, lunate prefrontals projecting posteriorly, and an absence of a cartilaginous union between the precoracoid ray of the epicoracoid and the scapula.

Russell (1972), however, has demonstrated that the stated reduction in the phalangeal formula of the pes from 2-3-4-5-4 does not occur in any of the New World species of the genus. This removes one of the most convincing arguments for the monophyly of New World *Phyllodactylus* as most of the other features are primitive, or at least broadly distributed among gekkonids as a whole. However, the absence of preanal pores is derived within gekkonids, and the ligamentous union of the scapula and precoracoid ray of the epicoracoid occurs elsewhere among leaf-toed genera only in *Asaccus* and some of the southern African *Phyllodactylus*, and might also be apomorphic. The reduction to a single egg per clutch seen in most New World *Phyllodactylus* (Dixon and Huey 1970) is probably derived at the level of gekkonids (Kluge 1987) but the presence of two-egg clutches has also been recorded (e.g., Kushlan 1981), and this character's variability within the group needs to be assessed.

Dixon (1960, 1964) recognized three species groups of *Phyllodactylus* in North and Central America: *Phyllodactylus unctus* (to which he believed some South American forms were related), *P. delcampi*, and *P. tuberculosus*, in which he included species occurring from southern California through western Mexico, Central America, and South America, as well as the Galapagos and the Caribbean. Dixon (1964) regarded the *unctus* and *delcampi* groups as closely related. Although Murphy (1983) presented evidence to the contrary, Dixon's conclusions have been supported by most data (e.g., Murphy and Papenfuss 1980; Grismer 1994).

Dixon's three species groups have been accepted by subsequent workers (e.g., Vanzolini 1968), although the monophyly of these units has not been rigorously established. Within the *P. tuberculosus* group several putatively monophyletic subunits have been proposed, including groups in the West Indies (Dixon 1961), Central America (Dixon 1968), and South America (Dixon and Huey 1970; Kroll and Dixon 1972). The Galapagos species are closely related to one another (Van Denburgh 1912) and to the South American west coastal forms (Dixon and Huey 1970; Wright 1983, 1984), although more than one invasion of the islands has been proposed.

We have not examined all New World *Phyllodactylus* in detail, nor have we critically evaluated the monophyly of this group as a whole, or that of any of its subunits, as this would have expanded the scope of the analysis significantly and would have duplicated the efforts of other workers more intimately involved with relationships among American *Phyllodactylus*. Rather, we have constrained our focus to Old World leaf-toed geckos. For this purpose confirmation of the monophyly of American *Phyllodactylus* is not essential. It is only necessary to demonstrate that putatively monophyletic Old World groups do not share a preponderance of derived characters with some or all of the American forms. *Phyllodactylus* has as its type species a West Indian form, *P. pulcher*, currently considered as a member of the *P. tuberculosus* group. The indentification of any clades of Old World leaf-toed geckos that can be diagnosed as monophyletic units distinct from New World forms

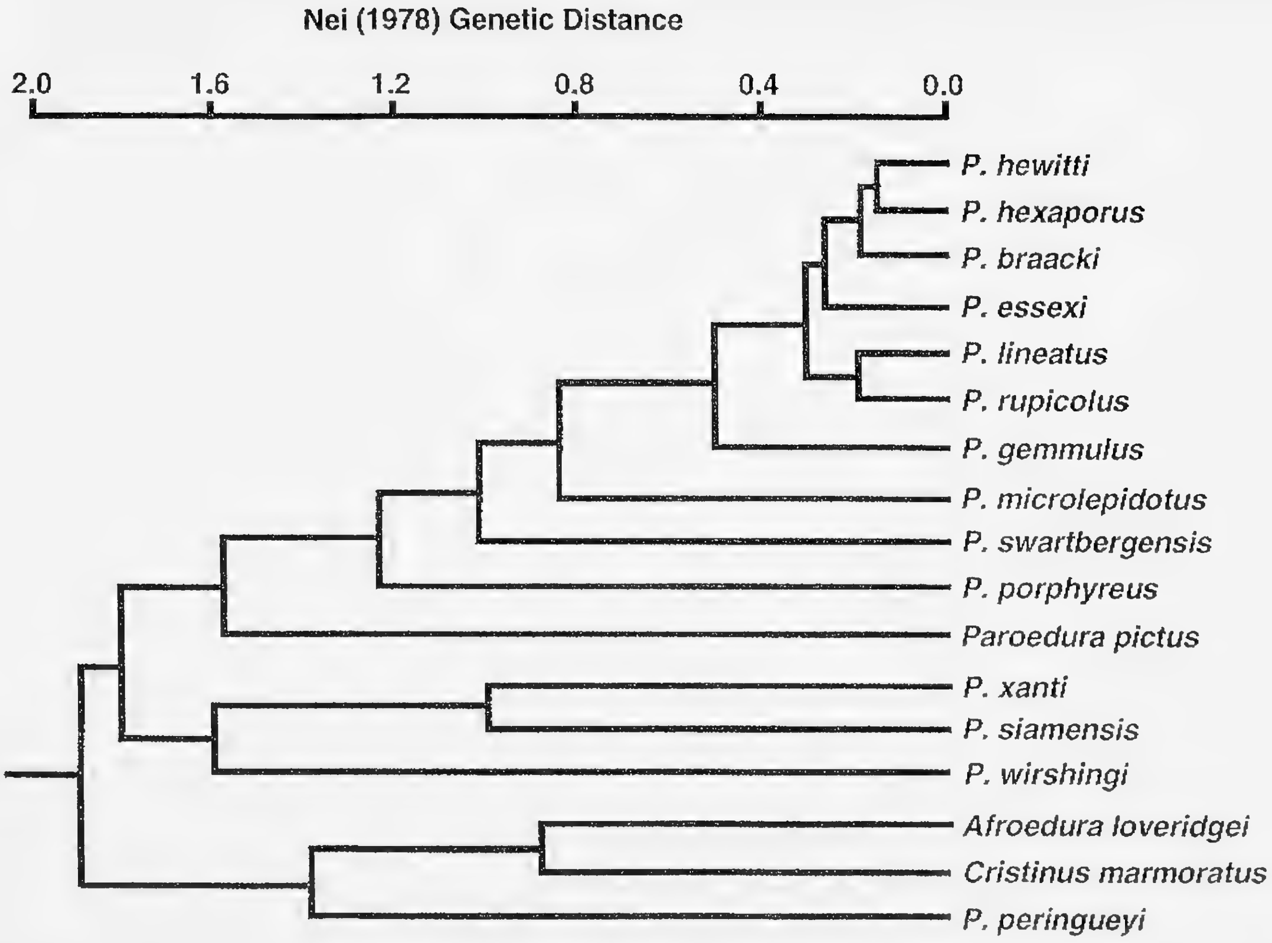


FIGURE 3. UPGMA phenogram illustrating Nei (1978) genetic distances among representative species of *Phyllodactylus* and other leaf-toed geckos. Note that only members of the *Phyllodactylus lineatus* complex of southern Africa cluster together closely, that *P. peringueyi*, also from southern Africa, is highly divergent from these forms, and that non-African *Phyllodactylus* do not cluster together.

therefore justifies the application of alternative (available or new) generic names.

Old World Leaf-toed Geckos

Asaccus Dixon and Anderson, 1973

The genus *Asaccus* was erected by Dixon and Anderson (1973) for two species of Middle Eastern leaf-toed geckos. The number of taxa now recognized is seven, distributed in eastern Arabia (Oman and the United Arab Emirates), Iraq, Iran, Syria and Turkey (Arnold and Gardner 1994; Rastegar-Pouyani 1996). This genus exhibits several derived features including a reduction in the phalangeal formula of the manus and pes to 2.3.4.4.3, a lack of preanal pores, loss of cloacal sacs and bones, and the loss of the left oviduct and associated reduction of clutch size to one (Arnold and Gardner 1994; Leptien 1994a, b, 1996). The reduction of phalangeal formula had been noted previously (Russell 1972). Arnold and Gardner (1994) reported that the reduced number of phalanges is a transient state in some species, and that three species eventually develop the normal phalangeal complement.

Urocotyledon Kluge, 1983

Kluge (1983) transferred the four species *inexpectata, wolterstorffi, palmata,* and *weileri* to the new genus *Urocotyledon.* The lack of the second ceratobranchial arch and possession of a well-formed scansorial pad on the ventral surface of the tail tip were used as apomorphic diagnostic characters for the genus. The insular species *U. inexpectata* occurs on the granitic Seychelles (Cheke 1984), whereas *U. wolterstorffi* is restricted to the eastern Usambara and Uluguru Mountains (Broadley and Howell 1991) and *U. weileri* and *U. palmata* occur in Cameroon and the adjacent Congo (Perret 1963).

Christinus Wells and Wellington, 1984

Australian "*Phyllodactylus*", including a complex of mainland forms involving several chromosome races (King 1981, 1987; King and Rofe 1976), were formally removed from *Phyllodactylus* by Wells and Wellington (1984) and placed in a new genus, *Christinus.* Wells and Wellington (1984) diagnosed *Christinus* on the basis of plesiomorphic or unpolarizable external features common to many leaf-toed geckos. Greer (1990) provided a preliminary diagnosis for *Christinus* that included osteological features, among them the unquestionably derived elevated number (27–28) of presacral vertebrae. We here present a more complete characterization and diagnosis of the genus.

TYPE SPECIES. — *Diplodactylus marmoratus* Gray, 1845, by original designation.

CONTENT. — *Christinus marmoratus* (Gray, 1845), *C. guentheri* (Boulenger, 1885). *Christinus marmoratus* contains several unnamed chromosomal races (King and Rofe 1976), which should be recognized at the species level (Bauer and Henle 1994).

CHARACTERIZATION AND DIAGNOSIS. — *Christinus* may be distinguished from all other gekkonids by the following combination of characteristics: digits bearing a single pair of enlarged ("leaf-toed") terminal scansors; dorsal scalation atuberculate; granules on snout slightly larger than those on body dorsum; rostral scale without median cleft; first supralabial enters nostril; enlarged chinshields and lateral gulars; margins of pupil crennelate in preserved specimens; preanal pores absent; series of 3–4 cloacal spurs present, better developed in males; subcaudal scales not transversely enlarged, tail without terminal scansorial pad; no sexual dichromatism; nasal bones fused; parietals paired; premaxilla with relatively rounded or pointed nasal projection of moderate length; frontal moderately broad, only slightly constricted over orbits, without maxillary contact; maxillary bone bearing approximately 30 teeth in adults; postfrontal bones with anterior and posterior projections subequal or with anterior longer than posterior, without pronounced lateral spine; stapes imperforate; coronoid bone strongly developed, raised well above the level of dentary tooth row; second ceratobranchial arch of hyoid present, inner proximal ceratohyal process present; neural arches of atlas paired or fused; 27–28 presacral vertebrae, 1 lumbar vertebra; 4 cervical ribs, 2–3 sternal ribs, 2–3 mesosternal ribs; one pair of clavicular fenestrae; interclavicle cruciform; union of scapula and precoracoid ray of epicoracoid cartilaginous; phalangeal formulae unreduced (2-3-4-5-3 manus, 2-3-4-5-4 pes); hypoischium bifurcate distally; cloacal sacs and a single pair of cloacal bones present. Clutch size variable (1–2 in

Christinus marmoratus, King 1977, How et al. 1987; 1–3 [mean of 1.3] in *C. guentheri*; Cogger et al. 1983).

Christinus may be diagnosed from all other leaf-toed geckos by the apomorphic increase in number (27–28) of presacral vertebrae (24–26 in all other taxa). In addition, the fusion of the nasals is a derived feature among gekkonids that distinguishes *Christinus* from all leaf-toed "ptyodactyline" forms except *Ebenavia,* the Socotran and some southern African *Phyllodactylus* and *P. brevipes. Christinus* differs from *Ebenavia, P. peringueyi* and *P. swartbergensis* in being atuberculate, and from the remaining forms in the presence of 4 (vs. 3) cervical ribs. The presence of cloacal sacs and bones further distinguishes it from the Socotran forms, whereas the absence of preanal pores and the imperforate condition of the stapes distinguishes it from *P. microlepidotus* and the *P. lineatus* complex, and the presence of more than two enlarged scales per cloacal spur and the presence of transverse projections on the interclavicle serve to diagnose it from the remaining southern African *Phyllodactylus.*

DISTRIBUTION. — *Christinus* occurs in temperate Australia from Shark Bay, Western Australia to northeastern New South Wales and in the Lord Howe and Norfolk Island groups in the Tasman Sea (Cogger 1992; Bauer and Henle 1994).

Paroedura Günther, 1879

Guibé (1956) reviewed the Madagascan leaf-toed geckos. The majority of the species he considered have since been removed to *Paroedura* by Dixon and Kroll (1974). Another species, *Phyllodactylus barbouri,* has been placed in the synonymy of *Diplodactylus granariensis,* an Australian species (Bauer and Henle 1994). Guibé also regarded *Phyllodactylus porphyreus* as occurring in Madagascar on the basis of his inclusion of Mocquard's (1900) *P. brevipes* in the synonymy of this species.

There are ten species in *Paroedura*, nine in Madagascar and one in the Comores. Relationships among the species remain unresolved (Nussbaum and Raxworthy 1994), but the monophyly of the group is well supported by a variety of osteological characters (Dixon and Kroll 1974; Nussbaum and Raxworthy 1994a) including: loss of the second ceratobranchial, paired atlas, imperforate stapes, cruciform interclavicle, 2–3 sternal ribs, 1–2 mesosternal ribs, and 3–4 cervical ribs.

"Phyllodactylus" brevipes Mocquard, 1900

Nussbaum and Raxworthy (pers. comm.) have rediscovered *Phyllodactylus brevipes* and conclude that it is very dissimilar from *P. Porphyreus* (contra Guibé 1956). A large series of this species is presently being studied (Nussbaum and Raxworthy, in prep.), but was unavailable to us during the preparation of the present manuscript. Dixon and Kroll (1974) regarded *P. brevipes* as being allied to its African congeners, but did not elaborate. Kluge and Nussbaum (1995), however, noted that *Phyllodactylus brevipes* "belongs to another part of the history of Gekkonini" relative to the southern African taxa of leaf-toed geckos.

Ebenavia Boettger, 1878

The generic separation of *Ebenavia* from *Phyllodactylus* was based on the absence of claws, enlarged chinshields, and enlarged midventral caudal scales in the former (Boettger 1878; Boulenger 1885). Most workers (e.g., Boettger 1878; Russell 1972) have regarded the two genera as closely allied. Bastinck (1981) further suggested that *Ebenavia* is derived from within *Phyllodactylus* but did not base this assumption on any repeatable analytical method. Dixon and Kluge (1964) provided some osteological data for this genus. These were confirmed by our observations except for the phalangeal formula of the pes, which was found to be unreduced (2-3-4-5-3 according to Dixon and Kluge 1964). Our observations differ considerably, however, from those of Wellborn (1933). Because the initial generic diagnosis was brief and published in Latin, we here provide an expanded redescription and diagnosis, incorporating both external and osteological features.

TYPE SPECIES. — *Ebenavia inunguis* Boettger, 1878, by monotypy.

CONTENT. — *Ebenavia inunguis* Boettger, 1878. An undescribed species is known from dry coastal habitats in Madagascar (R. A. Nussbaum, in litt. February, 1996).

CHARACTERIZATION AND DIAGNOSIS. — *Ebenavia* may be distinguished from all other gekkonids by the following combination of characteristics: digits bearing a single pair of enlarged ("leaf-toed") terminal scansors; dorsal scalation tuberculate, tubercles very high relative to width of base, keeled or mucronate; granules on snout mucronate, larger than those on dorsum of body; rostral scale without median cleft; first supralabial excluded from nostril; no enlarged chinshields; margins of pupil crennelate in preserved specimens; preanal pores absent; 1–2 enlarged scales on each cloacal spur, much more well developed in males; subcaudal scales not transversely enlarged, tail without terminal scansorial pad; no sexual dichromatism; nasal bones fused; parietals paired; premaxilla with moderately long, triangular nasal projection; frontal relatively thin, only slightly constricted over orbits, without maxillary contact; total number of maxillary tooth positions (unilateral) in adults greater than 40; postfrontal bones with posterior projection much thicker than anterior, without pronounced lateral spine; stapes imperforate; coronoid bone weakly developed, only slightly raised above the level of dentary tooth row; second ceratobranchial arch of hyoid present; neural arches of atlas fused; 26 presacral vertebrae, 1 lumbar vertebra; 3 cervical ribs, 2 sternal ribs, 2 mesosternal ribs; 1 pair of clavicular fenestrae; interclavicle cruciform; union of scapula and precoracoid ray of epicoracoid cartilaginous; phalangeal formulae unreduced (2-3-4-5-3 manus, 2-3-4-5-4 pes), some or all digits clawless; hypoischium not bifurcate; cloacal sacs and a single pair of cloacal bones present; clutch size usually two (Angel 1942; pers. observ.; but see Henkel and Schmidt 1991, 1995).

Ebenavia exhibits at least three derived diagnostic features relative to other leaf-toed geckos: the presence of amphicoelous vertebrae, a primitive condition for gekkonoids (Kluge 1967, 1987), but one that is most parsimoniously regarded as derived in gekkonids, the absence of claws on all digits (at least in males), and the very large number of marginal teeth (Bauer 1990; Kluge and Nussbaum 1995). Further, some of the dorsal tubercles in this genus are mucronate or multicarinate rather than simply keeled, and the snout granules are also mucronate. These conditions are not found in other tuberculate leaf-toed geckos. In addition to these features, *Ebenavia* may be distinguished from the superficially similar *Phyllodactylus peringueyi* by its lack of sexual dichromatism, presence of one versus two pairs of cloacal bones, 26 versus 24 presacral vertebrae, crennelate versus straight-edged pupil margins, and presence of transverse projections of the interclavicle. In all of these features, however, *Ebenavia* exhibits the apparently plesiomorphic conditions, and *P. peringueyi* the apomorphic ones. A more complete diagnosis and description of this genus will appear shortly (R. A. Nussbaum and C. Raxworthy, pers. comm.).

DISTRIBUTION. — The single described species of this genus occurs in Madagascar, the Comores, and Mauritius (Blanc 1971). It has also been reported from Pemba Island, off the coast of Tanzania (Loveridge 1957), although the validity of these records requires verification (Broadley and Howell 1991).

REMARKS. — Although *Ebenavia* possesses several uniquely derived characteristics among leaf-toed geckos (see diagnosis), its superficial similarity to *P. peringueyi* from littoral areas of the Eastern Cape, South Africa is striking (Branch and Bauer 1994). *Ebenavia inunguis* has been found in the littoral zone, as well as in forests at moderate to high elevation (Angel 1942; Raxworthy 1988; Andreone 1991). Certain aspects of the overall morphology of these forms is also reminiscent of some of the Peruvian species of *Phyllodactylus* that inhabit the arid littoral regions of the west coast (Huey 1979; Carillo de Espinoza et al. 1990). Such similarities appear to represent convergence towards activity on sand, soil or vegetation (as opposed to rock), rather than a real phylogenetic signal.

ADDITIONAL MONOPHYLETIC GROUPS OF LEAF-TOED GECKOS

The removal of *Asaccus, Paroedura, Urocotyledon,* and *Christinus* from *Phyllodactylus* leaves 18 recognized species of Old World *Phyllodactylus.* As indicated by earlier workers (e.g., Dixon 1964; Russell 1972; Kluge 1983) and suggested by the genetic distance data presented herein, there seems to be no support for the retention of these taxa within *Phyllodactylus.* As the type species of the genus, *P. pulcher,* is from Barbados, the name clearly is applicable to some or all of the New World species and new or resurrected names may be applied to diagnosable units of *"Phyllodactylus"* from the Old World. Three currently unused generic names have been proposed for leaf-toed geckos (Wermuth 1965; Kluge 1993, 1996). However, two of these, *Discodactylus* and *Gerrhopygus* are applicable to New World taxa and one of them (*Discodactylus* Fitzinger 1843) is preoccupied. The remaining available name, *Euleptes* Fitzinger 1843 has as its type species by original designation *Euleptes wagleri* Fitzinger 1843 (= *Phyllodactylus europaeus* Gené 1838). This name is therefore available for the Mediterranean species of leaf-toed gecko and is resurrected below.

Mediterranean Leaf-toed Geckos

Fitzinger's (1843) description of *Euleptes,* like those of many of the names proposed in *Systema Reptilium,* is brief and totally inadequate. We here provide a redescription and diagnosis of this monotypic genus.

Euleptes Fitzinger, 1843

TYPE SPECIES. — *Euleptes wagleri* Fitzinger, 1843 (= *Phyllodactylus europaeus* Gené, 1838), by original designation.

CONTENT. — *Euleptes europaea* (Gené, 1838).

CHARACTERIZATION AND DIAGNOSIS. — *Euleptes* may be distinguished from all other gekkonids by the following combination of characteristics: digits bearing a single pair of enlarged ("leaf-toed") terminal scansors; dorsal scalation atuberculate; granules on snout not larger than those on dorsum of body; no rostral crease or division; first supralabial enters nostril; no enlarged chinshields; a single large cloacal spur on each side of vent, especially well-developed in males; preanal pores absent; subcaudal scales not transversely enlarged, tail prehensile, but without well-developed terminal scansorial pad; margins of pupils crennelate in preserved specimens; no sexual dichromatism; nasal bones paired; parietals paired; premaxilla with relatively short, triangular nasal projection; frontal moderately broad, strongly constricted over orbits, without maxillary contact; approximately 25 maxillary tooth positions (unilateral) in adults; postfrontal bones with subequal anterior and posterior projections, or with thicker anterior projection, without pronounced lateral spine; stapes perforate; coronoid bone weakly developed, barely raised above the level of dentary tooth row; second ceratobranchial arch of hyoid present, inner proximal ceratohyal process lacking, medial projection of hyoid cornu much reduced; neural arches of atlas fused, at least in adults; 26 presacral vertebrae, 2 lumbar vertebrae; 3 cervical ribs, 2 sternal ribs, 2 mesosternal ribs; 0–1 pair of clavicular fenestrae, clavicles not strongly dilated; interclavicle dagger-shaped, with small transverse processes; union of scapula and precoracoid ray of epicoracoid cartilaginous; phalangeal formulae unreduced (2-3-4-5-3 manus, 2-3-4-5-4 pes); cloacal sacs and bones present, a second, irregular (second) set of cloacal bones is associated with the cloacal spur in males; clutch size two (Fretey 1975; Rieppel and Schneider 1981), or less frequently one (Wiedersheim 1876; Klingelhöffer 1957).

Euleptes may be distinguished from all other leaf-toed geckos except *Asaccus* and New World and southeast Asian *Phyllodactylus* by its perforate stapes. It may be differentiated from all of these by the absence of tubercular scales and the fusion of the atlantal arches. The presence of a second pair of cloacal ossifications, first noted by Wiedersheim (1876), is a derived condition appearing elsewhere among leaf-toed geckos only in *P. peringueyi* (Branch and Bauer 1994), in which it is variable, and in some *Paroedura* (contra Nussbaum and Raxworthy 1994). The prehensile tail of *Euleptes* has long been recognized (Fitzinger 1843; Wiedersheim 1876) and its superficial morphology has been investigated in some detail (van Eijsden 1983). *Urocotyledon* also has a prehensile tail, but Kluge (1983) considered the presence of a well-demarcated scansorial pad as synapomorphic for that genus only.

ETYMOLOGY. — From the Greek *eu-* (true or very) and *leptos* (small, thin, or delicate), apparently in reference to the overall shape and size of the type species, although this was not made explicit by Fitzinger (1843). The generic name is feminine.

DISTRIBUTION. — The single species of this genus occurs at several insular and near-coastal sites from the Gulf of Marseille in the west to coastal Tuscany in the east. It also occurs on Corsica and Sardinia and their satellite islands and on Cani Island and the Galite Archipelago just off the north coast of Tunisia (Fig. 1; Bruno 1980; Delaugerre and Dubois 1985).

REMARKS. — Although various aspects of population variation and distribution within the Mediterranean region have been discussed (e.g., Bruno 1980; Delaugerre and Dubois 1985; Delaugerre and Cheylan 1992), there have been no interpretations of the relationship of this form to other leaf-toed geckos.

Socotran Leaf-toed Geckos

The geographic isolation of the two Socotran *Phyllodactylus* from other members of the genus and their shared absence of cloacal sacs and bones has resulted in the general supposition that these two species are sister taxa, despite the fact that they differ from one another in size and in a number of obvious external characteristics. An analysis of both osteological and external characteristics supports the unity of the Socotran leaf-toed geckos and demonstrates that they can be separated from all other *"Phyllodactylus"* on the basis of apomorphic features. Consequently *Phllodactylus riebeckii* and *P. trachyrhinus* are here removed from *Phyllodactylus* to a new genus.

Haemodracon, new genus

TYPE SPECIES. — *Diplodactylus riebeckii* Peters, 1882.

CONTENT. — *Haemodracon riebeckii* (Peters, 1882), *H. trachyrhinus* (Boulenger, 1899).

CHARACTERIZATION AND DIAGNOSIS. — *Haemodracon* may be distinguished from all other gekkonids by the following combination of characteristics: digits bearing a single pair of enlarged ("leaf-toed") terminal scansors; dorsal scalation atuberculate; scales on snout smaller than those on dorsum of body (enlarged co-ossified snout scales present in *H. trachyrhinus*); enlarged chinshields present; rostral entire or completely divided; first supralabial enters nostril; margins of pupil crennelate in preserved specimens; preanal pores absent; subcaudal scales not transversely enlarged, tail without terminal scansorial pad; no sexual dichromatism; nasal bones fused; parietals paired; premaxilla with short triangular nasal projection; frontal broad, not strongly constricted over orbits, with extensive maxillary contact; 25–30 maxillary tooth loci in adults; postfrontal bones with longer posterior than anterior projection, without pronounced lateral spine; stapes imperforate; coronoid bone raised well above the level of dentary tooth row; second ceratobranchial arch of hyoid present; neural arches of atlas paired; 26 presacral vertebrae, 1 lumbar vertebra; 3 cervical ribs, 3 sternal ribs, 1–2 mesosternal ribs; 1 pair of clavicular fenestrae; interclavicle cruciform; union of scapula and precoracoid ray of epicoracoid cartilaginous; phalangeal formulae unreduced (2-3-4-5-3 manus, 2-3-4-5-4 pes); cloacal sacs and bones absent.

The absence of cloacal sacs and bones is a derived character state (Kluge 1967, 1982, 1987, 1995; Kluge and Nussbaum 1995) unique to *Haemodracon* among leaf-toed geckos, except for members of the genus *Asaccus* (Dixon and Anderson 1973; Arnold and Gardner 1994). *Haemodracon* is distinguished from the six species in the latter genus by the retention of the plesiomorphic states with respect to phalangeal formula of the manus (reduced to 2.3.4.4.3 in all *Asaccus,* at least during some stage in ontogeny), and presence of two oviducts (left oviduct lacking in *Asaccus*) (Arnold and Gardner 1994). The fused nasals of *Haemodracon* represent a derived condition shared with *Paroedura, Christinus,* some *Urocotyledon,* and some African *Phyllodactylus. Haemodracon* also differs from *Asaccus* in being atuberculate and in possessing an imperforate stapes.

ETYMOLOGY. — From the Latinized Greek *haema-* (blood) and *dracon* (dragon) signifying dragon's blood, in reference to the fact that members of this genus are endemic to the island of Socotra, known for an agave, *Dracaena cinnabari,* that produces a deep red resin referred to as dragon's blood. Socotra itself is sometimes called the "Island of the Dragon's Blood" (Botting 1958). The International Code of Zoological Nomenclature (Appendix D, VI.29) recommends that in generic names formed from compound Greek nouns the attribute in such a name (in this case "dragon" [draco] – the type of blood) should precede the substantive. However, since the resulting name is not particularly euphonious, we have chosen to reverse the order of the nouns. *Haemodracon* is masculine.

DISTRIBUTION. — The two species of this genus are confined to Socotra Island (Republic of Yemen), in the Gulf of Aden (Fig. 2).

Southeast Asian Leaf-toed Geckos

Taylor (1962), in describing *Phyllodactylus melanostictus,* compared it to *P. siamensis,* the only other east Asian leaf-toed gecko, but made no claims regarding its affinities to this or other leaf-toed geckos. Although clearly specifically distinct, these two taxa share a large number of traits, some apomorphic, that are rare or unique among leaf-toed gekkonids. As there is no evidence for the monophyly of a unit including both these forms and the New World leaf-toed geckos to which the name *Phyllodactylus* is correctly applied, the southeast Asian taxa are here removed from *Phyllodactylus* and described and diagnosed as a new genus.

Dixonius, new genus

TYPE SPECIES. — *Phyllodactylus siamensis* Boulenger, 1898.

CONTENT. — *Dixonius siamensis* (Boulenger, 1898), *D. melanostictus* (Taylor, 1962).

CHARACTERIZATION AND DIAGNOSIS. — *Dixonius* may be distinguished from all other gekkonids by the following combination of characteristics: digits bearing a single pair of enlarged ("leaf-toed") terminal scansors; dorsal scalation tuberculate, tubercles keeled longitudinally; granules on snout larger than those on dorsum of body; rostral scale with median cleft; first supralabial enters nostril; enlarged chinshields and lateral gulars; margins of pupil crennelate in preserved specimens; preanal pores present; series of three to seven cloacal spurs present, better developed in males; midventral row of transversely enlarged caudal scales, tail without terminal scansorial pad; no sexual dichromatism; nasal bones paired; parietals paired with a dorsomedial extension forming a prominent posteriorly-directed triangle; premaxilla with moderately long, lanceolate nasal projection; frontal moderately broad, only slightly constricted over orbits, with extensive maxillary contact; approximately 35 maxillary tooth positions in adults; postfrontal bones with posterior projection much thicker than anterior, without pronounced lateral spine; stapes perforate; coronoid bone weakly developed, barely raised above the level of dentary tooth row; second ceratobranchial arch of hyoid present, inner proximal ceratohyal process lacking, but ceratohyal inflated in the region where this structure typically appears, medial process of hyoid cornu elongate; neural arches of atlas paired; 26 presacral vertebrae, 1 lumbar vertebra; 3 cervical ribs, 3 sternal ribs, 1–2 mesosternal ribs; 1 pair of clavicular fenestrae; interclavicle cruciform; union of scapula and precoracoid ray of epicoracoid cartilaginous; phalangeal formulae unreduced (2-3-4-5-3 manus, 2-3-4-5-4 pes), but with phalanx 2 of digit IV of manus greatly reduced in length; ossifications present in the extensor tendons of digits II–V of manus and pes; hypoischium bifurcate proximally; cloacal sacs and a single pair of cloacal bones present.

The presence of preanal pores in this genus distinguishes it from all other leaf-toed geckos except the African *Phyllodactylus lineatus* complex. The tuberculate dorsum of *Dixonius* distinguishes it from *Christinus, Euleptes, Haemodracon, "Phyllodactylus" brevipes,* and all African *Phyllodactylus* except *P. swartbergensis* and *P. peringueyi,* which lack preanal pores. The reduction in length of phalanx 2 of digit IV of the manus, and the proximally bifurcate hypoischium are derived features that also serve to diagnose this genus from all other leaf-toed geckos.

ETYMOLOGY. — A patronym in honor of James R. Dixon of Texas A & M University, a long time student of the genus *Phyllodactylus* (*sensu lato*), a scholar, and a gentleman. Dr. Dixon has long expressed the belief that Old World *Phyllodactylus* were generically distinct from the New World taxa to which the name is correctly applied. The generic name is masculine.

DISTRIBUTION. — The two species of this genus occur in southeast Asia (Fig. 2). Although initially described from Thailand (Taylor 1963), both species have been recorded from elsewhere in the region. Both have been documented from southern Vietnam (Bobrov 1992, 1993, 1995), suggesting that their distribution also includes Cambodia (Kampuchea) and perhaps southern Laos. To the west, *D. siamensis* extends into Burma (Annandale 1905; Taylor 1963).

REMARKS. — Dixon (1964) erroneously stated that the Asian forms exhibited reduction in phalangeal formula of digit four of the manus. However, the second phalanx of this digit is extremely short, and the third is moderately so (Russell 1972). Russell (1972) considered that this condition might be a forerunner of the phalangeal loss seen in *Asaccus*. Kluge and Nussbaum (1995) incorrectly indicated that a derived condition of fewer than five phalanges in digit IV of the manus occurs in *Dixonius* and possibly *Haemodracon.*

Southern African Leaf-toed Geckos

The remaining Old World "*Phyllodactylus*" are native to southern Africa. Unlike the other geckos removed from *Phyllodactylus,* this group is both relatively speciose and highly morphologically diverse. Although no demonstration of the monophyly of this group has ever been put forward, it has been included as an operational unit in two phylogenetic analyses of African gekkonids (Bauer 1990; Kluge and Nussbaum 1995). Recent descriptions and resurrections of taxa have brought the number of recognized taxa to 12, including seven representatives of the *Phyllodactylus lineatus* complex, a group of small, morphologically similar geckos distributed through much of South Africa's Cape Provinces (Branch et al. 1995; Bauer et al. 1996; Good et al. 1996).

In order to evaluate the possible monophyly of the southern African *"Phyllodactylus,"* the characters used in diagnosing other leaf-toed genera were evaluated for all southern African taxa. Information for certain characters was lacking for *Phyllodactylus ansorgii,* for which the only osteological data are derived from radiographs of the two females types, and for Haacke's (1996) undescribed Angolan species, known to us only through his published partial data set.

Dorsal scalation. Among African *Phyllodactylus,* tubercles are present only in *P. swartbergensis* and *P. peringueyi.* Unlike all other leaf-toed geckos, the tubercles of the former are smooth and flattened. Those in the latter species are strongly keeled. We regard the smooth tubercles as autapomorphic for *P. swartbergensis* and thus of no phylogenetic value. The tubercles of *P. peringueyi* are similar to those seen in most tuberculate leaf-toed geckos. Dixon (1964) reported that dorsal tubercles are present in all New World *Phyllodactylus* except *P. unctus, P. leei,* and *P. gerrhopygus* and regarded this condition as derived within the New World taxa. However, the condition is variable among the gekkonids in general and cannot be assigned polarity at the hierarchical level under consideration here.

Rostral cleft. A dorsal rostral cleft is present in *P. microlepidotus, P. lineatus, P. braacki, P. gemmulus, P. hewitti, P. hexaporus, P. essexi,* and *P. rupicolus* and absent from the remaining taxa. Rostral creases occur in *Dixonius,* and *Haemodracon trachyrhinus.*

Nostril. The first supralabial is excluded from the nostril in *P. peringueyi, P. porphyreus,* and *P. swartbergensis* and enters the nostril in all other southern African species. Supralabial contact with the rim of the nostril is the most common condition among other leaf-toed geckos. It is excluded only in *Ebenavia, Urocotyledon,* and some New World *Phyllodactylus.*

Chinshields. Enlarged chinshields are absent in *P. peringueyi, P. ansorgii, P. porphyreus,* and *P. microlepidotus.* In *P. swartbergensis* the enlarged scales cover all of the anterior throat. In *P. gemmulus* there is a single enlarged scale posterior to the mental and in all remaining species there is a pair of enlarged scales behind the mental. The presence of enlarged chinshields in other leaf-toed geckos is variable, occurring in all groups except *Ebenavia, Euleptes,* and *Urocotyledon.*

Pupil. The shape of the margin of the pupil has long been debated as a character in systematic analyses (e.g., Underwood 1951, 1954; Cogger 1964; Kluge 1967; Bauer 1986). All leaf-toed geckos examined, except *P. peringueyi,* have a crennelated edge to the pupil in preserved specimens. This is also evident in living animals exposed to bright light. In *P. peringueyi,* however, the pupil margin is straight-edged (Branch and Bauer 1994; Haacke 1996) both in life and in preserved specimens. The latter condition would appear to represent a derived state for *P. peringueyi.*

Preanal pores. The African *Phyllodactylus* are the only geographic unit of leaf-toed geckos in which preanal pores are variably present. All other leaf-toed genera except *Dixonius* lack pores (Bastinck 1981; Kluge and Nussbaum 1995). Although some authors (e.g., Maderson and Chiu 1970) have considered the presence or absence of preanal glands and pores of little phylogenetic value, this is clearly dependent upon the hierarchical level being considered. On the basis of a composite leaf-toed outgroup, the presence of pores may be regarded as derived. However, using the broad African gekkonid outgroup of Kluge and Nussbaum (1995) the loss of pores is apomorphic. Pores are also absent in *Ptyodactylus* and *Uroplatus,* the "fan-toed" members of Russell's (1972) *Phyllodactylus* group.

Cloacal spurs. The cloacal spurs of all members of the *P. lineatus* complex, as well as *P. microlepidotus,* have 3–6 spinous scales in males, with 2–3 considerably smaller scales in females. In *P. peringueyi* there are two isolated spines on each spur, these being slightly larger in males. In both *P. porphyreus* and *P. swartbergensis* males possess a single enlarged, rounded scale on the spur. This is only slightly larger in males than in females and may be the same size in both sexes in the former species. *Euleptes europaea* males also have a single cloacal spur.

Sexual dichromatism. Sexual dichromatism is rare among nocturnal lizards, and is unique among African leaf-toed geckos in *P. peringueyi.* In this species females are primarily unicolored, whereas males are characterized by a lighter dorsal stripe (Branch and Bauer 1994). Dichromatism of the tail has been reported for some *Asaccus* (Arnold and Gardner 1994), but is a rare and derived condition within the Gekkonidae as a whole.

Color pattern variation in *P. porphyreus* may be extreme. Although most specimens are marbled or vaguely banded above, a vertebral stripe is sometimes present (Fig. 8a). FitzSimons (1957) noted a pale vertebral streak in a specimen from Hout Bay. This color morph is now known to be a common in many populations and we have examined specimens from Knysna and Port Elizabeth with bold white stripes. It is not related to sex.

Premaxilla. The nasal process of the premaxilla is short and rounded in *P. peringueyi, P. porphyreus,* and *P. swartbergensis.* In all other African *Phyllodactylus* it is moderately long and lanceolate in shape. The condition of this character could not be evaluated in *P. ansorgii.* Our observations are consistent with those of Haacke (1996), who also reported that the elongate, lanceolate process was present in the undescribed Angolan species. Short, rounded or somewhat pointed nasal processes are found in *Urocotyledon* and *Haemodracon.* A somewhat intermediate character state is present in *Christinus.*

Nasals. The nasals are primitively paired in gekkonids (Kluge 1967, 1987) with the azygous condition occurring only in *Afroedura, Ailuronyx, Cnemaspis* (part), *Ebenavia, Hemiphyllodactylus, Homopholis* (part), *Lepidodactylus, Lygodactylus, Microgecko, Nactus, Paroedura, Perochirus, Phelsuma, Pseudogekko, Uroplatus,* and some Old World *Phyllodactylus,* according to Kluge (1987). The azygous condition apparently also occurs in at least some *Urocotyledon* (J. R. Dixon, in litt., 1993). We found fused nasals in *Haemodracon* and *Christinus,* also in some African *Phyllodactylus.* The azygous condition occurs in *P. peringueyi, P. porphyreus,* and *P. swartbergensis,* and we tentatively record it as such in *P. ansorgii* as well, although this is not certain based on the radiographs available to us. Haacke (1996) recorded the fused condition in one of two individuals of *P. microlepidotus* he examined and in only one of six *P. porphyreus,* as well as in a single specimen of an undescribed Angolan species of leaf-toed gecko. Given our larger sample size for osteological observations we retain our assessment of character state distribution.

Although he rejected this character's utility at higher levels, Kluge (1987) suggested that it might be informative with respect to intergeneric relationships. Both Bauer (1990) and Kluge and Nussbaum (1995) interpreted the azygous condition as derived for African gekkonids.

Fronto-maxillary contact. The frontal is excluded from the maxillary bone by the prefrontal in *P. swartbergensis* and is excluded or meets at a single point in *P. porphyreus.* The remaining species exhibit extensive contact. The condition in *P. ansorgii* could not be evaluated. There is generally no contact in *Christinus, Euleptes* or *Ebenavia,* but other leaf-toed geckos exhibit extensive contact.

Postfrontal. Postfrontal shape varies considerably among leaf-toed geckos. In all African species the anterior and posterior projections of the postfrontal are subequal in length and width. This is in contrast to the conditions seen in New World *Phyllodactylus* and *Dixonius*, in which the posterior projection is much inflated and often somewhat longer than the anterior, and the condition seen in *Ebenavia* and *Christinus*, in which the anterior projection is larger. *Phyllodactylus peringueyi* is unique among African species in possessing a laterally projecting "spine" at the angle of the postfrontal. The entire bone, while still symmetrical, is often reduced to a thin crescent in the *P. lineatus* species complex.

Parietal. Kluge (1987) regarded the paired state of the parietals seen in most gekkonids as derived for gekkonoids. Thus the presence of the azygous condition within the Gekkonidae is a secondary derivation and apomorphic at this level. Among species of African *Phyllodactylus* the partial fusion of the parietals is autapomorphic for *P. swartbergensis.* Haacke (1996) noted difficulty in determining the condition of this character in this species. His observation of a single parietal or even a fused fronto-parietal plate in juveniles of other species is not supported by any of our observations and if correct would appear to suggest a unique pattern of skull development in these forms.

Stapedial foramen. Kluge (1987) reported the imperforate condition in *Ailuronyx, Cnemaspis, Ebenavia, Geckonia, Gehyra, Gekko, Hemiphyllodactylus, Homonota, Lepidodactylus, Perochirus, Ptenopus, Ptychozoon, Ptyodactylus, Thecadactylus, Urocotyledon, Uroplatus* and the perforate condition in *Afroedura, Aristelliger, Bunopus, Calodactylodes, Chondrodactylus, Cosymbotus, Cyrtopodion, Geckolepis, Gonydactylus, Hemidactylus, Heteronotia, Homopholis, Lygodactylus, Pachydactylus, Palmatogecko, Phelsuma, Pristurus, Quedenfeldtia, Rhoptropus, Saurodactylus, Stenodactylus, Tarentola, Teratoscincus,* and *Tropiocolotes.* Only in *Phyllodactylus* did he record both conditions as occurring.

Although the presence of a stapedial foramen is a derived feature at the level of the Squamata (Underwood 1971; Greer 1976), Bauer (1990) and Kluge and Nussbaum (1995) regarded the imperforate condition as derived within the southern African gekkonines. The stapes is imperforate in *P. peringueyi, P. swartbergensis,* and *P. porphyreus.* According to Haacke (1996) the stapes is also imperforate in the undescribed Angolan species. We were unable to score the condition of this character in *P. ansorgii,* and despite Kluge and Nussbaum's claim that the stapedial foramen is present in this species, we treat the condition as unknown. All remaining African *Phyllodactylus* have a stapedial foramen.

Hyoid. All of the southern African leaf-toed geckos retain the second ceratobranchial arch and thus exhibit the "ptyodactyline" condition (Kluge 1983). Joger (1985) criticized Kluge's tribal division based on variation in this character and proposed a hypothesis of relationship among Afro-Malagasy gekkonids that conflicted with Kluge's tribal assignments, but did not include any *"Phyllodactylus"* among his taxa. Bauer (1990) likewise criticized the accordance of special weight to the ceratobranchial character, but incorporated it into a broader data set. Kluge and Nussbaum (1995) themselves demonstrated that in light of a more complete data set the ceratobranchial arch character must have involved several independent evolutionary events. Thus the Gekkonini and Ptyodactylini previously hypothesized cannot be accepted as proven evolutionary entities.

The African species vary, however, with respect to the presence of the inner proximal ceratohyal process and the development of the medial process of the hyoid cornu. In *P. porphyreus, P. swartbergensis,* and *P. peringueyi* the former is present and the latter is elongate; in the remaining species the former is absent and the medial process of the hyoid cornu is only weakly to moderately developed. The condition in *P. ansorgii* could not be determined on the basis of available material. Prominent development of both processes is also typical of New World *Phyllodactylus* and *Christinus,* whereas both are poorly developed in *Euleptes.* In *Dixonius* the inner proximal ceratohyal process is lacking, but the associated region of the ceratohyal shaft is inflated, whereas in *Paroedura* this process is well-formed, but the hyoid cornu possesses only a short medial process. As noted by Fürbringer (1922) and Wellborn (1933), many attributes of the hyoid are intragenerically, or even intraspecifically variable. Nonetheless these features appear to be relatively stable in the taxa considered here.

Atlas. Bauer (1990) and Kluge and Nussbaum (1995) considered the paired condition of the atlas to be primitive among padded African gekkonids. Among African species of *Phyllodactylus* this state characterizes *P. ansorgii* (*fide* Kluge and Nussbaum 1995), *P. swartbergensis,* and *P. microlepidotus.* Some individuals of the *P. lineatus* species group also exhibit the paired condition, although the atlantal arches are generally fused in adults. Among other leaf-toed geckos, the derived condition is present in *Ebenavia, Urocotyledon, Euleptes, and Christinus* (may be variable in this genus). Haacke (1996) reported fused atlantal arches in *P. swartbergensis,* one *P. porphyreus,* one *P. lineatus,* and in the single specimen of an undescribed species from Angola. As this character is unambiguously scorable on cleared and stained material, we here ignore Haacke's observations in favor of our own based on larger samples.

Presacral vertebrae. The number of presacral vertebrae varies from 23 to 29 among fully-limbed gekkonoids (Wellborn 1933; Hoffstetter and Gasc 1969), although the majority of taxa possess 26. This would appear to be the primitive condition for gekkonids. *Phyllodactylus peringueyi* possesses 24 presacral vertebrae (Branch and Bauer 1994). All other species of African *Phyllodactylus* examined possess the primitive condition of 26 presacral vertebrae, except of 1 of 56 *P. lineatus* (25) and 4 of 39 *P. porphyreus* (1–25, 3–27). These exceptions are not regarded as phylogenetically significant. Haacke (1996) recorded 25 presacral vertebrae in an undescribed Angolan species. An elevated number of presacrals (27–28) is seen in *Christinus,* but all other leaf toed geckos have 26 presacrals, as do most African gekkonids in general.

The number of lumbar vertebrae is highly variable among the African species. One was recorded in *P. peringueyi, P. ansorgii, P. swartbergensis, P. microlepidotus* and some *P. porphyreus.* Two were recorded in the majority of *P. porphyreus* and all of the *P. lineatus* group geckos except *P. gemmulus,* which has three lumbars. Wellborn (1933) recorded a single lumbar as the most common condition among gekkonoids.

Ribs. The number of sternal vs. mesosternal ribs varies among African leaf-toed geckos. The most commonly encountered state in *P. ansorgii* and *P. porphyreus* is two sternal and two mesosternal ribs. Haacke (1996) reported the same condition in *P. swartbergensis* and an undescribed Angolan species. We also observed specimens of the former with one and two, and two and one sternal and mesosternal ribs, respectively. The *P. peringueyi* examined have two sternal and either one or two mesosternal ribs. In *P. microlepidotus* the most common condition was three sternal and two mesosternal ribs. All remaining species had either two sternal and two mesosternal or three sternal and two mesosternal ribs, with variation due primarily to the length of the mesosternal extension. The conditions are highly variable among extralimital leaf-toed taxa. Kluge and Nussbaum (1995) considered the primitive condition for African gekkonids to be 5–6 pairs of attached sternal and xiphisternal (= mesosternal) ribs, with reductions to totals of four and three pairs representing successive derived reductions.

Cervical rib number among most gekkonids, and most leaf-toed geckos is three. This number characterizes *P. porphyreus, P. swartbergensis, P. microlepidotus* and some specimens of the *P. lineatus* species group. Other individuals have four cervical ribs, a condition also seen in *Christinus,* some *Urocotyledon,* and some *Paroedura.* In *P. peringueyi* there are typically only two well-developed cervical ribs. An asymmetrical third rib was found anterior to the other two in a single specimen.

Clavicle. The shape of the clavicle and the presence of clavicular fenstrae is variable among African *Phyllodactylus.* As in most other leaf-toed geckos there is usually a single large fenestra occupying much of the dilated portion of each clavicle. However, at least some *P. porphyreus, P. swartbergensis,* and *P. lineatus* lack the fenestra entirely, although the clavicle is clearly very thin in the region where the fenestra would typically occur. In *P. swartbergensis* and, to a lesser extent, *P. porphyreus* the clavicle itself is not as strongly dilated as in other species. Among other leaf-toed geckos, fenestrae are sometimes absent in *Euleptes europaea,* which also exhibits relatively weak dilation of the clavicle. Two pairs of clavicular fenestrae, or bilateral asymmetry (two fenestrae on one side, one on the other) were observed in a small number of *P. peringueyi* and

P. porphyreus, and in some species of *Paroedura* and New World *Phyllodactylus.* Kluge (1995) considered one or more fenestrae to be primitive for sphaerodactyls, with the absence of fenestrae representing an apomorphic condition.

Interclavicle. Kluge and Nussbaum (1995) evaluated variation in interclavicle shape among African gekkonids and divided it into two character states, based on the retention (primitive) or reduction (derived) of lateral arms. According to them, *Euleptes* is intermediate and among African *Phyllodactylus* species *lineatus* shows the primitive condition and *porphyreus* the derived. While noting variability in the African *"Phyllodactylus"* they scored the genus as a whole as derived for the character. Within African species, a cruciform interclavicle with well-developed lateral processes is present in *P. microlepidotus* and all members of the *P. lineatus* group. The interclavicles of *P. peringueyi* and *P. swartbergensis* are without lateral projections, whereas that of *P. porphyreus* is somewhat intermediate. We agree with Kluge and Nussbaum, however, in scoring the splintlike condition in this species as derived. Radiographs suggest that the condition in *P. ansorgii* approximates that of *P. porphyreus* and Haacke (1996) indicated that an undescribed Angolan species has a similar structure.

Scapular-precoracoid connection. The nature of the union of these two pectoral elements was generally determined on the basis of Alcian blue stain uptake in cleared-and-stained specimens but could be inferred from radiographs based on the presence or absence of a tissue "shadow" (indicating cartilage) at the junction of the scapula and precoracoid. *Phyllodactylus microlepidotus* and all members of the *P. lineatus* group possess a ligamentous connection between these elements, whereas a cartilaginous connection is found in *P. peringueyi, P. swartbergensis* and *P. porphyreus.* The condition in *P. ansorgii* could not be determined on the basis of the radiographs of the types. Among other leaf-toed gekkonids a ligamentous connection is found only in *Asaccus* and New World *Phyllodactylus.* The condition is variable among potential African outgroup taxa.

Extraphalangeal digital ossifications. Russell and Bauer (1988) recorded paraphalanges as present only in *Uroplatus* among members of the *Phyllodactylus* group of Russell (1972). Among other African genera they were recorded in *Homopholis, Lygodactylus* and *Palmatogecko.* In each case the pattern of these elements is different and is assumed to have evolved independently. As Kluge and Nussbaum (1995) noted, the appendix in Bauer (1990) presented the distribution of character states for this character incorrectly. The data were, however, entered correctly in Bauer's (1990) original analysis based on the data reported by Russell and Bauer (1988), accounting in part for the discrepancy in Bauer's cladogram and that derived by Kluge and Nussbaum (1995) by rerunning the data as incorrectly listed in the appendix.

Small, nodular ossifications were noted in the digits of *P. swartbergensis and P. microlepidotus.* In both they are associated with digits II–V of both manus and pes. In general form these elements resemble the paraphalanges reported in *Lygodactylus* and *Calodactylodes* by Russell and Bauer (1988); however, in the African taxa (and in *Dixonius*), such elements are dorsally, rather than laterally situated and are not associated with the scansorial apparatus and appear rather to be ossifications in the extensor tendons of the digits. We do not accept the presence of these elements as evidence of shared ancestry as their presence in the only two large African species of *Phyllodactylus* suggests that their ossification may be attributable to size alone.

Hypoischium. Kroll and Dixon (1972) reported that the distal end of the hypoischium is forked in members of the *P. gerrhopygus* group that possess abdominal plaques. We found a pronounced distal bifurcation in *P. swartbergensis* and a weakly developed bifurcation in one specimen of *P. lineatus.* In most non-African leaf-toed geckos the hypoischium is undivided, although in *Dixonius* there is a proximal rather than distal bifurcation.

Cloacal bones. The occurrence of these structures has been reviewed on several occasions (Smith 1933, Kluge 1967, 1982; Rieppel 1976; Russell 1977; Kluge and Nussbaum 1995). Typically a single pair of elements is present in gekkonids. The presence of an irregular second pair of ossifications associated with the cloacal spurs is unique to *P. peringueyi* among the African leaf-toed geckos and occurs elsewhere among former *Phyllodactylus* only in the genus *Euleptes*. In the latter genus the second ossification is usually conspicuous, whereas in *P. peringueyi* it is small or even absent in some specimens.

Chromosomes. Karyological data have been published for a variety of leaf-toed geckos outside of Africa (King, 1981, 1987; King and Rofe 1976 for *Christinus;* McBee et al. 1984; Navarro et al. 1981 for Neotropical forms). Four South African taxa have been investigated by Gordon (unpublished). *Phyllodactylus porphyreus* and *P. swartbergensis* have a diploid number of 34 with one large pair of submetacentric elements, one medium-sized pair with short p-arms, one pair of small metacentric elements and 14 pairs of acrocentric or subtelocentric elements. For *P. microlepidotus* 2N = 36, the karyotype differing by the presence of one additional intermediate-sized biarmed pair. Gordon examined three specimens of *P. lineatus*. These also had a diploid number of 36, but an additional two or three pairs of small elements are biarmed and pair 2 exhibits female sex-correlated heteromorphism.

Comparing the African *Phyllodactylus* to two members of the *Pachydactylus* clade (*Pachydactylus capensis* and *Rhoptropus afer)* Gordon concluded that the four leaf-toed geckos he examined were relatively similar and probably monophyletic. Following Joger (1985), Gordon accepted 2N = 36 as a derived condition of a monophyletic Southern African gekkonine group. He regarded the 2N = 34 condition of *P. porphyreus* and *P. swartbergensis* as a synapomorphy uniting these two taxa. Further, he regarded the loss of biarmed chromosome pair four as synapomorphic of this species pair. However, in light of the more recent phylogeny of Kluge and Nussbaum (1995), the claim for polarizing the diploid number is called into question. Indeed, there appear to be numerous exceptions to 2N = 36, even among the southern African clade as defined by Joger (1985). Since the position of *Phyllodactylus* relative to other African or extralimital geckos remains unclear, there is no basis at present for assigning polarity to this character. One or the other, or perhaps both states may be apomorphic relative to an appropriate outgroup. The sex chromosome heteromorphism recorded in *lineatus* was regarded as autapomorphic by Gordon, but might apply at a higher level, and could be a synapomorphy of the *lineatus* complex of seven species. Similar ZZ/ZW heteromorphisms have been demonstrated in *P. lanei* (King 1981) and *Christinus marmoratus* (King and Rofe 1976).

A review of the characters presented here reveals that there are no demonstrably apomorphic features that unite all of the southern African leaf-toed geckos. Indeed, these geckos are variable in character state for a variety of features (such as stapedial perforation, presacral vertebral count, and interclavicle shape) that are generally invariant in other gekkonid genera (Bauer 1990; Kluge 1995; Kluge and Nussbaum 1995). Although this in itself is not evidence for the para- or polyphyly of the group, it clearly provides no support for monophyly. Further, the genetic distance data presented here and previously (Bauer et al. 1996) demonstrate that distances within the *P. lineatus* group, and between members of this group and *P. microlepidotus,* are small relative to those between these species and other African *Phyllodactylus*. Indeed, distances to *P. peringueyi* are as large as those to any *"Phyllodactylus"* elsewhere in the world, or even to representatives of other genera. Character state distributions among southern African *"Phyllodactylus"* support the recognition of three monophyletic units of uncertain affinity to one another. Because no names are available for these taxa we here present descriptions and diagnoses for three new genera.

Cryptactites, new genus

TYPE SPECIES. — *Phyllodactylus peringueyi* Boulenger, 1910.

CONTENT. — *Cryptactites peringueyi* (Boulenger, 1910) (Fig. 4a).

CHARACTERIZATION AND DIAGNOSIS. — *Cryptactites* may be distinguished from all other gekkonids by the following combination of characteristics: body size minute; digits bearing a single pair of enlarged ("leaf-toed") terminal scansors; dorsal scalation tuberculate, tubercles keeled longitudinally, granules on snout larger than those on dorsum of body; median rostral cleft; enlarged chinshields and gulars absent; no midrostral crease or division; first supralabial excluded from nostril; margins of pupil straight-edged in preserved specimens; preanal pores absent; cloacal spurs with two enlarged spinous scales, larger in males than females; midventral caudal scales not transversely enlarged, tail without terminal scansorial pad; sexually dichromatic; nasals fused; parietals paired; premaxilla with moderately short, broad, spatulate nasal projection; frontal moderately broad, only slightly constricted over orbits, with maxillary contact at only a single point; approximately 25–28 maxillary tooth loci; postfrontal bones with posterior projection somewhat thicker than anterior, with pronounced lateral spine; stapes imperforate; coronoid bone moderately well developed, raised above the level of dentary tooth row; second ceratobranchial arch of hyoid present, inner proximal ceratohyal process present, medial process of hyoid cornu elongate; neural arches of atlas fused; 24 presacral vertebrae, 1 lumbar vertebra; 2–3 cervical ribs, 2 sternal ribs, 1–2 mesosternal ribs; 1–2 pairs of clavicular fenestrae; interclavicle splintlike without lateral processes; union of scapula and precoracoid ray of epicoracoid cartilaginous; phalangeal formulae unreduced (2-3-4-5-3 manus, 2-3-4-5-4 pes): hypoischium without terminal bifurcations; cloacal sacs and bones present, a second cloacal ossification is present in association with the cloacal spur in males (apparently individually variable); clutch size two.

The reduction to 24 presacral vertebrae is unique among leaf-toed geckos, and rare among gekkonids in general (Hoffstetter and Gasc 1969). The presence of a second pair of cloacal bones is derived and occurs elsewhere among leaf-toed geckos only in *Euleptes* and at least some *Paroedura*. *Cryptactites* differs from *Euleptes* in the presence of dorsal tubercles, fused nasals, and imperforate stapes. Branch and Bauer (1994) reviewed those osteological features that differentiated this genus from *Asaccus, Paroedura, Christinus, Urocotyledon* and *Haemodracon.* Significant differences with respect to *Ebenavia* are discussed in the redescription of that genus.

ETYMOLOGY. — From the Latinized Greek *crypto-* (hidden) and *actites* (shore dweller) in reference to the habitat of this inconspicuous gecko, which was "lost" to science for more than 80 years (Branch and Bauer 1994). The generic name is masculine.

DISTRIBUTION. — The single species in the genus is confined to coastal and riverine habitats (Fig. 4b) along the Kromme River estuary (Branch and Bauer 1994) and near Port Elizabeth (Willows, Schoenmakerskop, Chelsea Point; Branch 1996) in the Eastern Cape Province of South Africa (Fig. 5). The single record from "Namaqualand" is almost certainly in error.

REMARKS. — The diagnosis above reflects several corrections relative to the previously published redescription of *C. peringueyi* by Branch and Bauer (1994). The initial observations were based on radiographs of the two poorly-preserved types only, whereas the present information is derived from radiographs of specimens in better condition and a single cleared and stained specimen. Branch and Bauer (1994) indicated a paired condition for the nasal bones and tentatively regarded the stapes as perforate. In adult specimens examined the nasals are at least partially fused, but this condition may be individually variable. The stapes is always imperforate.

Goggia, new genus

TYPE SPECIES. — *Phyllodactylus lineatus* Gray, 1838.

CONTENT. — *Goggia braacki* (Good, Bauer, and Branch, 1996), *G. essexi* (Hewitt, 1925) (Fig. 6b), *G. gemmula* (Bauer, Branch, and Good, 1996), *G. hewitti* (Branch, Bauer, and Good, 1995), *G. hexapora* (Branch, Bauer, and Good, 1995), *G. lineata* (Gray, 1838) (Fig. 6a), *G. microlepidota* (FitzSimons, 1939), *G. rupicola* (FitzSimons, 1938) (Fig. 6c).

CHARACTERIZATION AND DIAGNOSIS. — *Goggia* may be distinguished from all other gekkonids by the following combination of characteristics: digits bearing a single pair of enlarged ("leaf-toed") terminal scansors; dorsal scalation atuberculate; granules on snout larger than those of dorsum of body; enlarged chinshields present or absent; rostral partially divided; first supralabial enters nostril; margins of pupil crennelate in preserved specimens; cloacal spurs consisting of 3–7 enlarged scales, better developed in males; preanal pores present; subcaudal scales not transversely enlarged, tail without terminal scansorial pad; no sexual dichromatism;

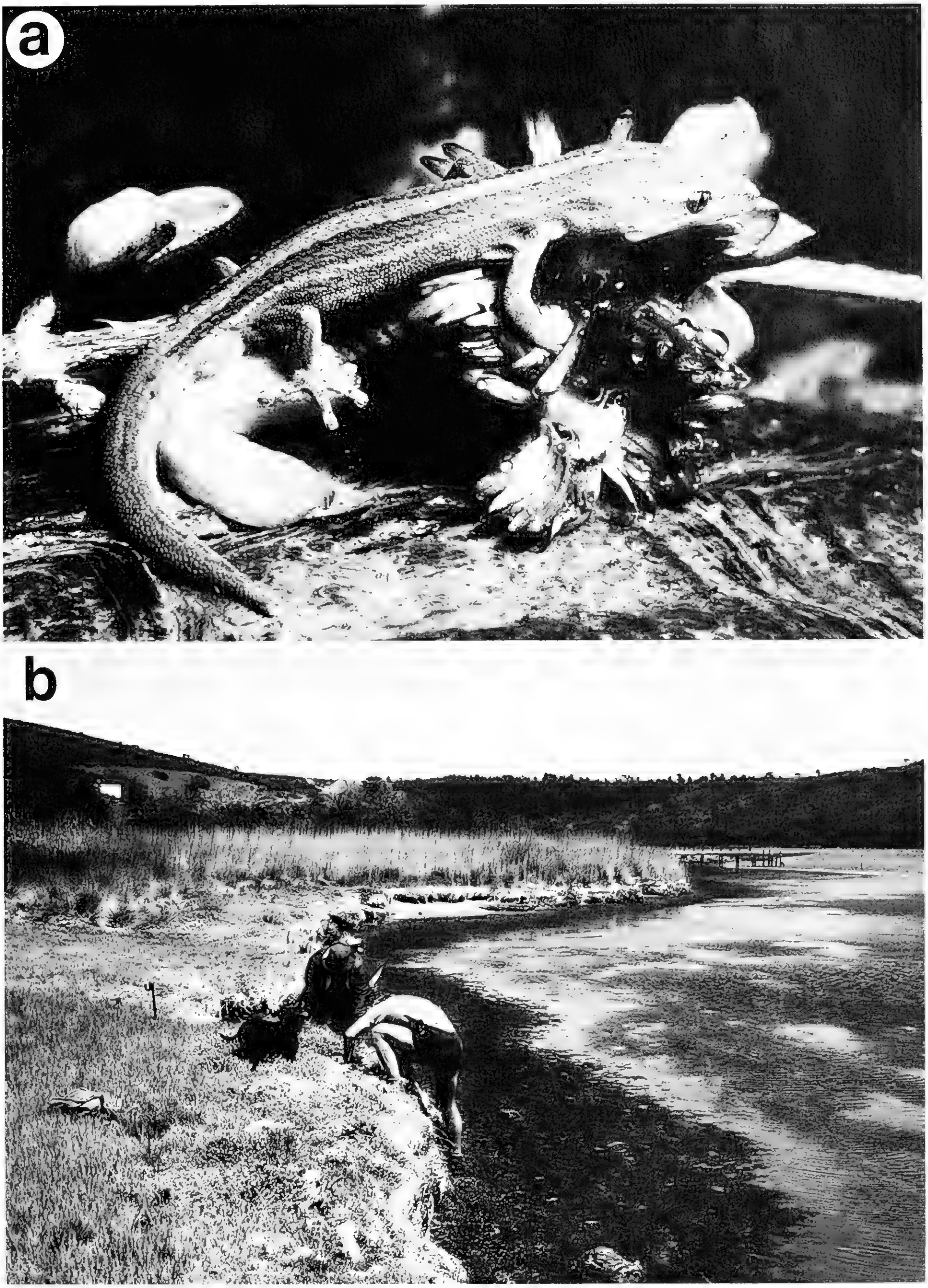


FIGURE 4. a) *Cryptactites peringueyi* (maximum SVL 29 mm) from Kromme River, Eastern Cape Province, South Africa. This specimen illustrates the straight-edged pupil and keeled dorsal tubercles that distinguish this genus from *Goggia* and *Afrogecko*. Note the striped dorsal pattern typical of males. Females have a unicolored dorsum. b) Habitat of *C. peringueyi* along the Kromme River Estuary. The species has so far been found only along the lower reaches of the Kromme and near Port Elizabeth.

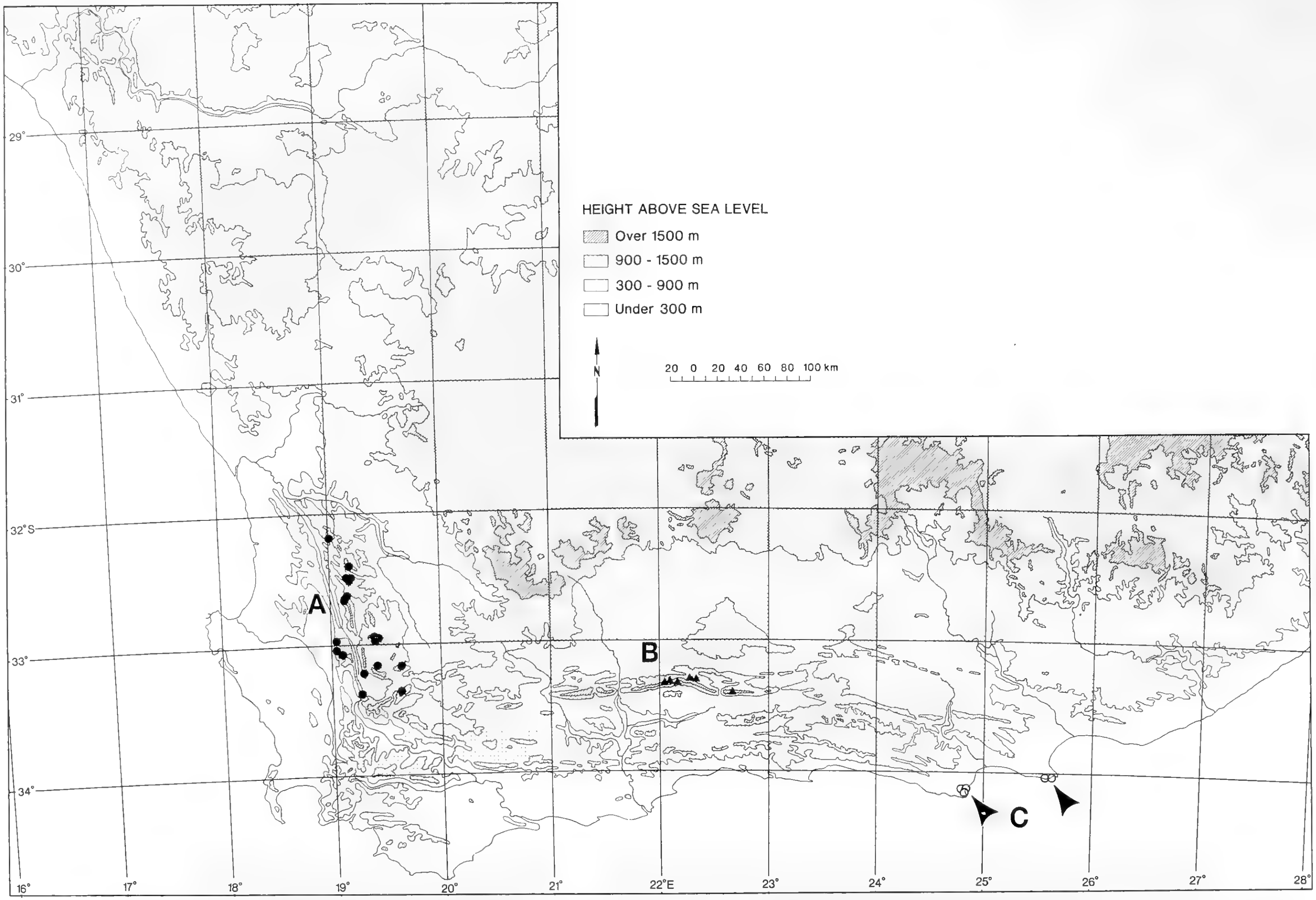


FIGURE 5. Distribution of African leaf-toed geckos. A = *Goggia microlepidota* (solid circles). B= *Afrogecko swartbergensis* (solid triangles), and C = *Cryptactites peringueyi* (open circles with arrows) in South Africa. See Appendix A for a complete list of localities.

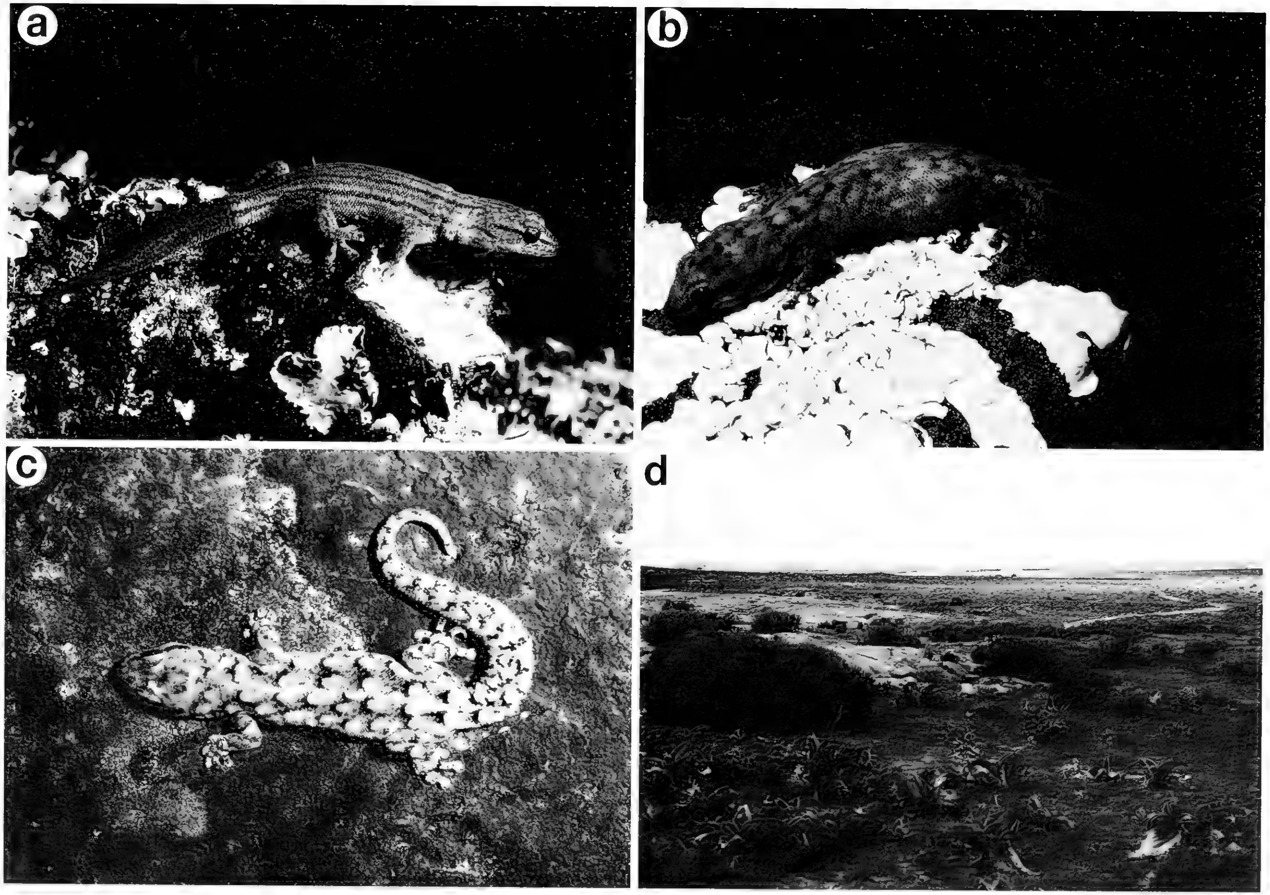


FIGURE 6. Representative members of the genus *Goggia*. a) *G. lineata* (maximum SVL 32 mm) from Warmwaterberg, Little Karoo, Western Cape Province, South Africa. This is the most widespread species in the genus and does not exhibit the depressed body form of most of its congeners. The striped pattern is not always present in this species but representatives of no other *Goggia* ever exhibit such a pattern. b) Topotypical *G. essexi* (maximum SVL 29 mm SVL) from Farm Hounslow, Eastern Cape Province, South Africa (gravid female). This species is restricted to the Suurberg and adjacent rocky areas in valley bushveld vegetation. c) *G. rupicola* (maximum SVL 32 mm) from near Steinkopf, Northern Cape Province, South Africa. The relatively bright (usually orange) markings of the dorsum are typical of this species, which lives under flakes of exfoliating granite on exposed domes in areas of succulent Karoo vegetation (d).

nasal bones paired; parietals paired; premaxilla with moderately long, lanceolate nasal projection; frontal moderately broad, moderately strongly constricted over orbits, with extensive maxillary contact; 25–32 maxillary tooth loci in adults; postfrontal bones with anterior and posterior projections subequal, without pronounced lateral spine; stapedial foramen present; coronoid bone moderately well-developed, raised well above the level of dentary tooth row; second ceratobranchial arch of hypoid present, inner proximal ceratohyal process absent, medial process of hyoid cornu short to moderate in length; neural arches of atlas fused or paired; 26 presacral vertebrae, 1–3 lumbar vertebrae; 3 (or rarely 4) cervical ribs, 2–3 sternal ribs, 1–2 mesosternal ribs; clavicular fenestrae variable, usually one pair of large fenestrae; interclavicle cruciform, with prominent lateral projections; union of scapula and precoracoid ray of epicoracoid ligamentous; phalangeal formulae unreduced (2-3-4-5-3 manus, 2-3-4-5-4 pes); ossifications in digital extensor tendons usually absent (present in *G. microlepidota*); hypoischium not, or only weakly bifurcate distally; cloacal sacs and a single pair of bones present; clutch size two.

The presence of preanal pores in male *Goggia* is shared with only *Dixonius* among the leaf-toed geckos. These genera differ in many aspects of scalation (tuberculation, subcaudal scales) and osteology (scapular-precoracoid union, coronoid height, hypoischial shape, postfrontal shape, maxillary tooth loci). The reduction of both the inner proximal ceratohyal process and medial process of the hyoid cornu occurs only in *Goggia* and *Euleptes*. The midrostral crease occurs only in *Goggia*, *Dixonius*, and *Haemodracon trachyrhinus*. *Goggia* differs from *Cryptactites* and the remaining southern African *"Phyllodactylus"* in possessing a rostral crease, preanal pores, cloacal spurs consisting of three or more enlarged scales, ligamentous rather than cartilaginous scapular-precoracoid connection, a perforate vs. imperforate stapes, paired vs. fused nasal bones, elongate lanceolate nasal process of the premaxilla, extensive fronto-maxillary contact, prominent transverse processes of the interclavicle, and reduced processes of the hyoid cornu and ceratohyal. It is further differentiated from *Cryptactites* by its atuberculate scales, crennelate pupil margin, unreduced presacral vertebral count, postfrontal shape, and lack of sexual dichromatism.

ETYMOLOGY. — The name is derived from the Afrikaans word "gogga" meaning a "creepy-crawly," usually an arthropod or reptile. In recent years the word has taken on connotations of endearment. The word has a Khoisan derivation and may have also given rise to the Xhosa term "rho-rho" meaning something to be feared. Because the modification of the noun "gogga" to form *Goggia* yields a feminine Latin ending to the word, we treat *Goggia* as feminine. The specific epithets of the constituent species have been modified accordingly. Note that in Afrikaans the letter "g" is guttural and is always pronounced like the "ch" in the Scottish word "loch."

DISTRIBUTION. — The genus as a whole is distributed in southwestern Africa, including extreme southern Namibia and parts of the Northern, Western and Eastern Cape Provinces of South Africa (Figs. 5, 7). The distribution of *Goggia* is essentially congruent with the winter rainfall area of South Africa (Haacke 1996). *Goggia lineata* is by far the most widespread species, ranging from southern Namibia (Arusberg Mountains and Karas District) south to the level of Mamre and Tulbagh, Western Cape Province, South Africa. This species is primarily found at elevations of less than 300 m, although there are records as high as at least 745 m. It is chiefly associated with plant debris, but may also be found under stones or bark (Branch and Braack 1989; Branch and Bauer 1995; Branch et al. 1995).

The large species *G. microlepidota* occurs in the sandstones of the Cedarberg (Visser 1979; Mouton and van Wyk 1981; Mouton et al. 1987; Branch and Bauer 1997) from Pakhuis Pass south to Ceres (Fig. 5). It is sympatric with *Goggia hexapora,* which occupies the Cedarberg and adjacent ranges, including the isolated Piketberg (Branch et al. 1995). A northern extension of this species range since its description is Farm Kliprivier, near Nieuwoudtville, represented by a single specimen in the National Museum, Bloemfontein (NMB 7169). All remaining species are allopatric (Fig. 7). *Goggia hewitti* occurs in the quartzitic sandstones of the southern Cape Fold Mountains, *G. essexi* in the Suurberg near Grahamstown, and *G. rupicola* is limited to isolated granite koppies in succulent Karoo vegetation in upland areas of Little Namaqualand (Fig.

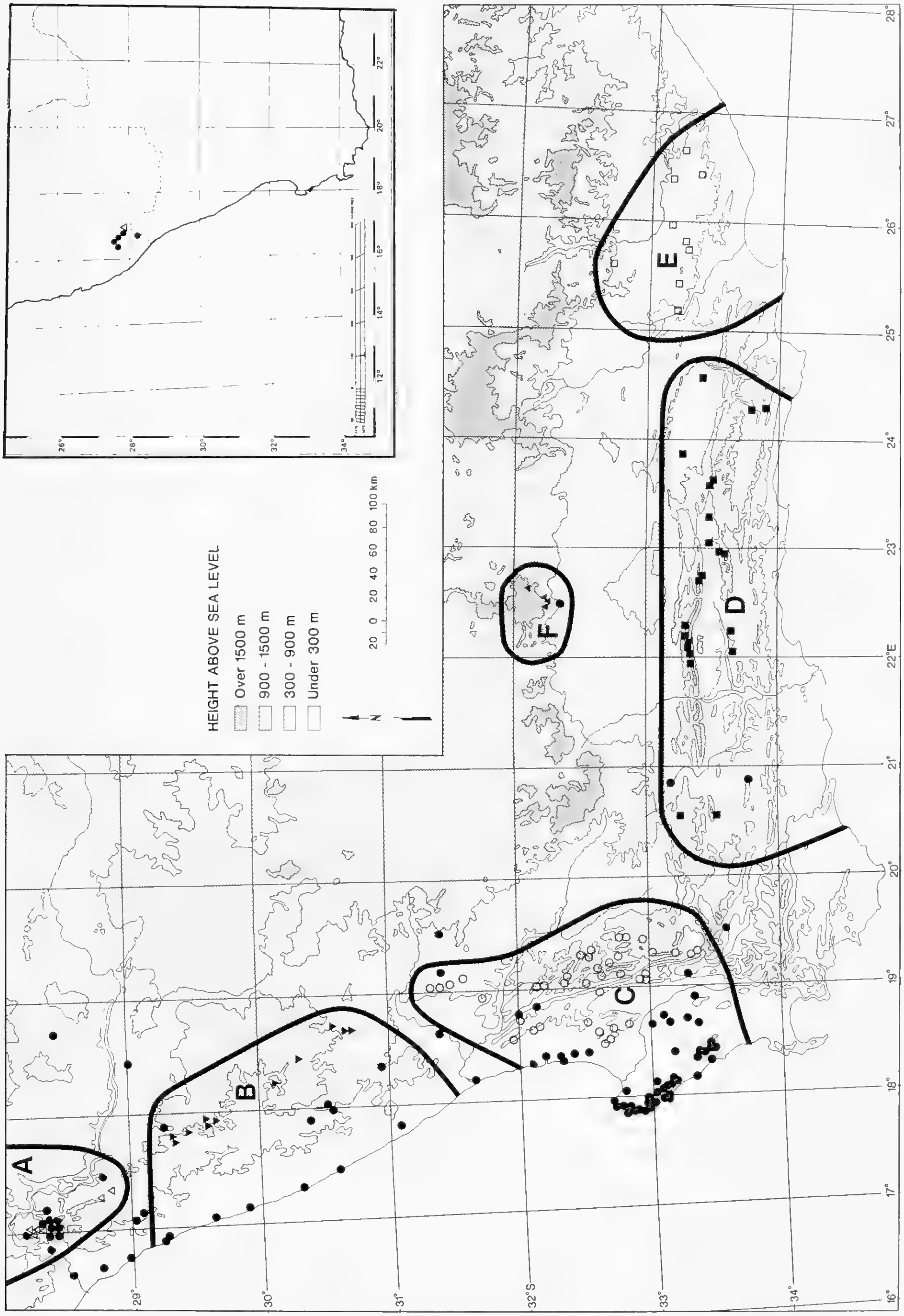


FIGURE 7. Distribution of the *Goggia lineata* complex in southern Africa. A = *G. gemmula* (open triangles), B = *G rupicola* (inverted solid triangles), C = *G hexapora* (open circles), D = *G. hewitti* (solid squares), E= *G. essexi* (open squares), F = *G. braacki* (solid triangles). Remaining (mostly coastal) localities = *G. lineata* (solid circles). Inset map shows the southern Namibian localties for *G. lineatus* and *G. gemmulus*. See Branch et al. (1995), Bauer et al. (1996), and Good et al. (1996) for complete list of localities.

6d) including the Kamiesberg and Komaggas Hills (Branch et al. 1995). *Goggia gemmula* occurs on granite boulders in the Richtersveld and adjacent southern Namibia (known in Namibia only from Macmillan's Pass near Rosh Pinah, Karas District; Bauer et al. 1996). Only *G. braacki* inhabits the inland escarpment of southern Africa, being found on dolerite outcrops in the Nuweveldberg near Beaufort West (Good et al. 1996).

Afrogecko, new genus

TYPE SPECIES. — *Gecko porphyreus* Daudin, 1802.

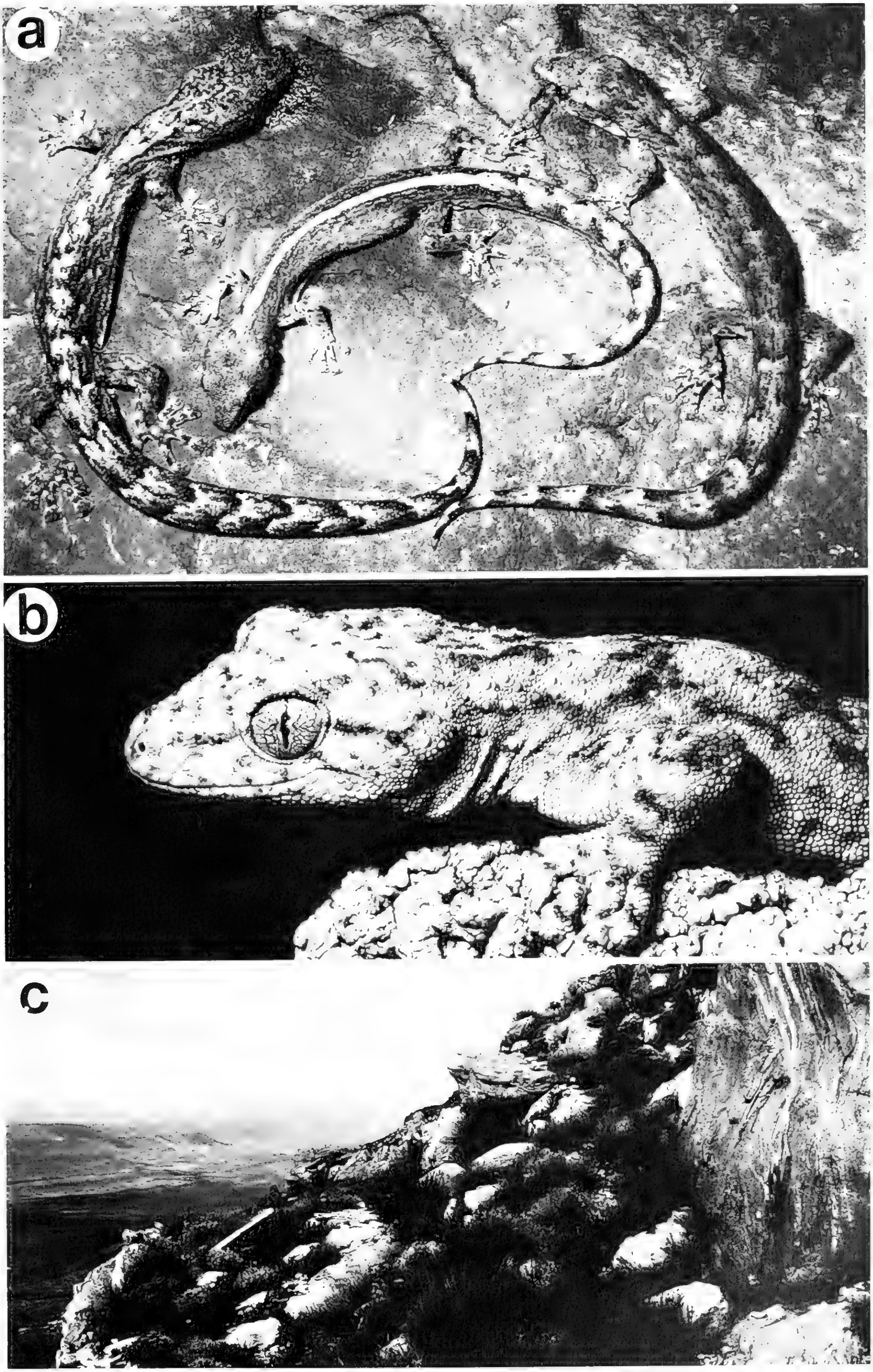
CONTENT. — *Afrogecko porphyreus* (Daudin, 1802) (Fig. 8a), *A. ansorgii* (Boulenger, 1907), *A. swartbergensis* (Haacke, 1996) (Fig. 8b). Haacke's (1996) undescribed Angolan species is tentatively referred to this genus, although the data he presented do not permit this to be done with confidence.

CHARACTERIZATION AND DIAGNOSIS. — *Afrogecko* may be distinguished from all other gekkonids by the following combination of characteristics: digits bearing a single pair of enlarged ("leaf-toed") terminal scansors; dorsal scalation atuberculate or with low, rounded tubercles; granules on snout larger than those on dorsum of body; enlarged chinshields present or absent; rostral entire; first supralabial excluded from nostril (enters nostril in *A. ansorgii);* margins of pupil crennelate in preserved specimens; cloacal spurs consisting of a single enlarged scale (sometimes flanked by much smaller scales that are somewhat larger than adjacent body granules), more well-developed in males; preanal pores absent; subcaudal scales not transversely enlarged, tail without terminal scansorial pad; no sexual dichromatism; nasal bones fused; parietals paired (partially fused in *A. swartbergensis);* premaxilla with short rounded nasal projection; frontal moderately broad, only slightly constricted over orbits, with maxillary contact absent or reduced to a single point; 26–36 maxillary tooth loci in adults; postfrontal bones with anterior and posterior projections subequal, without pronounced lateral spine; stapedial foramen absent; coronoid bone moderately well-developed, raised well above the level of dentary tooth row; second ceratobranchial arch of hyoid present, inner proximal ceratohyal process present, medial process of hyoid cornu elongate; neural arches of atlas paired or fused; 26 presacral vertebrae (rare individual variation from 25–27 occurs), 1–2 lumbar vertebrae; 3 cervical ribs, 1–3 (usually 2 sternal ribs, 1–2 (usually 2) mesosternal ribs; clavicular fenestrae variable, may be absent or consist of one or two pairs of fenestrae; interclavicle without prominent lateral projections (character with high individual variability); mesoscapula-precoracoid union cartilaginous; phalangeal formulae unreduced (2-3-4-5-3 manus, 2-3-4-5-4 pes); ossifications present (*A. swartbergensis*) or absent in digital extensor tendons; hypoischium bifurcate distally or not; cloacal sacs and a single pair of cloacal bones present; clutch size two.

Afrogecko differs from all other leaf-toed geckos except *Cryptactites* (and some specimens of *Euleptes*) in the absence of prominent transverse processes of the interclavicle. The short, broad nasal process of the maxilla is found elsewhere only in *Cryptactites* and *Urocotyledon.* Although numerous features are shared with *Cryptactites, Afrogecko* differs from this form in possessing smooth dorsal scales or rounded tubercles (vs. keeled tubercles), a crennelate pupil margin, 26 prescral vertebrae, no postfrontal spine, and no sexual dichromatism. All species of *Afrogecko* are also much larger than *Cryptactites peringueyi,* with even hatchlings of the former approaching or surpassing maximal adult sizes of the latter.

→

FIGURE 8. Representatives of the genus *Afrogecko.* a) Three specimens of *A. porphyreus* (maximum SVL 56 mm) from Walmer, Port Elizabeth, Eastern Cape Privince, South Africa illustrating variation in dorsal pattern within a single population. b) *A. swartbergensis* (maximum SVL 75 mm) from the Groot Swartberge, Western Cape Province, South Africa. Note the smooth, enlarged, rounded tubercles unique to this species. The crennelated pupil margin is typical of all southern African leaf-toed geckos except *Cryptactites peringueyi.* c) Typical habitat of *A. swartbergensis* in the north-facing slopes of the Groot Swartberge. This habitat is alos typical of *Goggia hewitti,* although the latter species typically occupies smaller rock cracks and crevices.


a
b
c

ETYMOLOGY. — The name refers to the restriction of this genus to the African continent and is masculine.

DISTRIBUTION. — The distribution of the genus is disjunct in southwestern Africa. *Afrogecko ansorgii* and an undescribed species (Haacke 1996) occur in southern Angola (Fig. 9) and the remaining species occur in the temperate regions of the Western and Eastern Cape Provinces of South Africa. *Afrogecko ansorgii* is known only from the types obtained from "Maconjo, Benguella" (= Maconge, Mocamedes Province, 15°01′S 13°12′E, 700 m), Angola. *Afrogecko swartbergensis* described from the Swartberg Pass, is now known to have a wider distribution in the Groot Swartberge, Cape Fold Mountains, Western Cape Province (Branch and Bauer 1997) (Figs. 5, 8c).

Afrogecko porphyreus is widespread in the southern and southwestern portions of the Cape (Fig. 9) chiefly in association with mesic mountain fynbos (De Kock, undated). The South African distribution of this species was previously mapped at the quarter degree square level by Visser (1984). The species is commensal under some conditions and has expanded its range with human assistance. Within South Africa the range has expanded to the east. Branch and Hanekom (1987) recorded the easternmost locality for the species in the Tsitsikamma National Park, but populations are now well-established in Port Elizabeth (pers. observ.). This species is also known from a number of islands off of the west coast of South Africa (Robben Id., Jutten Id., Dassen Id., Meeuw Id., Marcus Id., Malgas Id., and Schappen Id.; Branch 1991). It has also been recorded from St. Helena (FitzSimons 1943), although these specimens represent an introduction. Madagascan records (Angel 1942; Guibé 1956; Blanc 1971) are in error as they refer to *Phyllodactylus brevipes,* a distinctive, and probably endemic Malagasy species (Dixon and Kroll 1974; Glaw and Vences 1994; R. A. Nussbaum, pers. comm.).

The absence of *Afrogecko* from the Northern Cape and Namibia (except as introduced populations) is probably real, although additional collecting may reveal its presence in the southern Northern Cape and/or extreme northern Namibia.

REMARKS. — In addition to the nominate form, two subspecies of *Afrogecko porphyreus* have been described, *A. p. cronwrighti* (Hewitt 1937), and *A. p. namaquensis* (Hewitt 1935). Loveridge (1947) questioned the validity of the former, and recent reviews (e.g., Branch 1988) have not recognized either form. Both forms were described from the periphery of the species' distribution. *Afrogecko p. cronwrighti* was described from Cape St. Francis and probably represents the easternmost non-human-assisted limit of the range of the species. The Bitterfontein type locality of *A. p. namaquensis,* is also peripheral. Records from north 32°30′S are very scarce and the only records north of Bitterfontein are Werner's (1910) record from Warmbad, a record from Swakopmund, and an old record from Damaraland (Boulenger 1885). The literature record for Warmbad has since been regarded as referring to *Goggia lineata* (Mertens 1955; Branch et al. 1995), and the Damaraland record is considered a locality error. The Swakopmund record probably represents an introduction. The validity of the two subspecies of *Afrogecko porphyreus* will be examined in more detail elsewhere (Branch and Bauer 1997), but neither form is here accorded specific or subspecific rank.

KEY TO LEAF-TOED GECKOS OF SOUTHERN AFRICA

Earlier reviewers (FitzSimons 1943; Loveridge 1947) published keys to the southern African *Phyllodactylus* then recognized. However, five additional species have since been described and additional material has become available for all species except *Afrogecko ansorgii.* Although a key to a subset of the *Goggia lineatus* complex species has been published recently (Branch et al. 1995), no comprehensive key for all southern African leaf-toed geckos exists. With the new generic allocations of the 12 recognized southern African species, we take this opportunity to present such a key, based primarily on easily determined external characters.

1a. Dorsal scalation homogeneous 3
b. Dorsal scalation heterogeneous, with enlarged tubercles 2
2a. Dorsal tubercles keeled, body size small . . . . *Cryptactites peringueyi*
b. Dorsal tubercles flattened and smooth, body size large *Afrogecko swartbergensis*

3a. Rostral scale entire, preanal pores absent in males 4
b. Rostral scale with dorsal midline crease, preanal pores present in males 5
4a. Preanal scales enlarged, first supralabial . . . enters nostril. . . . . *Afrogecko ansorgii*
b. Preanal scales not enlarged, first suprala-bial excluded from nostril. . . . . *Afrogecko porphyreus*
5a. No enlarged chinshields, body size large, midbody scale rows >95. . . . . *Goggia microlepidota*
b. 1-2 enlarged postmental scales, body size small, midbody scale rows <90 6
6a. Midbody scale rows usually fewer than 80 7
b. Midbody scale rows usually more than 80 8
7a. Usually 5 preanal pores in males; usually fewer than 10 granules between nostril and anterior border of orbit; body rounded, head deep . . . . *Goggia lineata*
b. Usually 4 preanal pores in males; usually more than 10 granules between nostril and anterior border of orbit; head and body depressed . . . . *Goggia gemmula*
8a. Six preanal pores in males (Kouebokkeveld and Cedarberg region) . . . . *Goggia hexapora*
b. Four preanal pores in males 9
9a. Nasorostrals usually 2; maximum SVL rarely more than 30 mm. 10
b. Nasorostrals usually 1 (rarely 0 or 2); maximum SVL 37 mm 11
10a. Nasorostrals 2–3 (rarely 1); granules around midbody about 85 (80–90); dorsum usually with bright orange sports (Namaqualand) . . . . *Goggia rupicola*
b. Nasorostrals 1-2 (rarely 3); granules around midbody usually about 80 (78–84); dorsum without bright markings (Eastern Cape). . . . . *Goggia essexi*
11a. Southern Cape Fold Mountains* . . . . *Goggia hewitti*
b. Nuweveldberg. . . . . *Goggia braacki*

**G. hewitti* and *G. braacki* are not distinguishable on the basis of discrete morphological characters, but may be separated on the basis of several fixed allelic differences (Good et al. 1996). Because the taxa are entirely allopatric, their distributions have been substituted in lieu of key morphological characters.

RELATIONSHIPS AMONG AFRICAN LEAF-TOED GECKOS

Until recently the only statements regarding relationships among the southern African leaf-toed geckos were limited to subjective interpretations of external morphology. For example, Werner (1910) considered *Afrogecko ansorgii* and *A. porphyreus* to be closely related and FitzSimons (1939) regarded *Goggia microlepidota* as most closely allied to *G. lineata. Cryptactites peringueyi,* because of its radically different morphology and uncertain provenance (see Branch and Bauer 1994) attracted particular attention. Hewitt (1937) and subsequent authors (FitzSimons 1943; Loveridge 1947; MacLachlan 1978) questioned the validity of the taxon and doubted that it was indigenous to southern Africa. The African origin of this genus is still questioned by some workers (see Haacke 1996).

Gordon (unpublished), using karyological data supplemented by morphological data from other sources, investigated relationships among four species of South African "*Phyllodactylus*." His data suggested the pattern (*lineatus* (*microlepidotus* (*porphyreus, swartbergensis*))). Affinities of *P. porphyreus* with *P. brevipes* were also suggested, although not investigated. Gordon, however, warned of limitations in the karyological data set and considered data insufficient to examine broader patterns of relationship. This analysis was weakened by the absence of an appropriate outgroup, an a priori assumption on ingroup monophyly, and the use of the criterion of commonality to assign polarity.

Most systematic work has focused on the species now assigned to *Goggia,* particularly those small species constituting the *G. lineatus* group. Following suggestions that *Goggia lineata* was probably a composite species (Branch and Braack 1989; Oelofsen et al. 1987) Branch, Bauer and Good (1995) reviewed the status of this taxon on the basis of both morphological and allozyme characters. They resurrected *G. rupicola* and *G. essxi* to specific status, described two additional species, *G. hewitti* and *G. hexapora,* and concluded that the *G. lineata* complex was a natural unit and provided a diagnosis for this species group. Subsequent analysis of the *G.*

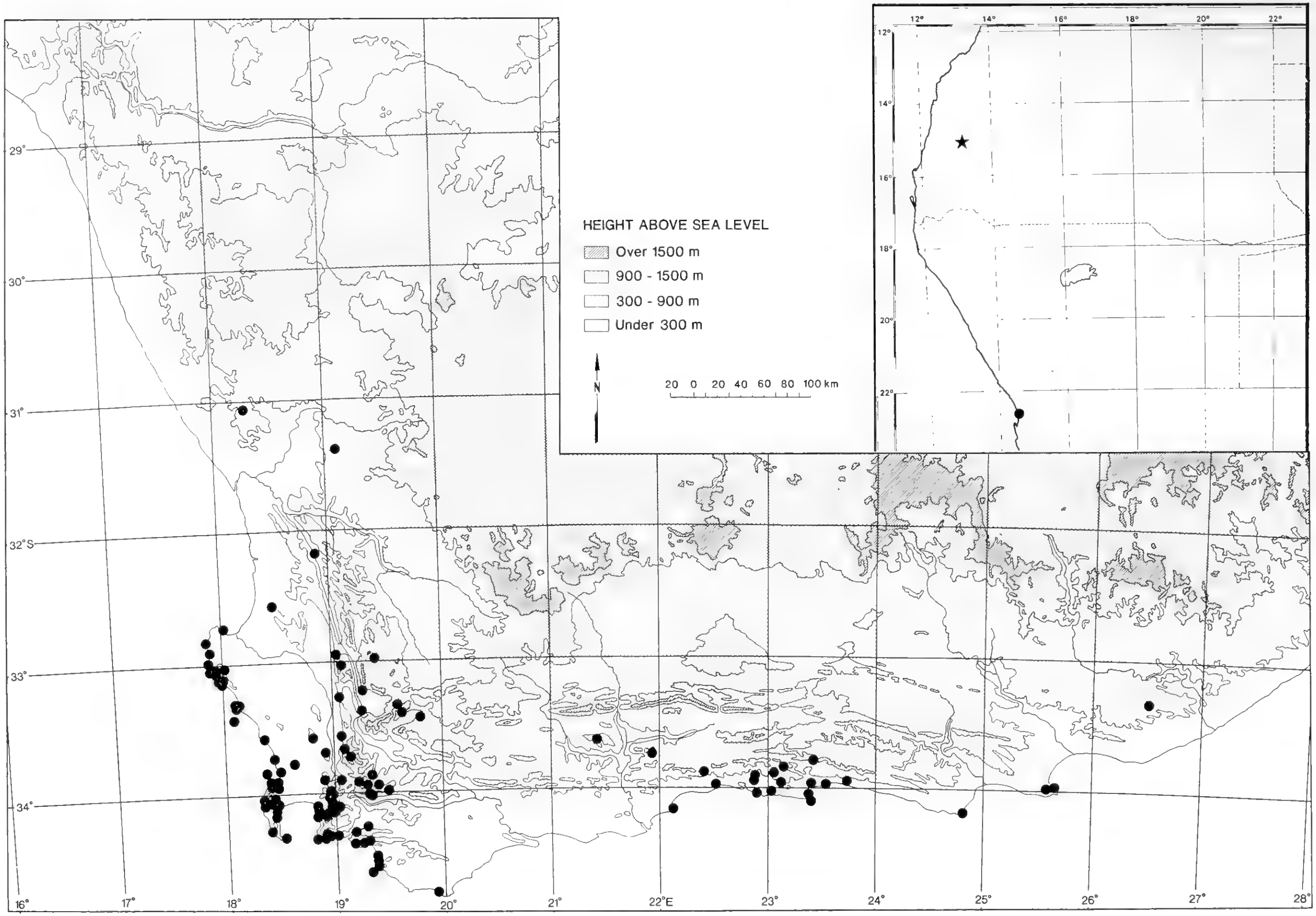


FIGURE 9. Distribution of *Afrogecko porphyreus* (solid circles) in South Africa. Inset map shows an introduced population is Swakopmund, Namibia and the only known locality of *Afrogecko ansorgii* (star) in southern Angola. See Appendix A for a complete list of localities for *A. porphyreus.*

lineata group has revealed two additional species, *G. gemmula* (Bauer et al. 1996), and *G. braacki* (Good et al. 1996). The latter species is morphologically indistinguishable from *G. hewitti* and differs from *G. hexapora* only in the number of preanal pores in males, although fixed allozyme differences unambiguously support its specific recognition.

Any attempt at reconstructing the phylogeny of the African leaf-toed geckos is hindered by the lack of an identified suitable outgroup, or series of outgroups. Among African gekkonid genera, only the monophyly of the *Pachydactylus* clade, first identified by Underwood (1954) and modified by Russell (1972), has been supported by subsequent analysis (Haacke 1976; Joger 1985; Bauer 1990; Kluge and Nussbaum 1995; Bauer and Good 1996). Another group of African gekkonid genera, including *Pristurus, Narudasia, Quedenfeldtia, and Saurodactylus* has been allied with the New World sphaerodactyline genera (Kluge 1995; Kluge and Nussbaum 1995), although relationships among the Old World genera remain unclear (Kluge 1995).

Bauer (1990) presented a phylogeny of Afro-Malagasy gekkonines that he characterized as preliminary and non-comprehensive. In this preliminary analysis he excluded a number of genera (*Gehyra, Lepidodactylus, Nactus, Tarentola, Geckonia, Saurodactylus, Tropiocolotes, Quedenfeldtia, Pristurus, Hemidactylus*) that are peripheral or extralimital to southern Africa, but which occur in the greater Afro-Malagasy region. These taxa were explicitly excluded, not because he regarded them as irrelevant or outside the southern African and Malagasy radiations (as assumed by Nussbaum and Raxworthy 1994b), but because the analysis was preliminary and operationally so constrained. Bauer (1990:277) noted that the assumptions of the monophyly of the group as a whole and the monophyly of the constituent genera were likely not to be valid.

In Bauer's (1990) analysis *Phyllodactylus* formed a trichotomy with *Afroedura* and the group including *Phelsuma, Lygodactylus, Urocotyledon, Ailuronyx, Homopholis, Geckolepis, Ebenavia, Paroedura, and Uroplatus.* The trichotomy was supported by the presence of fused nasals, and fused atlantal arches. These characters are variable within the African *"Phyllodactylus"* and do not provide strong support for even this most general grouping of genera.

Kluge and Nussbaum's (1995) reanalysis of Bauer's (1990) data yielded a somewhat different pattern of relationship, but one that still provided no resolution of the affinities of *Phyllodactylus.* They retrieved the pattern (*Afroedura, Phyllodactylus,* (*Phelsuma, Rhotropella*), (*Lygodactylus, Urocotyledon*), (*Ailuronyx, Homopholis*), *Geckolepis,* (*Ebenavia, Paroedura, Uroplatus*)). Using their own data set, the same authors presented a consensus cladogram for the endemic Ethiopian region ingroup taxa. According to this, *Phyllodactylus* forms a trichotomy with (*Lygodactylus + Rhotropella + Phelsuma),* and a group containing *Afroedura, Paragehyra, Ailuronyx, Blaesodactylus, Paroedura, Ebenavia, Uroplatus,* and *Urocotyledon.* The inclusion of the extralimital ingroup taxa *Gehyra, Gekko,* and *Hemidactylus* yielded a consenus cladogram in which *Phyllodactylus* was the sister group of *Parogehyra,* with this pair forming an unresolved trichotomy with *Afroedura* and a group including all of the scansor-bearing geckos in the analysis except *Paroedura* and *Ptyodactylus,* which were sequentially more distant sister taxa of the trichotomy. Kluge and Nussbaum (1995) admitted, however, that their initial first run results were poorly resolved and that fewer than half of the clades in their final results are supported by two or more synapomorphies. Further, as they indicated, the coding of polymorphic data as missing (Platnick et al. 1991) ignores the independent evolution of certain character states and makes the data appear more robust than they actually are.

We agree with Kluge and Nussbaum (1995) that much more research on the higher classification of the Gekkonidae is required. On the basis of either Bauer's (1990) or Kluge and Nussbaum's (1995) results, an outgroup including nearly all African gekkonids with padded digits (perhaps excluding *Ptyodactylus,* which the latter authors found to be outside of all other padded genera) would have to be employed in any analysis of relationships among southern African leaf-toed geckos. This, of course, assumes the monophyly of the Ethiopian region gekkonids (a dubious assumption at best). Alternatively, an approach like that of Arnold and Gardner (1994), using other leaf-toed geckos as the outgroup could be employed. There is, however, no reason to assume the monophyly of these units or to hypothesize some structured pattern of relationships among them. Recognizing these difficulties we present below the results of analyses using a number of different combinations of in- and outgroup taxa. We reiterate that there is no strong support for accepting the appropriateness of these outgroups. Rather we employ them because they are the only outgroups that have been suggested (Bauer 1990; Kluge and Nussbaum 1995), or assumed (Arnold and Gardner 1994) by previous phylogenetic analysis, or because they are suggested (albeit weakly) by the phenetic analysis of leaf-toed geckos presented herein. Further, it should be noted that the uniformity of the *Goggia lineata* group with respect to the morphological characters included in the analysis dictates that analyses employing only morphological data cannot yield resolution within this clade. This fact also necessarily yields multiple output trees of identical topology.

For the two polytypic genera *Goggia* and *Afrogecko* there are a number of intragenerically variable characters. Of the six variable morphological characters in *Afrogecko* for which character states could be determined in all three described species (condition of chinshields, dorsal scalation, and extraphalangeal ossifications, number of lumbar vertebrae, atlantal fusion, and circumnarial scalation) each pair of species share a common state for two. Polarity for most of these characters cannot be established using either *Goggia* or *Goggia* + *Cryptactites* as the outgroup. Likewise, using all leaf-toed gekkonids, or all African gekkonids does not clarify matters. The only character for which polarity has been established in the context of African gekkonids (atlantal arch fusion; see Kluge and Nussbaum 1995) exhibits the derived state in only *A. porphyreus*. Likewise, the presence of more than one lumbar vertebra, which, on the basis of general distribution in leaf-toed geckos, if not gekkonids as a whole (Wellborn 1933), may also be derived, is unique to *A. porphyreus* among *Afrogecko*. The large size, enlarged chinshields, and tuberculate dorsum of *A. swartbergensis* make this species the most distinctly different in the genus, but whether this reflects an early division from an *A. porphyreus* + *A. ansorgii* clade, or merely the accumulation of autapomorphies remains unclear. The phenetic analysis of allozyme data (Fig. 3) suggests that *A. porphyreus* and *A. swartbergensis* are rather dissimilar, but until additional material becomes available for *A. ansorgii* no phylogenetic resolution within the genus is possible.

Relationships within *Goggia* are more tractable as data, both morphological and allozyme, are available for all eight species. Only five of the morphological characters scored for all leaf-toed geckos were variable within *Goggia* (atlantal arch fusion, chinshield presence, number of mesosternal and sternal ribs, number of lumbar vertebrae, and presence of extraphalangeal ossifications). Using *Afrogecko* as the outgroup (weakly suggested by the phenetic allozyme analysis, Fig. 3) suggests only that *G. microlepidota* possesses a derived condition in having a total of five versus four ribs connecting to the sternum either directly or via the mesosternal extension. Using all leaf-toed geckos as the outgroup suggests that the presence of extraphalangeal ossifications in *G. microlepidota* is derived and that all remaining taxa share the apomorphic condition of and increased number (2–3) of lumbar vertebrae. If African gekkonids are chosen as the outgroup the fusion of the atlas and reduction to four sternal and mesosternal pairs of ribs seen in the *G. lineata* group would be interpreted as derived.

If all southern African leaf-toed geckos (excluding *Cryptactites*) are regarded as part of a single clade (suggested in the context of the phenetic allozyme analysis of leaf-toed gekkonids only, but unsupported by morphological data) thirteen allozyme loci (Table 5) provide possible evidence of relationships. All others were either monomorphic or could be mapped onto any phylogenetic hypothesis equally parsimoniously. The single phylogenetic hypothesis resulting from these data, with all other leaf-toed geckos (Appendix B), including *Cryptactites,* as outgroups, yielded five most parsimonious trees (35 steps, c.i. 0.857) all of which placed the group (*A. swartbergensis* (*A. porphyreus, G. microlepidota*)) as the sister group of the remaining species of *Goggia* (the *G. lineata* complex). In this analysis the monophyly of the *G. lineata* group is suggested by the presence of three allele combinations (Ck-b/c, Icdh1-b/c, and Icdh2-b) among its species that are unique among leaf-toed geckos. This is also reflected in the much smaller genetic distances within this group relative to other distances among leaf-toed geckos (Table 3; Fig. 3). The species pair *G. lineata* + *G. gemmula*

TABLE 5. Distribution of allozyme character states among the southern African leaf-toed geckos.

Locus	Taxa										Out
	BRA	ESS	GEM	HEW	HEX	LIN	MIC	RUP	POR	SWA	
Acon-1	0	0	2	0	0	2	3	0	3	1	0
Ak	0	0	0	0	0	0	1	0	1	0	–
Ck	1	1	2	1	1	2	4	2	3	0	–
Fum	2	2	2	2	2	2	2	2	0	1	0
Gpi-1	0	2	4	0	0	3	5	0	1	1	0
Gpi-2	0	0	1	0	0	0	0	0	1	0	0/1
Icdh-1	1	1	1	1	1	1	2	1	0	0	0
Icdh-2	1	1	1	1	1	1	0	1	2	0	0
Ldh-1	2	2	2	0	2	2	2	2	0	1	0
Me	0	1	0	0	0	0	0	0	1	0	0
Pep-2	1	1	0	1	1	0	2	0	0	0	0
Pgdh	2	2	2	2	2	2	0	2	3	1	0
Pgm-2	0	0	0	0	2	0	1	0	1	1	0

is also retrieved in all five trees, but there is no further resolution among the *G. lineata* complex.

Employing only *Afrogecko* species as an outgroup to *Goggia* reduces the number of potentially informative allozyme characters to twelve, as only one allele is present at the Fum locus in all *Goggia.* This analysis yields 24 most parsimonious trees (length 14, c.i. 0.658). The strict consensus of these trees is largely unresolved, although the clade (*lineata* (*gemmula, microlepidota*)) is always retrieved.

Using only the five morphological characters that are not monomorphic among *Goggia* and assigning *Afrogecko* as the outgroup it is not possible to produce a tree which maintains the monophyly of the ingroup. The expansion of the morphological data set to 18 characters (Appendix C) that vary within the group *Afrogecko* plus *Goggia,* however, yields a single most parsimonious tree (length 22, c.i. 0.864) when *G. braacki, G. essexi, G. hewitti, G. hexapora, G. lineata,* and *G. rupicola,* which are identical for all characters scored, are treated as a single taxon. *Goggia microlepidota* is the sister species of the unresolved clade containing all of its congeners.

Examining only morphological data but expanding the outgroup to include all of the leaf-toed geckos yielded 225 equally most parsimonious trees each with a length of 40 and a consistency index of 0.500. In the resulting strict consensus cladogram the monophyly of *Goggia* was not corroborated, as there is an unresolved trichotomy involving the *Goggia lineata* complex, *G. microlepidota,* and *Dixonius. Afrogecko, Cryptactites, Euleptes, Urocotyledon,* and *Ebenavia* formed another, distantly related clade.

The incorporation of both allozyme and morphological data (30 characters) for *Goggia* and *Afrogecko* produced 102 trees of 60 steps and a consistency index of 0.700. The strict consensus of these trees collapsed most of the *lineata* complex species into a polychotomy but retrieved *lineata* and *rupicola* as sister taxa and *microlepidota* as the sister species of the entire *lineata* complex. Expanding the analysis of the full data set to include all of the leaf-toed geckos as outgroups yielded 45 most parsimonious trees (length 184, c.i. 0.880). A single strict consensus tree yielded the pattern (*microlepidota* ((*gemmula, lineata*), *rupicola,* (*braacki, essexi, hewitti, hexapora*))) (Fig. 10).

These results are largely consistent with the results of analyses performed by Good, Bauer, and Branch (1996). In their study *Goggia hewitti, G. hexapora, G. braacki* and *G. essexi* cluster together both phylogenetically and phenetically. In the phenetic analysis this group was next most

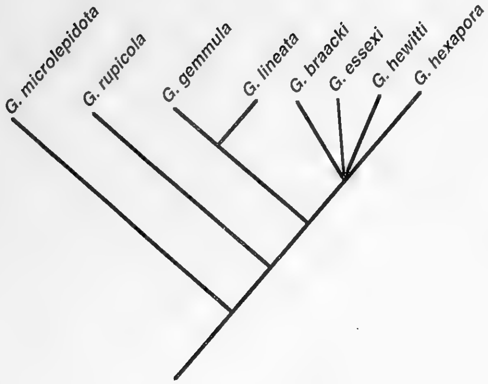


FIGURE 10. Consensus cladogram of relationships within the genus *Goggia* produced from the complete data set of allozyme and morphological characters. Note that there is no strong evidence that the outgroup taxa employed in this analysis (all other leaf-toed geckos) are monophyletic, or even paraphyletic.

similar to the group *G. lineata* + *G. rupicola,* with *G. gemmula* being the most dissimilar. The phylogenetic analysis yielded no resolution within the clade *essexi* + *hewitti* + *hexapora* + *braacki,* but placed *G. rupicola, G. lineata,* and *G. gemmula* as sequentially more distant sister taxa to this group. Using a technique developed by Good and Wake (1992, 1993), and de Queiroz and Good (1997), Good, Bauer, and Branch (1996) further analyzed the geographic patterns of geographic distance and demonstrated that at least some of the genetic distance that had accumulated between species reflected initial genetic divergence with geographic distance within the ancestral species prior to vicariance and subsequent speciation. Thus, the genetic distance of 0.288 between *G. essexi* and *G. rupicola* reflects an initial within species divergence of 0.25 Nei (1978) genetic distance units per 1000 km plus the accumulation of a post-vicariance genetic distance of approximately 0.13 genetic distance units. The distance between *G. essexi* and the geographically closer *G. braacki* (0.213) is less because of the lower initial geographic distance between populations in the ancestral form, not because of a difference in time of divergence. Taking this information into account their preferred phylogeny was (*gemmula* (*lineata* (*braacki, essexi, hewitti, rupicola*))) (Fig. 11).

The five species of the *Goggia lineata* complex that Good, Bauer, and Branch (1996) believed to have separated from each other essentially simultaneously are each endemic to a single montane or upland rocky region. Based on minimum and maximum calibrations of 8.9 and 26 MY per Nei genetic distance unit (see Branch et al. 1995 for a review of the literature on this topic in the context of African gekkonids), this divergence probably took place 1.2–3.4 MYA. The calibration of 18 MY per unit first proposed by Brody et al. (1993) for cordylids in southern Africa yields an estimate of 2.3 MYA for the divergence. The divergence of the ancestor of these five taxa from *G. lineata* may be similarly calculated at 3.2 MYA (1.6–4.7 MYA), and that of *G. gemmula* from all remaining *lineata* complex species at 5.8 MYA (2.9–8.3 MYA). Because of the broad range of possible calibration values and the questionable validity of dating cladogenic events on the basis of distance data, we do not intend to attempt to tie these divergence estimates to particular candidate vicariant events in southern Africa. However, these results are broadly suggestive that events spanning from the Miocene to Pleistocene may have produced the observed patterns of diversity in *Goggia.* The Late Miocene cooling of the Atlantic Ocean and development of the Benguela Current produced increasing aridity in the region and resulted in the

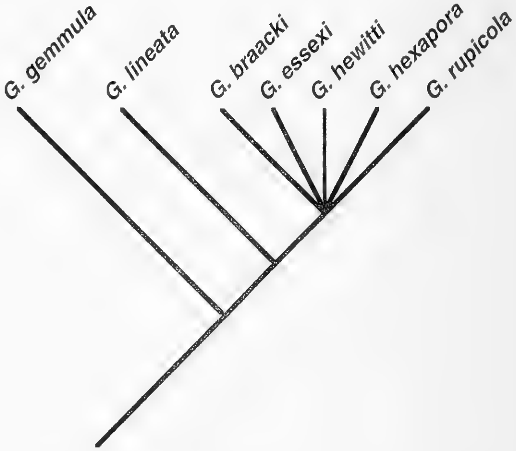


FIGURE 11. Preferred pattern of relationships among the *Goggia lineata* complex of species based on a combination of phylogenetic results and the analysis of genetic distance in relation to geographic distance (see Good et al. 1996). Under this hypothesis the group of five small *G. lineata* complex species cannot be resolved because they diverged simultaneously as a result of climatic changes affecting the entire range of the ancestral form.

cooler, more xeric southern African climate of the early Pliocene (Tyson 1986). Floral extinctions during this period yielded the contraction and fragmentation of formerly continuous habitat types that may have isolated ancestral populations of members of the *G. lineata* complex.

The much larger genetic distances between *Goggia microlepidota* and its congeners, as well as its overall morphological distinctness, suggest that the initial cladogenic event in the *Goggia* lineage took place well before the Late Miocene. Candidate events include secondary orogenic activity in the Cape Fold Mountains or earlier climatic changes.

Divergence distance between the two species of *Afrogecko* for which allozymes were examined is greater still (Fig. 3). Further, the highly disjunct distribution of this genus as a whole and the morphological disparity among species suggest that diversification within this group took place earlier in the Tertiary than that of *Goggia.* The origin of both genera, however, remains obscure and there are no obvious candidates for the immediate sister group of either.

Both *Afrogecko and Goggia* have radiated in southern Africa and include species endemic to remote montane areas, suggesting a long history in the region. The known distribution of *Cryptactites,* however, includes only two small areas of littoral and estuarine habitat near prominent headlands in the Eastern Cape. This pattern of distribution, as well as the fact that only a single species appears to occur in Africa, has raised the possibility that *Cryptactites peringueyi* may have arrived on the Eastern Cape by recent overwater dispersal (McLachlan 1988). A coastal headland distribution pattern is seen elsewhere in southern African lizards only in *Cryptobelpharus boutonii africanus,* apparently a relatively recent derivative of a widespread Indo-Pacific lineage known for overwater dispersal capabilities (Branch 1988; Haacke 1989). Very recent arrival appears unlikely for *C. peringueyi* because the species is clearly not conspecific with gekkonids from anywhere else in the world. Further, we have demonstrated that it differs significantly, both in allozyme and morphological characters from all other groups of leaf-toed geckos. Nonetheless, its affinities may lie with Madagascan or Asian groups rather than with other African gekkonids. It is interesting to note in this regard that the Port Elizabeth area, specifically the type locality of *C. peringueyi,* received a large influx of floating pumice and associated organic debris following eruption of Krakatau in 1883 (Simkin and Fiske 1983; Oelofsen et al. 1986) and might be expected to receive propagules originating from Asia or the southern Indian Ocean.

Because the goal of this study was not to resolve relationships among leaf-toed geckos, but to delineate probable monophyletic groups among the Old World *"Phyllodactylus,"* we cannot propose a reconstruction of the evolutionary history of each of these groups. However, the large genetic and morphological gaps separating each of the generic level taxa, diagnosed herein, from one another strongly suggest that the leaf-toed morphology has evolved on many occasions in many parts of the world, and that each clade of leaf-toed geckos may have had a long history independent of other superficially similar groups. We believe that the break-up of suspect polyphyletic groups, such as *Phyllodactylus,* into monophyletic units is a necessary first step in resolving relationships within higher order taxa. The future use of the monophyletic units *Euleptes, Haemodracon, Dixonius, Afrogecko, Cryptactites,* and *Goggia* should thus facilitate the resolution of patterns of affinity within the Gekkonidae.

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Appendix A

SPECIMENS EXAMINED. — Except for the southern African leaf-toed geckos, only skeletal specimens examined are listed. Specimens examined osteologically by means of radiographs are indicated by an asterisk (*), dry skeletal specimens are indicated by (sk) and cleared and stained specimens by (c&s). Locality data are provided for those southern African species that have not been recently revised. Named localities as well as quarter degree square coordinated are provided (see Leistner and Morris [1976] for an explanation of the quarter degree notation). A complete list of specimens examined for *Goggia lineata, G. rupicola, G. essexi, G. hewitti,* and *G. hexapora* was provided in Branch et al. (1995). Specimens examined for *G. gemmula* were given by Bauer et al. (1996) and those for *G. braacki* were listed by Good et al. (1996).

Afrogecko ansorgii: BMNH 1946.8.24.52-53*. ***Afrogecko porphyreus***: Namibia: Swakopmund (2214Da) AMNH 47898; South Africa, Northern Cape Province: Nieuwoudtville (3119Ac) SAM 3078; Western Cape Province: Bitterfontein (3118Ab) PEM-AM 6943; Jacobsbaai (3217Dd) CAS 167586-7*, 167589-90*, 173911*, 173912, 143913*, 175286-7*, 175408*, 176041, 176044, 176051*; Hoedklip, 32°49′45″S 17°51′07″E, 20 m (3217Dd) JEM FB 511; Maritzbaai, 32°58′37″S 17°52′50″E, <20 m (3217Dd) JEM FB 527; Clanwilliam (3218Bb) SAM 18564; Klein Tafelberg, 32°33′08″S 18°27′50″E, 320 m (3218Cb) JEM FB 837; Helenabaai, 32°45′52″S 18°01′48″E, 30 m (3218Cc) JEM FB 617; Kouebokkeveld Mts. (3219Cc) SAM 2408; Dasklip Pass, 13 km NE of Porterville (3219Cc) CAS 175319; Farm Excelsior, 32°57′26″S 19°25′23″E (3219Cd) AMB H8585 (c&s); Hoedjies Point, Saldanha (3317Bb)

SAM 45138-40; Saldanha, 33°01′15″S 17°56′57″E, >20 m (3317Bb) JEM FB 23-4; Marcuseiland, 33°02′32″S 17°58′11″E, <20 m (3317Bb) JEM FB 291-5, SAM 44776-7; Malgaseiland, 33°03′09″S 17°55′35″E, <20 m (3317Bb) JEM FB 333-4; Jutteneiland, 33°04′57″S 17°57′19″E, <20 m (3317Bb) JEM FB 323-5, SAM 19431 (2 specimens), 19432, 44827-9; Plankiesbaai, 33°07′54″S 17°58′22″E, <15 m (3317Bb) JEM FB 255-6; Vondelingeiland, 33°09′08″S 17°58′00″E, <20 m (3317Bb) JEM FB 310-3; Meeuw Island (3318Aa) SAM 44770-1; Schaapen Island (3318Aa) JEM FB 125-6, PEM 1572-3, 1575-8, 1580, 1588-89; Boomgat, 33°01′42″S 17°57′37″E, <20 m (3317Bb) JEM FB 297; Leentjiesklip, 33°02′44″S 18°02′31″E, <20 m (3318Aa) JEM FB 286; Leentjiesklip, 33°04′09″S 18°02′25″E, <20 m (3318Aa) JEM FB 289-90; Konstabelberg 33°07′53″S 18°01′16″E, 120 m (3318Aa) JEM FB 269; Yzerfontein (3318Ac) SAM 44998-9; Dassen Island, 33°25′18″S 18°05′02″E, <20 m (3318Ac) JEM FB 862-3, PEM 4607-23, SAM 44830, 44833-4; Matroosbaai, 33°36′09″S 18°22′13″E, <20 m (3318Cb) JEM FB 450; Blouberg, 33°44′57″S 18°27′47″E, 188 m (3318Cb) JEM FB 192-3; Robben Island (3318Cd) PEM 10682, SAM 42979-80; Platteklip Gorge, Table Mountain (3318Cd) SAM 144; Table Mountain (3318Cd), AMNH 47899-900, SAM 2053-4; Range Cottage nr. Cape Town (3318Cd) MCZ 20980; Cape Town (3318Cd) AMNH 47901-6, MCZ 11930-1, PEM 10579-86, SAM 1174-6, 13588, 17679, 18856, 45496, ZMB 44028; Mowbray (3318Cd) SAM 43536; Cape Town, 33°49′06″S 18°22′22″E (3318Cd) SAM 47797-8; Betel, 33°34′24″S 18°48′35″E, 520 m (3318Db) JEM FB 146-7; Paarlberg, 33°42′47″S 18°55′30″E, 580 m (3318Db) JEM FB 196-7; Meerendal, 33°47′07″S 18°37′00″E, 380 m (3318Dc) JEM FB 100-1; Milnerton (3318Dd) SAM 43999; Jonkershoek (3318Dd) CAS 167605, PEM 4985, 5012; Simonsberg, 33°53′05″S 18°55′33″E, 1300 m (3318Dd) JEM FB 501; Groot-Winterhok, 33°03′50″S 19°05′40″E, 660 m (3319 Aa) JEM FB 1052; Slagboom, 33°14′21″S 19°17′09″E, 960 m (3319Ab) JEM FB 960-3; Obiekwa, 33°15′58″S 19°04′07″E, 420 m (3319Ac) JEM FB 965; Skurweberg, 33°21′48″S 19°16′35″E, 580 m (3319Ad) JEM FB 986; Lakenvleidam, 33°221′17″S 19°34′40″E, 1000 m (3319Bc) JEM FB 603; De Doorns, 33°22′30″S 19°39′53″E (3319Bd) PEM 663, SAM 47795-6; Matroosberg, slopes between ski huts and "conical peak" (3319Bd) PEM 3602-8; Du Toitskloof (3319Ca) SAM 43877-8; Eerste Tol Bainskloof, 33°37′31″S 19°06′13″E, 675 m (3319Ca) JEM FB 1048-9; Hawekwaberge, 33°41′05″S 19°05′42″E, 1140 m (3319Ca) JEM FB 920-1; 300 ft below Franshoek Pass on road to Fishoek (3319Cc) CM 64516; Hottentotsholland Nature Reserve, 8 km E of Franschhoek (3319Cc) CAS 175317; La Motte, 33°52′16″S 19°04′33″E, 400 m (3319Cc) JEM FB 484-5; Mont Rochelle, 33°53′35″S 19°09′17″E, 1120 m (3319Cc) JEM FB 1533-6; Stettyn, 33°52′31″S 19°20′25″E, 540 m (3319Cd) JEM FB 1547; Elandskloofdam, 33°57′11″S 19°17′33″E, 760 m (3319Cd) JEM FB 1260; Kleinfontein, 33°57′11″S 19°24′19″E, 880 m (3319Cd) JEM FB 1263-4; Jonaskop, 33°58′S 19°30′E, 1640 m (3319Dc) JEM FB 877-8; Baileys Peak, Rooiberg, 33°38′11″S, 21°26′04″E (3321Cb) PEM 8569, 8672-3; Bailey's Peak, Rooiberg, Little Karoo, 33°38′15″S, 21°26′22″E (3321Cb) 1166 m, CAS 195398; Gamka Mountain Reserve, 33°44′S, 21°56′E (3321Db) PEM 6746-8; Montagu Pass, Outeniquaberg (3322Cd) PEM1057; Saasveld Forest Station (3322Dc) PEM 3678; Goukamma Nature Reserve, Groenvlei, Knysna District (3422Bb) PEM 1038, 1045, 1056; Karatara (3322Dd) PEM-AM 5922; Leisure Island, Knysna, 33°48′S, 23°03′E (3323Cc) PEM 11788; Knysna, 33°57′00″S, 23°06′30″s (3323Cc) PEM 10124; Prince Alfreds Pass (3323Cc) PEM 1454; Formosa Conservation Area, 33°47′19″S, 23°23′58″E (3323Cd) PEM 9326; Steenoondrug, Grootrivier Pass, 33°57′50″S, 23°33′30″E (3323Dc) PEM 1928; Wynberg (3418Ab) SAM 1968; St. James (3418Ab) PEM 10597; Bergvliet, Cape Town (3418Ab) PEM 1554; Hout Bay (3418Ab) SAM 6096, ZFMK 20729-30; Simonstown (3418Ab) ZMB 23562 (2 specimens); Fischoek (3418Ab) PEM 1574, 1579, 1581-2, 1584-7; Cape Peninsula (3418Ab) CAS 111943*, PEM 10587-9; Constantia Nek (3418Ab) SAM 17969 (2 specimens); Cape Peninsula, Noordhoek (3418Ab) CAS 106039*, USNM 159123-4; Kalk Bay (3418Ab) PEM 10594-6; Cape of Good Hope (3418Ad) AMNH 47907, ZMB 408 (2 specimens); Olifantsbosch, Cape Point (3418Ad) SAM 44368-9; 1.4 km N of Steenbrasrivier on Rt. 44 (3418Bb) CAS 193647-49; S side of Steenbrasrivier at Rt. 44 (3418Bb) CAS 193650-1; Hottentots Holland above Sir Lowry's (3418Bb) SAM 3939; Somerset West (3418Bb) PEM 660, 666, 1436 [3 specimens]; Jonkershoek, 34°00′06″S 18°59′38″E, 1640 m (3418Bb) JEM FB 902; Rooskraal, 34°04′37″S 18°58′31″E, 680 m (3418Bb) JEM FB 1019-20; Strand, 34°06′08″S

18°49′13″E, 20 m (3418Bb) JEM FB 869, 913; Verkykerskop, 34°06′08″S 18°58′04″E, 1200 m (3418Bb) JEM FB 996-7; Verkykerskop, 34°06′08″S 18°58′21″E, 880 m (3418Bb) JEM FB 1015-6; Gandoupas, 34°07′52″S 18°56′60″E, 560 m (3418Bb) JEM FB 1024-5; Kogelberg, 34°10′40″S 18°55′52″E, 500 m (3418Bb) JEM FB 1034-5; Kogelberg, 34°12′14″S 18″55′48″E, 800 m (3418Bb) JEM FB 1031-2; Cape Point (3418bC) CAS 85909-10*, SAM 43234, 44604; Die Mond (3418Bd), MCZ 45471-9; Cape Hangklip (3418Bd) AMB 2140 (c&s), 2144 (c&s), 2146 (c&s), H8523 (c&s), H8530 (c&s), CAS 167591-603*, 167605*, 175299-300, 175301-12*, 200120-24, LSUMZ 57239-43, SAM 44025; Mountain Rose, 34°19′39″S 18°58′27″E, 140 m (3418Bd) JEM FB 1454-5; Rooielsrivier, 34°17′47″S 18°51′06″E, 220 m (3418Bd) JEM FB 1460; Cape Flats (3418Dc) SAM 428, ZMB 22898 (7 specimens); Boskloof, 34°00′24″S 19°20′56″E, 1000 m (3419Ab) JEM FB 1550-1; Boskloof, 34°01′48″S 19°21′38″E, 760 m (3419Ab) JEM FB 1549; Onrust, on beach (3419Ac) SAM 44800; Perdekloof, 34°17′45″S 19°13′38″E, 180 m (3419Ac) JEM FB 1530; Kleinmond, 34°20′37″S 19°16′33″E, 250 m (3419Ad) JEM FB 1516-8; Platberg, 34°22′16″S 19°16′21″E, 520 m (3419Ad) JEM FB 1321-2; Riviersonderend Mts. (3419Ba) SAM 18009, 18340; just W Cape Agulhas (3419Bd) SAM 44788; Die Kelders, Hermanus (3419Cb) SAM 18352; Franskraal, 34°35′27″S 19°23′25″E, 110 m (3419Cb) JEM FB 1419; Danger Point, 34°37′29″S 19°19′37″E, 20 m (3419Cb) JEM FB 1415-6; Wydgele, 34°29′25″S 20°25′48″E, De Hoop Nature Reserve (3420Ad) SAM 47794; Plettenberg Bay (3421Ac) PEM 1567-71, 7892; Mossel Bay (3422Aa) PEM 10590-3; Groenvlei, Sedgefield (3422Bb) PEM 1515; Goukamma Nature Reserve (3422Bb) PEM 6529; Knysna (3423Aa) SAM 13583 (2 specimens), 13585; 14329 (2 specimens); Robberg Nature Reserve (3423Ab) PEM3134-8; Eastern Cape Province: Coldstreams (3323Dc) PEM 1583; Walmer, Port Elizabeth (3325Cd) CAS 199986-8, LSUMZ 57244-6, PEM 7052-3, 8058, 8076-9; Humewood Road, Port Elizabeth (3325Dc) PEM 2686; Grahamstown, 33°18′55″S, 26°31′50″E (3326Bc) PEM 6531, 7743; Cape St. Francis (3424Bb) PEM-AM 7649, 7791; Imprecise or untraceable localities: Tygerberg and Hout Bay ZFMK 21921-3; Langekuil near Don R., Clanwilliam SAM 2856-7; Meyverhouts Kraal, Clanwilliam SAM 3392; Riversdale Mts., 4000-4500 ft. SAM 17654 (2 specimens); Cape Province, ZMB 25045 (2 specimens); Namaqualand SAM 778; Cape SAM 545, 547, 1365; no locality, PEM 1929. Africa AMNH 6. ***Afrogecko swartbergensis**:* [all localities in Western Cape Province, Republic of South Africa] Gouekranshut, 33°19′16″S, 22°14′32″E (3322Ac) PEM 6876, 6879, 7834; 1.6 km along Summit track, Groot Swartberg, 33°21′S 22°03′E (3322Ac) PEM 6754, 6756, 6876; Head of Mooikloof, Groot Swartberg, 33°20′S, 22°18′E (3322Ad) CAS 180418*, 180419 (c&s), PEM 6877; Blesberg radio mast, 33°24′55″S, 22°41′34″E (3322Ad) PEM 7843. ***Assaccus elisae**:* BMNH 1961.15.01*, CAS 86525-7*, 86528 (sk), 86529*. ***Asaccus gallagheri**:* BMNH 1973.1847-9*, 1973.2894-5*. ***Asaccus griseonotus**:* CAS 170817-8*. ***Christinus marmoratus**:* CAS 74995*, 75029*, 83512-58, 83560-69, CAS 83570 (sk). ***Cryptactites peringueyi**:*[all records in Eastern Cape Province, Republic of South Africa] Kromme River Estuary (3424Bb) CAS 186374-5*; Kaia da Balaia, upper Kromme River, 34°07′S, 24°47′E (33424Bb) PEM 6886*, 6887, 6916*, 7210; bridge at Kromme River mouth, 34°08′S, 24°48′E (3424Bb) PEM 10875-6, 11334; 50 m NW kromme River Bridge, 34°08′S, 24°48′E (3424Bb) CAS 186383*, PEM 6910, 6911 (c&s), 6912-15*; 200 m W of Kromme River Bridge, 34°08′S, 24°48′E (3424Bb) PEM 6908, 6909; west bank of Kromme River mouth, 34°09′S, 24°49′E (3424Bb) PEM 8068; Willows, Port Elizabeth, 34°03′S, 25°37′E (3425Ba) PEM 12207-8; Chelsea Point, 34°03S, 25°38′E (3425Ba) PEM 12206, SAM 8628* [paralectotype]; Schoenmakerskop, 34°04′S, 25°35′E (3425Ba) PEM 12209; Imprecise locality [in error]: Little Namaqualand (no specific locality) SAM 777* [lectotype]. ***Dixonius melanostictus**:* FMNH 178232*. ***Dixonius siamensis**:* BMNH 1946.8.24.51*, 1946.8.24.40-41*, 1931.10.13.3-4*, 1931.10.13.6, CAS 95254-5*, 95256 (sk), 95257*, FMNH 177696*, 177730 (c&s), 177732*, 177735*, 177766 (c&s). ***Ebenavia inunguis**:* CAS 66195-6*, ZMB 19007* (4 specimens), 19008* (2 specimens), 19009*, 19200* (4 specimens), 19460* (3 specimens), 19461* (8 specimens), 19462* (11 specimens), 19521* (11 specimens), 22598* (5 specimens), 30631* (6 specimens). ***Euleptes europaea**:* MZUF 19119-19139*, 19721*, USNM 014861(2 specimens), 037216. ***Goggia braacki**:* CAS 199989-91*, PEM R3270*, 4323*. ***Goggia essexi**:* CAS 186376-7*, PEM R664 (c&s), PEM R665*. ***Goggia gemmula**:* CAS 186352*, 200080*, 200090 (c&s), 200095*. ***Goggia hewitti**:* CAS 167607*, 175273*, 180353*, 180354 (c&s), 180357 (c&s), 180358*, 180369*, 180371-2*, PEM R 3623*. ***Goggia hexapora**:* CAS 113537*, 167606*, 167608 (c&s), 167609*, 175420*, 157421 (c&s), 200114*. ***Goggia lineata**:*

AMB H8611 (c&s), CAS 85926-7*, 167578-85*, 167588*, 173899*, 157288-99*, 157319*, 154415-9*, 176042-50*, 186319-21*, 200013*, 200015-6*, 200027*, 200068*, 200106*, 5 specimens (no number, c&s); PEM R3609*, 4588*. ***Goggia microlepidota***: [all records in Western Cape Province, Republic of South Africa] Pakhuis Pass (3219Aa) - SAM 20531 (holotype), 45494-5; Engelmanskloof Gorge (3219Ac) PEM 6399; Waboomskloof, 32°24′00″S 19°12′30″E, 1370 m (3219Ac) JEM FB 687; Hoogvertoon, 32°29′11″S 19°09′35″E, 1260 m (3219Ac) JEM FB 606, 611; Sneeuberghut, 32°29′13″S 19°10′30″E, 1340 m (3219Ac) JEM FB 938; Bokveldskloof, 32°29′40″S 19°09′5 0″E, 1465 m (3219Ac) JEM FB 688; Skurweberg 3, 33°22′11″S 19°16′27″E, 780 m (3319Ad) JEM FB 994; Buffelsberg, 32°36′52″S 19°11′07″E, 820 m (3219Ca) JEM FB 1393-4; Middelbergpas, 32°37′53″S 19°09′06″E, 1100 m (3219Ca) AMB 2438 (c&s), CAS 167637*, 176035*, 180430-2*, JEM FB 1174-6; Zuurvlakte, 32°58′08″S 19°03′04″E, 1030 m (3219Cc) JEM FB 598; Skurweberg, 32°56′37″S 19°23′42″E, 1125 m (3219Cd) JEM FB 1608-9; Skurweberg, 32°57′S 19°24′E,(3219Cd) JEM 1780; Excelsior, 32°57′26″S 19°25′23″E, 1020 m (3219Cd) JEM FB 1076-7; Op-den-berg, 32°58′05″S 19°24′35″E, 960 m (3219Cd) JEM FB 631; Louws Legplek, 32°02′40″S 19°03′29″E, 940 m (3319Aa) JEM FB 1056-8, 1072; Groot-Winterhoek, 33°03′50″S 19°05′40″E, 660 m (3319Aa) JEM FB 1050-1; Slagboom 33°14′21″S 19°17′09″E, 960 m (3319Ab) JEM FB 957-8; 33°11′29″S 19°37′42″E (3319Bc) JEM FB 1939; Grootvlakte, 33°21′13″S 19°37′14″E (3319Bc) JEM FB 2227; Imprecise locality: Cedarberg, SAM 43746. ***Goggia rupicola***: CAS 19331-6*, 200003 (c&s). ***Haemodracon riebeckii***: BMNH 1953.1.7.95 (c&s), ZMB 10109*. ***Haemodracon trachyrhinus***: BMNH 1946.819.81*, 1967.496-7. ***Paroedura guibeae***: FMNH 73051*, 73059-60*. ***Paroedura pictus***: ZMB 18983 (3 specimens). ***Paroedura stumpfi***: CAS 156898-9*. ***Phyllodactylus galapagensis***: CAS 10357 (sk). ***Phyllodactylus gerrhopygus***: CAS 84761*, 84763*, 84765 (sk). ***Phyllodactylus gilberti***: CAS 12676*, 12679 (sk), 12681*. ***Phyllodactylus homolepidurus nolascoensis***: CAS 98534 (sk). ***Phyllodactylus leei***: CAS 10062 (sk), 11053*, 11993*. ***Phyllodactylus pumilus***: FMNH 197831*. ***Phyllodactylus tuberculosus saxatilis***: CAS 58953 (sk). ***Phyllodactylus unctus***: CAS 91343 (SK), 91352*, 91355*, 147376 (c&s). ***Phyllodactylus ventralis***: FMNH 165833-5*. ***Phyllodactylus wirshingii***: CAS 175498 (c&s), 175500*. ***Phyllodactylus xanti xanti***: CAS 98509 (sk), 98510*, 98514*, 147377 (c&s). ***Urocotyledon inexpectatus***: ZMB 9381* (3 specimens) - skulls examined by superficial dissection.

Appendix B

Tissue samples used in phenetic and phylogenetic allozyme analysis of leaf-toed geckos. Frozen tissue collection numbers (if different from corresponding whole specimen numbers) are listed parenthetically. Collection abbreviations are detailed in the Materials and Methods section except GVH (= Gerald V. Haagner field series, to be deposited in PEM).

Afroedura loveridgei (n = 1) GVH 3969; ***Afrogecko porphyreus*** (n = 5) CAS 193647-50, 195398 (LSUMZ H2800-4); ***Afrogecko swartbergensis*** (n = 1) CAS 180419 (LSUMZ H1508); ***Christinus marmoratus*** (n = 1) unnumbered; ***Cryptactites peringueyi*** (n = 2) CAS 186374-5 (LSUMZ H1666-7); *Dixonius siamensis* (n = 1) MVZ uncatalogued; ***Goggia braacki*** (n = 10) CAS 199989-91, LZUMZ 57330-2, PEM R11890, 11922, 12379-80; ***Goggia essexi*** (n = 2)CAS 186376-7 (LSUMZ H1655-56); ***Goggia gemmula*** (n = 5) CAS 186352 (LSUMZ H1658), 193364-5, 193641-2; ***Goggia hewitti*** (n = 7) CAS 180353-4, 180356-7, 180360, 180371-2 (LSUMZ H1501-7); ***Goggia hexapora*** (n = 4) CAS 200114, LSUMZ 57360, PEM R 12381-2; ***Goggia lineata*** (n = 5) CAS 193254, 193351-4 (LSUMZ H2794-8); ***Goggia microlepidota*** (n = 1) CAS 180432 (LSUMZ H2799); ***Goggia rupicola*** (n = 5) CAS 193341-6 (LSUMZ H2805-9); ***Paroedura picta*** (n = 1) AMB 4176; ***Phyllodactylus wirshingi*** (n = 1) SBH 101730; ***Phyllodactlyus xanti*** (n = 2) MVZ FC 13226-7.

Appendix C

Morphological characters used in analyses of the phylogeny of the genus *Goggia*. Character states for outgroup taxa, except *Afrogecko* spp. are based on composites for the entire genus.

	Characters																	
Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
G. braacki	0	0	0	0	1	1	0	0	1	0	0	0	0	1	1	0	1	0
G. essexi	0	0	0	0	1	1	0	0	1	0	0	0	0	1	1	0	1	0
G. gemmula	0	0	0	0	1	1	0	0	1	0	0	0	0	2	1	0	1	0
G. hewitti	0	0	0	0	1	1	0	0	1	0	0	0	0	1	1	0	1	0
G. hexapora	0	0	0	0	1	1	0	0	1	0	0	0	0	1	1	0	1	0
G. lineata	0	0	0	0	1	1	0	0	1	0	0	0	0	1	1	0	1	0
G. rupicola	0	0	0	0	1	1	0	0	1	0	0	0	0	1	1	0	1	0
G. microlepidota	0	0	0	1	1	1	0	0	1	0	0	0	1	0	0	0	1	1
A. porphyreus	0	1	1	1	0	0	1	1	0	0	1	1	0	9	1	1	0	0
A. swartbergensis	1	1	1	0	0	0	1	1	0	1	1	1	1	0	1	1	0	1
A. ansorgii	0	1	0	1	0	0	1	1	0	0	1	1	1	0	1	1	0	0
Phyllodactylus	2	1	9	0	0	1	0	0	1	0	0	1	1	0	0	0	1	0
Asaccus	2	1	0	0	0	0	0	0	0	0	0	9	1	9	0	0	1	0
Dixonius	2	0	0	0	1	1	0	0	1	0	0	0	1	0	9	0	0	1
Cryptactites	2	1	1	1	0	0	1	1	0	0	1	1	0	0	1	1	0	0
Haemodracon	0	9	0	0	0	9	1	1	1	0	1	9	1	0	9	0	0	0
Ebenavia	2	1	1	1	0	0	0	1	0	0	1	9	0	0	1	0	0	0
Christinus	0	1	0	0	0	1	9	1	0	0	1	1	9	0	0	0	0	0
Euleptes	0	1	0	1	0	0	1	0	0	0	0	0	0	1	1	0	0	0
Urocotyledon	0	1	1	1	0	0	1	9	1	0	1	9	0	0	1	0	0	0
Paroedura	0	1	0	0	0	0	0	1	1	0	1	1	1	9	0	0	0	0

Note that characters states were arbitrarily assigned numerical values and that polarity was established on the basis of choice of outgroup (see text).

1. Dorsal body scales atuberculate (0), tuberculate - smooth (1), or tuberculate - keeled (2).
2. Rostral cleft present (0), or absent (1).
3. First supralabial enters nostril (0), or excluded from nostril (1).
4. Enlarged chinshields present (0), or absent (1).
5. Preanal pores absent (0), or present (1).
6. Cloacal spurs consisting of 1-2 enlarged scales (0), or a comb of 3-7 scales (1).
7. Nasal process of premaxilla long and lanceolate (0), or short and broad (1).
8. Nasal bones paired (0), or fused (1).
9. Frontal bone not or barely contacting maxilla (0), or broad fronto-maxillary contact (1).
10. Parietal bones paired (0), or fused (1).
11. Stapes perforate (0), or imperforate (1).
12. Inner proximal ceratohyal process absent (0), or present (1).
13. Atlantal arches fused (0), or paired (1).
14. Lumbar vertebrae 1 (0), 2 (1), or 3 (2).
15. 5 or more (0), or 4 or fewer (1) pairs of sternal + mesosternal ribs.
16. Interclavicle with (0), or without (1) well-developed lateral processes.
17. Precoracoid-mesoscapular connection cartilaginous (0), or ligamentous (1).
18. Extraphalangeal digital ossifications absent (0), or present (1).

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A REVIEW OF THE OCTOCORALLIAN GENUS *LEPTOGORGIA* (ANTHOZOA: GORGONIIDAE) IN THE INDIAN OCEAN AND SUBANTARCTIC, WITH DESCRIPTION OF A NEW SPECIES AND COMPARISONS WITH RELATED TAXA

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A remarkable new species of the large and widespread gorgoniid genus *Leptogorgia* is described from the southwestern Indian Ocean. A variant of *L. gilchristi* is described from the Mozambique/South African border region, the only known record of the genus as a member of an Indo-Pacific coral reef community. The subantarctic *L. lutkeni* is redescribed and compared to a similar species in South Africa. The genus *Leptogorgia* is compared with related taxa in the family Gorgoniidae (including the genus *Pseudopterogorgia*), and new distributional data are provided for the Indo-West Pacific species. A dichotomous key is included for all southern African and subantarctic species of *Leptogorgia* that are currently recognized as valid.

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Leptogorgia is a large genus of gorgonian octocorals (family Gorgoniidae) representing approximately 54 valid species. The genus is distributed throughout most of the Panamic Province, much of the Atlantic Ocean including the Caribbean and Mediterranean seas, and around southern Africa into the southwestern fringe of the Indo-Pacific. One species is present in the subantarctic.

Twelve tropical western Atlantic species are considered valid by Bayer (1961). Carpine and Grasshoff (1975) and Grasshoff (1982, 1986, 1988, and 1992) recognized 24 species as valid from the eastern Atlantic, which includes Europe, the Mediterranean, the Atlantic archipelagoes, and the west coast of Africa. The southern African and subantarctic taxa (at least 6 valid species) are reviewed by Williams (1992a) and the present paper. Three other southern African species described by Kükenthal, 1919, *Leptogorgia abietina*, *L. tenuissima*, and *L. pusilla*, all from Francis Bay, Cape Province, at 100 m depth, are of questionable validity. The eastern Pacific species (southern California to Chile and the Galapagos Islands) are in major need of revision. Hardin (1979) provided an unpublished review of these taxa (approximately 12 species).

The present account provides the description of a new species of *Leptogorgia* from central Natal in the Indian Ocean. The species is remarkable in having an expanded coenenchyme, unlike any other species of the genus. A relatively small, brick-red variant of the southern African endemic species, *Leptogorgia gilchristi*, is described from the coral reefs of northern Natal near the Mozambique/South African border. In addition, *Leptogorgia lutkeni* from subantarctic Prince Edward Island is here redescribed and compared with a superficially similar variant of the South African species *Leptogorgia palma*. Lastly, certain species of *Leptogorgia* are compared with related gorgoniid taxa including *Pseudopterogorgia*, *Pterogorgia*, and *Hicksonella*. New distribution data are provided concerning the geographic ranges of *Leptogorgia* and *Pseudopterogorgia* in the Indo-West Pacific.

MATERIAL AND METHODS

Some of the preserved material used in this study was acquired on loan from the Natural History Museum, London (NHM) and the South African Museum, Cape Town (SAM). Other material was examined from the collections of the California Academy of Sciences, Department of Invertebrate Zoology, San Francisco (CAS). All material was preserved in ethanol. Sodium hypochlorite was used to dissociate sclerites from tissue. Permount mounting medium was used to make permanent microscope slides of sclerites. An Olympus CH-2 compound microscope with drawing tube and a Nikon SMZ-10 zoom dissecting microscope with drawing tube were used to produce the figures. A Hitachi S-510 scanning electron microscope was used to make sclerite micrographs. Terminology used throughout the paper corresponds to that of Bayer, Grasshoff, and Verseveldt (1983).

SYSTEMATIC ACCOUNT

Key to the Southern African and Subantarctic Species of *Leptogorgia*

1. Branches conspicuously flattened with expanded coenenchyme and biserial polyps throughout. Color lemon yellow . . *L. bayeri*
—Branches cylindrical, or if somewhat flattened, then coenenchyme not expanded. Polyps mostly disposed uniformly over entire surface of branches or in several rows on opposite sides of lower branches, but not biserially arranged. Color variable: mauve, red, orange, yellow, pink, or white 2
2. Branching dichotomous or somewhat lateral 3
—Branching pinnate 6
3. Color deep red 4
—Color yellow or white 5
4. Largest sclerites 0.10 mm in length *L. palma*
—Largest sclerites 0.10–0.17 mm in length . . . . *L. lutkeni*
5. Color white. Sclerites mostly slender and symmetrical with well-separated whorls of tubercles, up to 0.16 mm in length. . . . . *L. barnardi*
—Color yellow. Sclerites mostly robust, many of them slightly curved with asymmetrical tuberculation. . . . . *L. capensis*
6. Color bright orange to deep red. Sclerites mostly 0.1 mm long . Anastomoses never present. . . . . *L. palma*
—Color yellow, white, pink, mauve, rust orange, or dark brick red. Sclerites up to 0.14 mm in length. Anastomoses occasional . . . . *L. gilchristi*

Family **Gorgoniidae** Lamouroux, 1812

Genus **Leptogorgia** Milne Edwards and Haime, 1857

Leptogorgia Milne Edwards and Haime, 1857:163; Verrill, 1868:387; Verrill, 1869:420; Kükenthal, 1924:324; Bielschowsky, 1929:81; Stiasny, 1943:87; Bayer, 1956:212; Bayer, 1961:214; Grasshoff, 1988:97; Grasshoff, 1992:54; Williams, 1992a:231. Type species *Gorgonia viminalis* Pallas, 1766, by subsequent designation of Verrill, 1868:387; Eastern Atlantic.

Lophogorgia Milne Edwards and Haime, 1857:167; Kükenthal, 1924:322. Bielschowsky, 1929:73; Stiasny, 1943:87. Bayer, 1956:212. Bayer, 1961:194. Type species by monotypy: *Gorgonia palma* Pallas, 1766; South Africa.

Filigorgia Stiasny, 1937:307. Stiasny, 1939:301. Bayer, 1956:206. Type species by monotypy: *Filigorgia riodouroi* Stiasny, 1937; West Africa.

REVISED DIAGNOSIS. — Gorgoniid octocorals with branching planar and variable: pinnate, lateral, dichotomous, or filiform. Anastomosis absent in all but two species. Coenenchymal sclerites are radiates and/or spindles with symmetrically or asymmetrically sculptured tuberculation. In elongated spindles, tubercles may appear in whorls. Disc spindles may be present. Anthocodial sclerites often ovoid platelets or flat rods. Color highly variable: white, pink, yellow, orange, red, violet, or brownish; sometimes bicolored.

DIVERSITY AND DISTRIBUTION. — Approximately 53 species in the eastern Pacific, Atlantic, and southwestern Indian oceans, and one species in the subantarctic; mostly shallow-water benthic communities (<100 m), with one species recorded at 567 m.

Leptogorgia bayeri sp. nov.
(Figs. 1–5)

TYPE MATERIAL. — Holotype: SAM-H4834, Landers Reef, 7 km off Park Rynie, Durban region, Natal, South Africa, 50 m depth, December 1984, collected by W. R. Liltved by means of SCUBA.

DIAGNOSIS. — Axis cylindrical. Growth form upright, planar. Branching copious and mostly dichotomous, lateral branching rare. Anastomosis occasional between neighboring branches. Branches ribbon-like from laterally expanded coenenchyme. Polyps biserial along lateral margins of expanded coenenchyme, retractile, not forming calyces. Anthocodial sclerites flat, irregularly shaped rods and plates (0.03–0.12 mm long). Sclerites of the outer coenenchyme compact eight radiates (0.03–0.10 mm long) and elongate spindles (0.10–0.18 mm long); tuberculation symmetrical. Sclerites of inner coenenchyme mostly radiates and robust spindles (0.04–0.10 mm long). Color lemon yellow.

DESCRIPTION. — **Growth form and branching.** The holotype is 295 mm in height and 195 mm in width. The colonial growth form is upright, multiply-branched from a single trunk, and planar (Fig. 1A). The holdfast is spreading, 26 mm at its maximum diameter. The trunk arises 28 mm above the holdfast before the origin of the first branch. The trunk is 7.5 mm in width by 4.5 mm in depth.

The branching pattern is for the most part dichotomous. Lateral branching is also evident in a few areas. The distance between branching nodes varies from 8 to 55 mm. The maximum distance between branching node and distal terminus of the branches is 65 mm. Branch width varies from a minimum of 2.5 mm immediately below a distal terminus to a maximum of 11 mm at a node.

The branches appear flattened and ribbon-like from the lateral expansion of the coenenchyme, which forms opposite wing-like extensions of tissue (Fig. 1B). This lateral compression of the edges results in a somewhat elliptical shape to the branches in cross section (Fig. 1C). The apices of the branches each have a single acute projecting point produced by the terminus of the axis (Fig. 1B).

Several adjacent branches fuse to form occasional anastomoses. The fusions occur not at the branch tips, but below the terminus of each branch, or between branching nodes. The anastomoses are only occasional, and in no way do the branches form a net-like appearance, as in species of the American gorgoniid genera *Gorgonia* and *Pacifigorgia*. The fusions apparently incorporate the axis as well as the coenenchyme.

Polyps. The polyps are arranged biserially and are contained in two opposite longitudinal rows along any particular branch. The polyps are restricted to the edges of the branches and do not appear on the flat broad surfaces of the branches, except for a few polyps in three longitudinal rows along one side of the trunk. The numerous and minute slit-like openings to the polyps are approximately 0.6 mm in length and are separated from adjacent slits by an average of 1.0 mm. The slit-like openings are arranged more-or-less parallel to the longitudinal axis of a particular branch. Most of the polyps havea slightly swollen appearance (Fig. 1B). All of the polyps are completely retracted in the holotype, and thus, aspects of polyp morphology are not distinguished. The retracted polyps do not form conspicuous calyces.

Sclerites. The sclerites are of three main types: plate-like forms, radiates, and spindles.

The sclerites of the anthocodiae are irregularly-shaped, flattened rods or plates, 0.03–0.12 mm in length (Figs. 2A, 4A and B). The margins are not smooth but rather are scalloped or irregularly dentate.

Sclerites of the outer coenenchyme are of two main types (Fig. 2B). Firstly, there are numerous compact, ovoid radiates (mostly eight-radiates), 0.03–0.05 mm in length, with some up to 0.10 mm (Figs. 3A, B, D, G; 4E–N). In contrast to these hightly ornamented forms, some of the radiates are sparsely tuberculated (Fig. 3C–F). Secondly, many elongate spindles are also present, 0.10–0.18 mm in length. These spindles are narrow to more robust, and have several parallel whorls of tubercles (Figs. 2B, 4C, D). Although some of these spindles may be slightly curved,

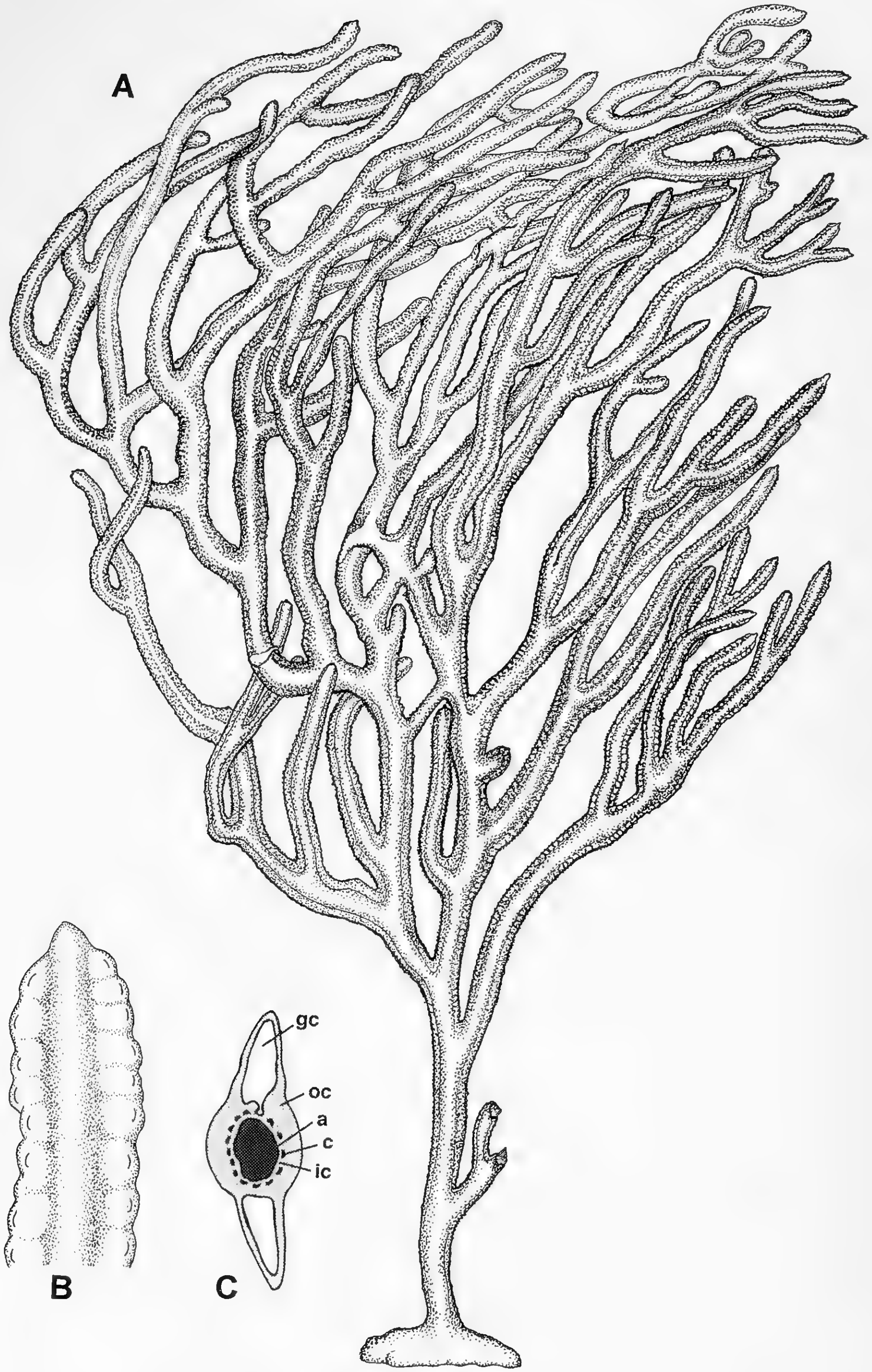


FIGURE 1. Holotype of *Leptogorgia bayeri*. A. Entire holotype, 295 mm in height. B. Terminal branch tip, 11 mm in length. C. Transverse section of terminal branch, 5 mm in length; **a** - axis, **c** - canal, **gc** - gastric cavity, **ic** - inner coenenchyme, **oc** - outer coenenchyme.

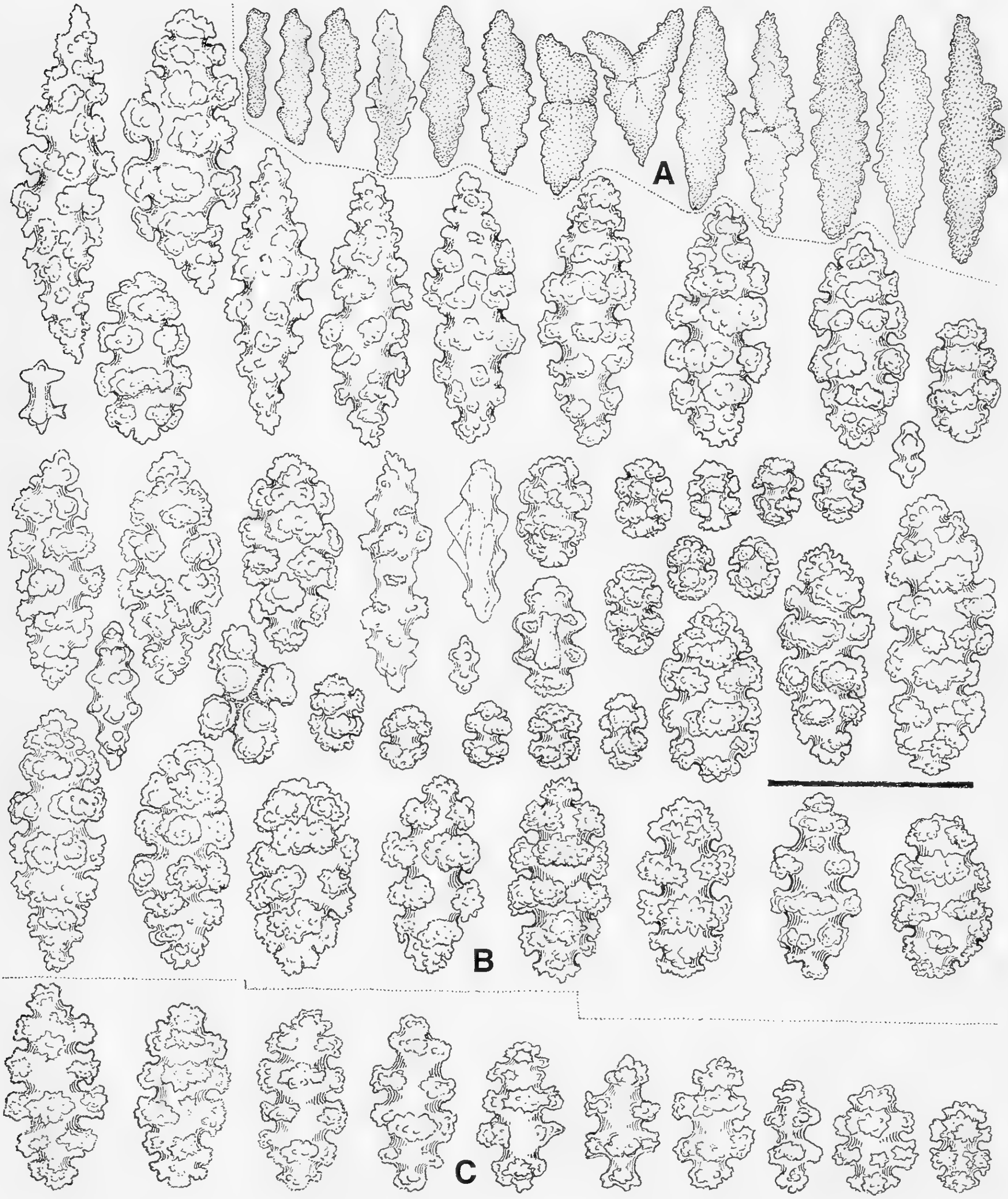


FIGURE 2. Sclerites of *Leptogorgia bayeri* (holotype). A. Polyp sclerites. B. Sclerites of the outer coenenchyme. C. Sclerites of the inner coenenchyme. Scale bar = 0.1 mm.

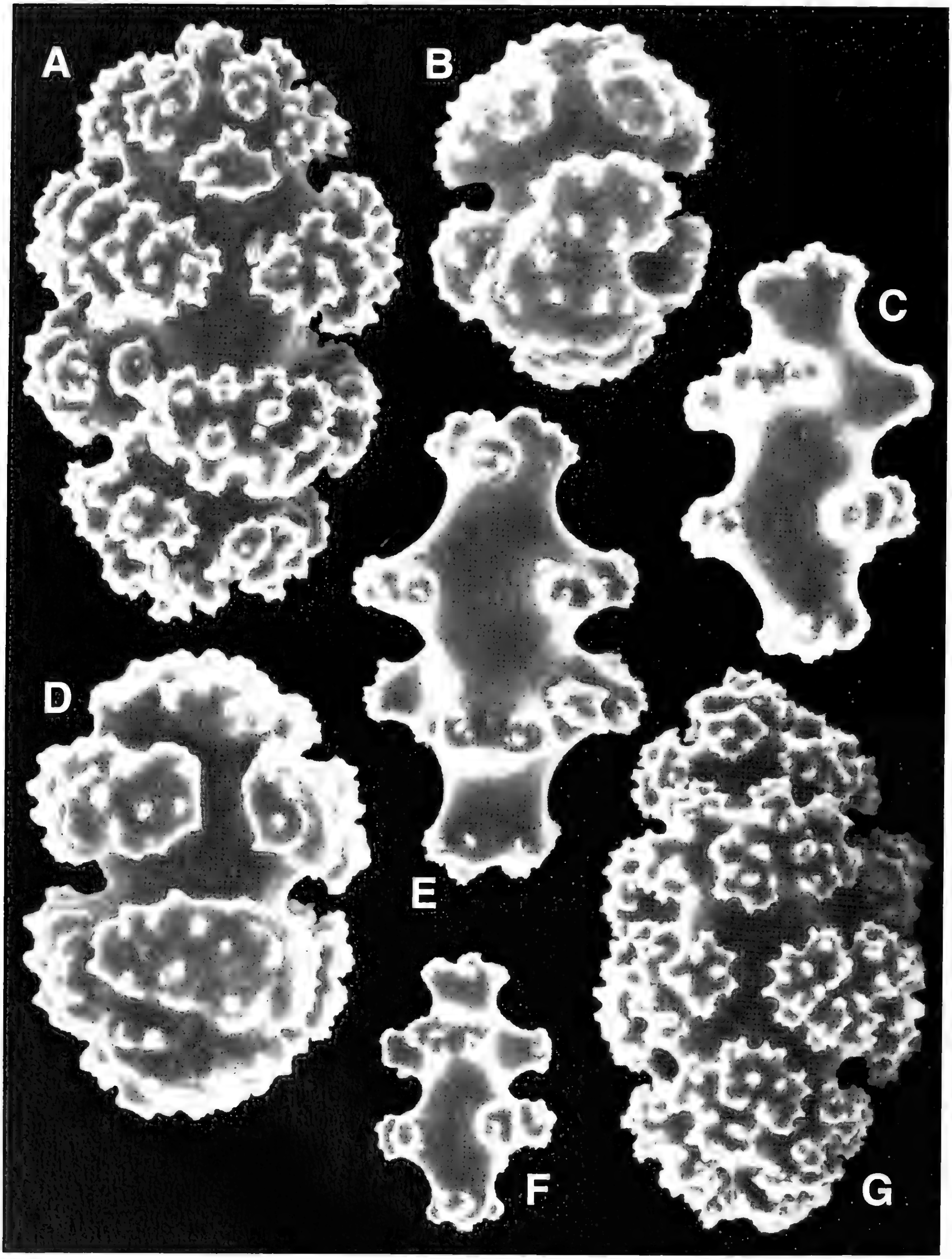


FIGURE 3. *Leptogorgia bayeri* (holotype). Scanning electron micrographs of coenenchymal sclerites. A. 0.075 mm. B. 0.028 mm. C. 0.052 mm. D. 0.035 mm. E. 0.059 mm. F. 0.060 mm. G. 0.085 mm.

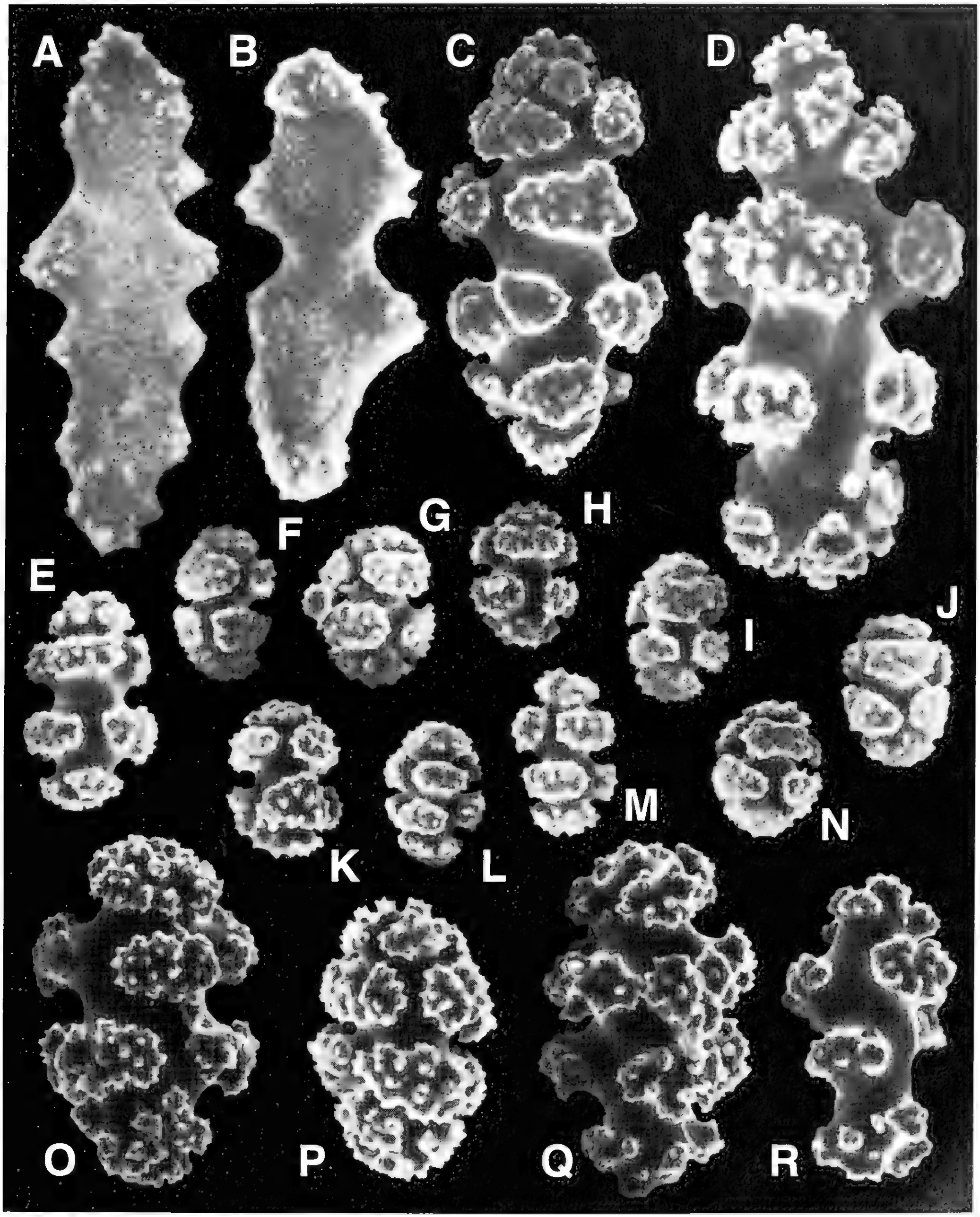


FIGURE 4. *Leptogorgia bayeri* (holotype). Scanning electron micrographs of polyp sclerites (A-B), and coenenchymal sclerites (C-R). A. 0.052 mm. B. 0.030 mm. C. 0.092 mm. D. 0.081 mm. E. 0.047 mm. F. 0.031 mm. G. 0.032 mm. H. 0.030 mm. I. 0.031 mm. J. 0.031 mm. K. 0.033 mm. L. 0.032 mm. M. 0.036 mm. N. 0.030 mm. O. 0.074 mm. P. 0.058 mm. Q. 0.073 mm. R. 0.064 mm.

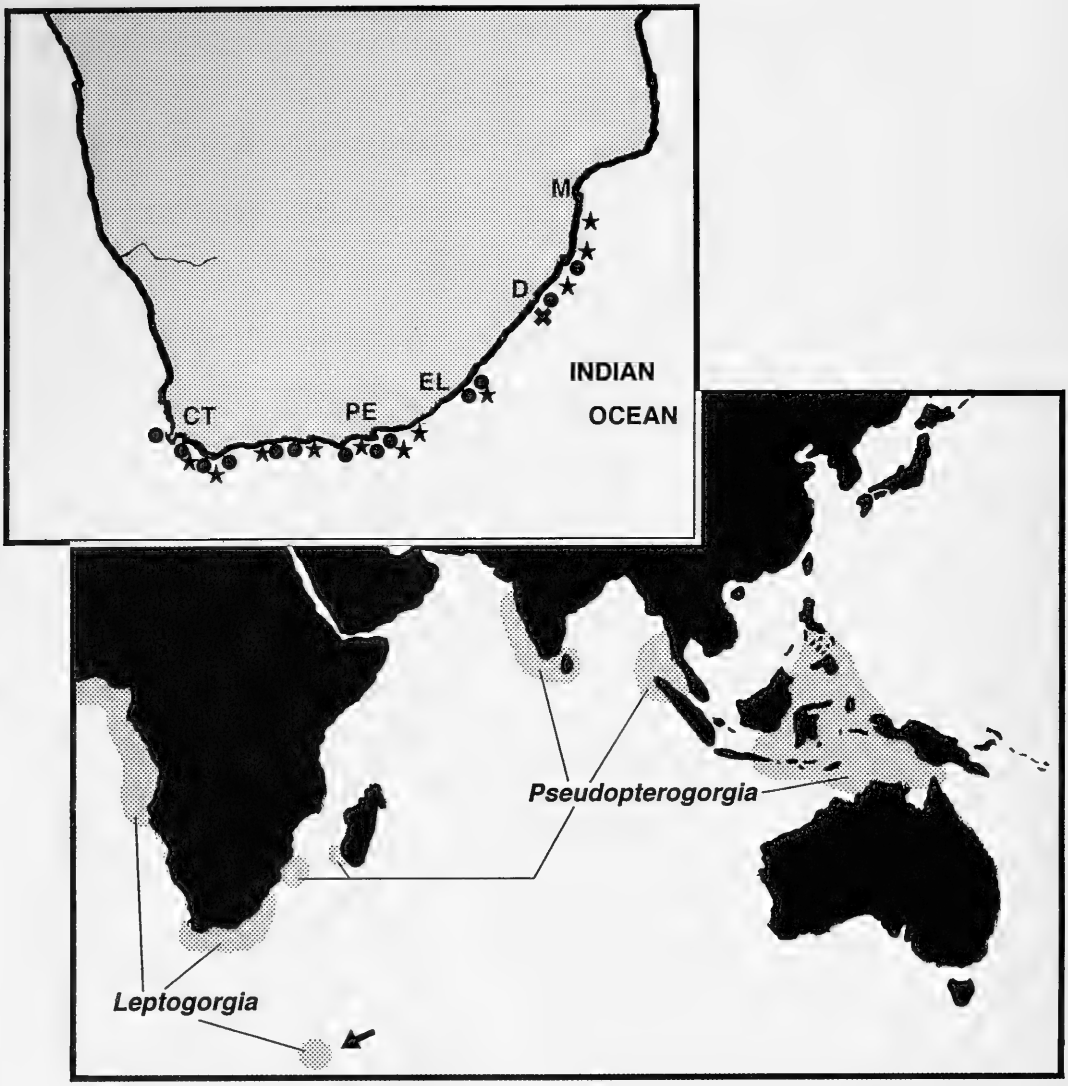


FIGURE 5. Distribution of *Leptogorgia* and *Pseudopterogorgia* in the Indo-West Pacific. Arrow shows distribution of *L. lutkeni*. Inset at top shows distribution of three species of *Leptogorgia* in southern Africa: *L. palma* (●), *L. gilchristi* (★), and *L. bayeri* (×); **CT** - Cape Town, **PE** - Port Elizabeth, **EL** - East London, **D** - Durban, **M** - Maputo.

the tuberculation is symmetrical; one side is not modified relative to the other. In addition, adjacent tubercles do not fuse to form disk spindles, as in some species of the genus.

The sclerites of the inner coenenchyme are radiates and robust spindles, mostly 0.04–0.10 mm in length (Fig. 2C). The elongate spindles found in the outer coenenchyme do not seem to be present in the inner coenenchyme.

Color. The holotype is a vivid lemon yellow throughout. The coenenchymal sclerites are lemon yellow, while the plate-like sclerites of the polyps are salmon pink to pale orange.

Internal Anatomy. A transverse section at a level approximately 10 mm below a branch terminus reveals the following internal anatomy (Fig. 1C). The axis is cylindrical throughout, circular to ovoid in cross section. It is not markedly flattened or laminar. In this particular transverse section, the axis measures 1.2 by 0.8 mm. Large, conical gastric cavities occupy the wing-like expansions of the coenenchyme. These two deltoid expansions emanate laterally from the axis, and are disposed opposite one another. The long plane of this entire complex is parallel to the growth plane of the whole colony (Fig. 1A). The inner coenenchyme immediately surrounds the axis and occupies the area between the axis and a single ring of canals. This inner coenenchyme is approximately 0.08 mm thick. Between the canal ring and the surface is the outer coenenchyme, which averages 0.3 mm in thickness. The canals that compose the canal ring are approximately 15–16 in number and do not exceed 0.1–0.2 mm in diameter.

DISTRIBUTION. — The new species is at present known only from the type locality: Park Rynie, Durban, Natal, South Africa (Fig. 5).

ETYMOLOGY. — This species is named in honor of Dr. Frederick M. Bayer, Curator of Coelenterates (National Museum of Natural History, Smithsonian Institution, Washington, D. C.) and diligent student of the Octocorallia.

REMARKS. — *Leptogorgia bayeri* sp. nov. is distinguished from other species in the genus in two main ways. Occasional anastomosis is known to occur in only one other species of the genus, *Leptogorgia gilchristi*. Therefore, the presence of anastomosis in *L. bayeri* sp. nov. distinguishes it from the remaining 52 species of genus. The laterally expanded coenenchyme along all the flattened branches together with biserial polyps distinguishes the new species from all other members of the genus. This is a major difference and might seem to be enough for the creation of a new genus. However, as Alderslade (1986) has shown in the original description of *Hicksonella expansa*, which has a remarkably leaf-like coenenchyme expansion, the species should still be retained in the genus *Hicksonella*, since the sclerites are so similar to those of the type speces, *H. princeps* Nutting, 1910, which has cylindrical branches with no expansion of coenenchyme.

The ribbon-like branches give the holotype of *Leptogorgia bayeri* sp. nov. a superficial resemblance to species of the West Indian gorgoniid genus *Pterogorgia*, such as *P. citrina* and *P. anceps*, in which the polyps also retract into the edges of the branches. Both *Leptogorgia bayeri* and species of *Pterogorgia* have flattened branches with expanded coenenchyme and biserially arranged polyps. However, a comparison of Figs. 2–4 with Fig. 12D and E shows that *Leptogorgia bayeri* may have curved or C-shaped spindles, but not scaphoids, which are numerous in *Pterogorgia citrina* and *P. anceps*.

Grasshoff (1988:105) reports that several West African species of *Leptogorgia*, such as *L. gaini* (Stiasny 1940), may have strongly flattened branches (at least in the proximal regions of the colonies), and Bayer (1961:222) records the occurrence of biserial polyps in the West Indian species *L. euryale* (Bayer 1952). However, neither *Leptogorgia gaini* or *L. euryale* has markedly expanded coenenchyme as in *L. bayeri*.

Leptogorgia gilchristi (Hickson, 1904)
(Figs. 5–8)

Eugorgia Gilchristi Hickson, 1904:230. pl. 9 (figs. 15, 19). J. S. Thomson, 1917:38.

?*Leptogorgia africana* J. S. Thomson, 1917:28, pl. 5 (fig. 7).

Leptogorgia alba var. *capensis* J. S. Thomson, 1917:29.

Leptogorgia aurata J. S. Thomson, 1917:32, pl. 1 (fig. 5), pl. 4 (fig. 2).

Eugorgia lineata J. S. Thomson, 1917:39, pl. 2 (fig. 3), pl. 5 (fig. 2).

?*Leptogorgia abietina* Kükenthal, 1919:639, text fig. 289, p. 32 (fig. 15).

Eugorgia gilchristi Kükenthal, 1924:347. Stiasny, 1940:27, text fig. E.

Leptogorgia gilchristi Grasshoff, 1992:79, text fig. 141; pl. 7 (fig. 4). Williams, 1992a:244; figs. 46–49. Williams, 1992b:383, 397, fig. 24G.

Leptogorgia: Williams, 1993:53, figs. 9H, I, 25A–C.

MATERIAL. — SAM-H4016, Sodwana Bay, Natal, South Africa, 18-19 m depth, 4 July 1986, collected by G. C. Williams by means of SCUBA, six whole and five partial specimens. CAS 108559, permanent microscope slide of sclerites from holotype, Saint Francis Bay, Cape Province, South Africa, 95 m depth, 1 November 1898, *S.S. Pieter Faure*.

DESCRIPTION. — The following description is based on the six entire specimens from lot SAM-H4016.

Growth form and branching. The six whole specimens vary in height from 47 to 143 mm and 35-135 mm in width. The colonial growth form is upright, copiously branched from a single

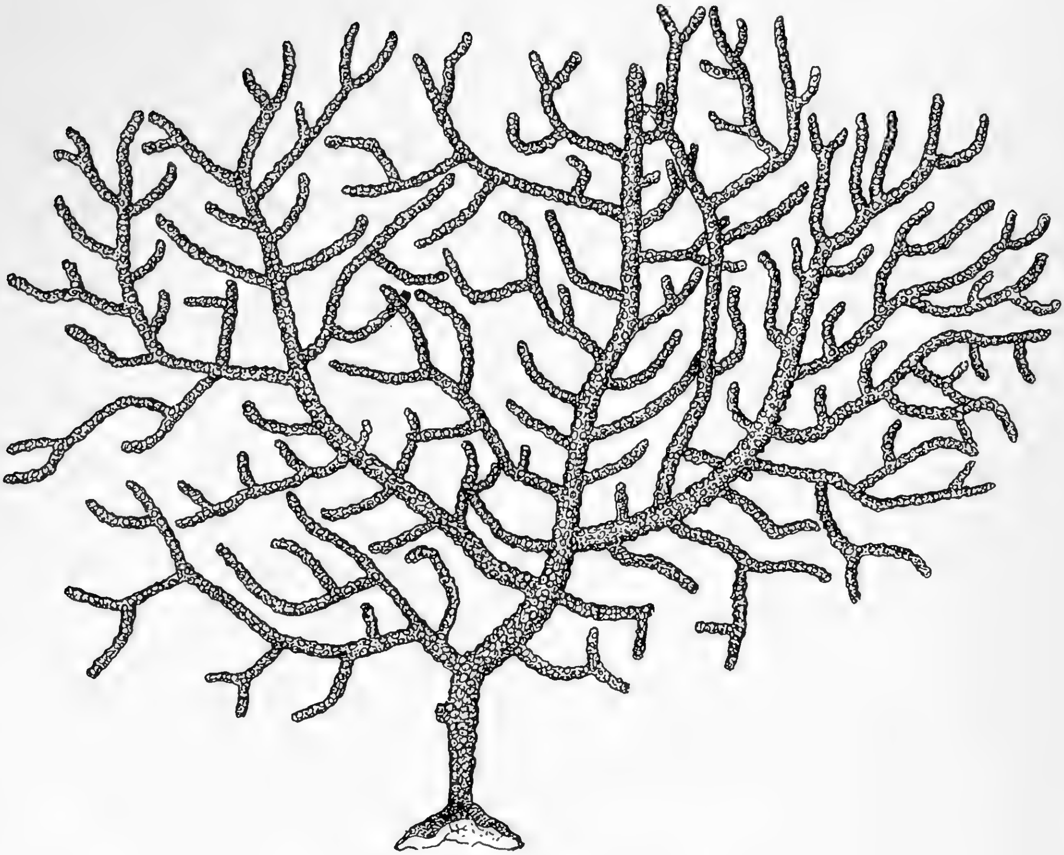


FIGURE 6. *Leptogorgia gilchristi* (SAM-H4016) from Sodwana Bay, Natal; 100 mm in height, 132 mm in width.

trunk, and planar (Fig. 6). The holdfasts are spreading and vary in diameter from 5 to 15 mm. The trunks vary in length from 12 to 26 mm between the holdfasts and the first branching node, and from 1 to 3 mm in diameter.

The branching pattern is pinnate throughout (Fig. 6). Many of the branches are curved or somewhat sinuous. The lower branches are more-or-less flattened with a slightly flattened axis in the proximal regions of the main branches. This contrasts with the distal regions of the ultimate branches, which are for the most part cylindrical, not distinctly flattened. The distance between branching nodes varies from 2 to 15 mm. The ultimate branches vary from 3 to 13 mm in length and from 1.0 to 1.5 mm in width. Anastomoses occur occasionally between adjacent branches, but do not form a reticulated pattern anywhere on the specimens. The coenenchyme is thin throughout and is not differentially expanded or spreading.

Polyps. The polyps in all the material examined are tightly retracted into the coenenchyme, and therefore, features of their morphology were not observed. The retracted polyps form rounded or conical protuberances (calyces) approximately 0.5 mm in diameter, each with a single, minute, slit-like opening (0.2–0.3 mm in length). In the proximal region of the specimens and in the proximal regions of the branches, the polyps are arranged in two opposite series of one or more rows per side. In the distalmost portions of the ultimate branches, the polyps are disposed on all sides of the cylindrical or nearly cylindrical branches. The branch tips are blunt and rounded or are terminated with a minute apical point.

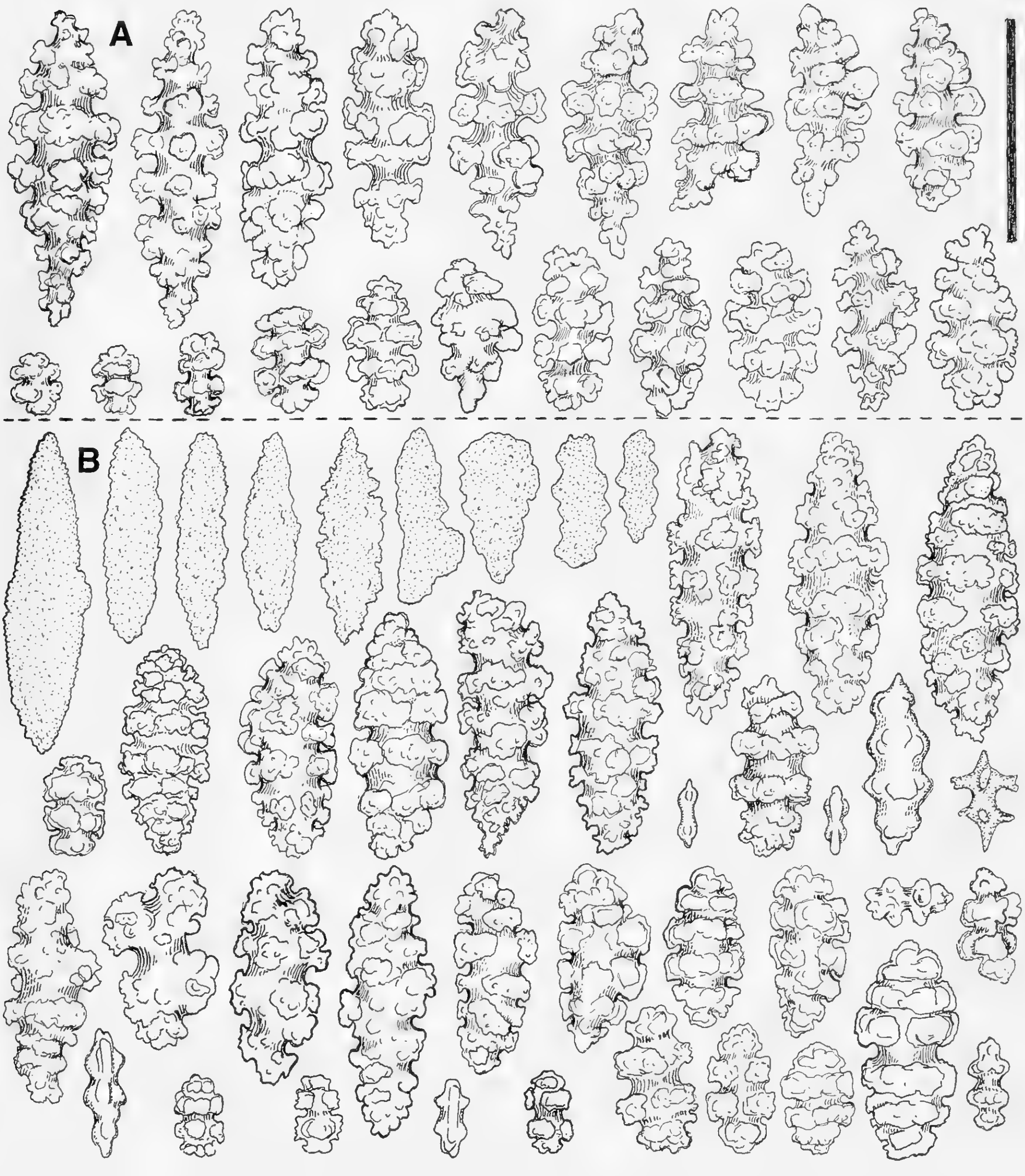
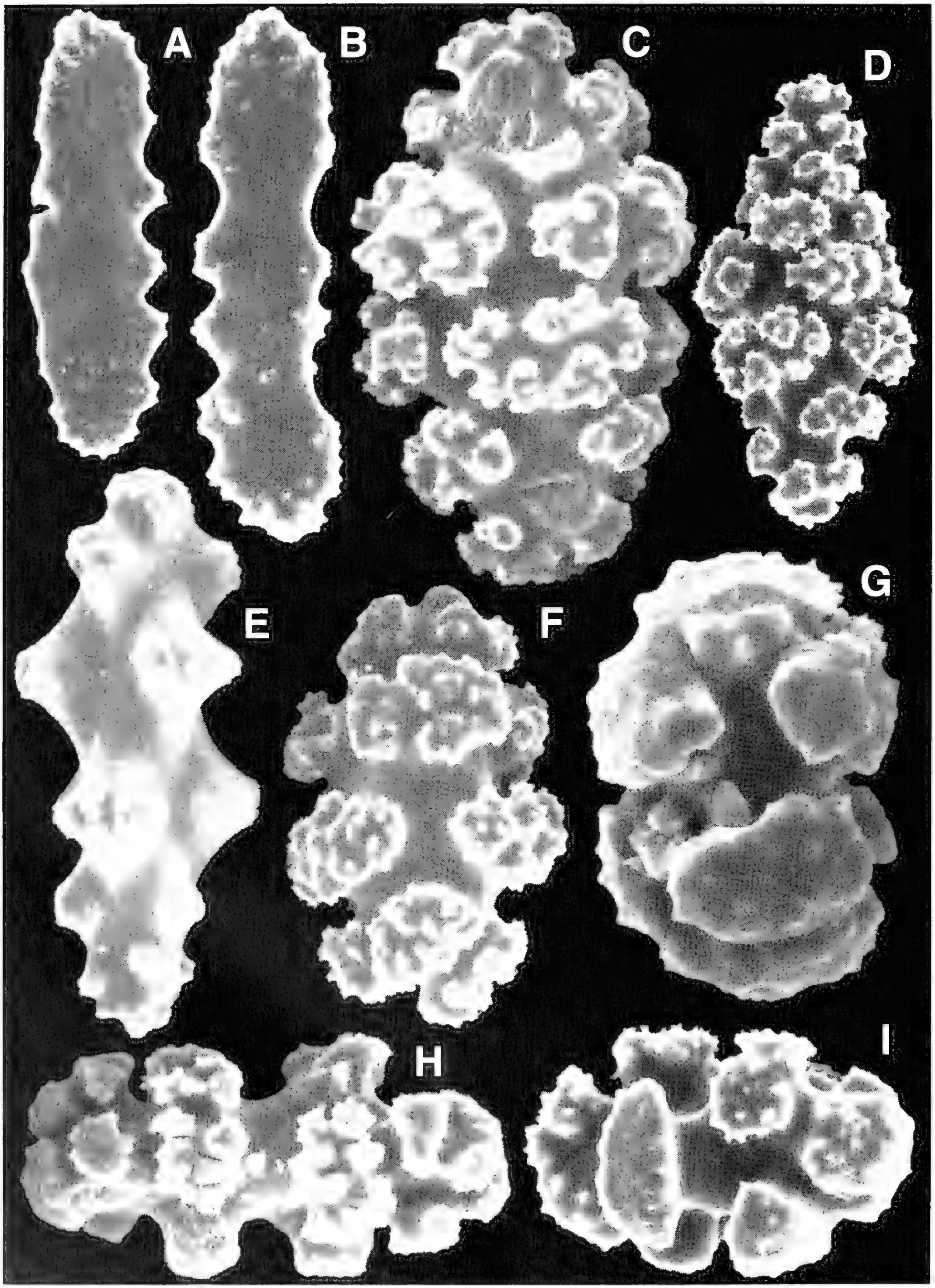


FIGURE 7. Sclerites of *Leptogorgia gilchristi*. A. Coenenchymal sclerites (holotype). B. Polyp and coenenchymal sclerites of Sodwana Bay material (SAM-H4016). Scale bar = 0.1 mm.

Sclerites. The form and size of the sclerites closely resemble those of the holotype (Fig. 7B vs. 7A). The sclerites are of three main types: anthocodial plate-like forms, and coenenchymal eight radiates and spindles.

The anthocodiae contain plates and flattened rods, 0.05–0.15 mm in length. These sclerites are mostly elliptical in shape. They have irregularly shaped margins, which may be somewhat scalloped or toothed but not smooth (Fig. 7B top left; 8A, B).

The radiates are mostly eight radiates, which are variously shaped: compact (Fig. 8G) to relatively elongate (Fig. 8H), ranging in length from


A
B
C
D
E
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G
H
I

0.04 to 0.06 mm (Figs. 7B, 8E–I). Some radiates are only sparsely ornamented (Fig. 8E).

The spindles are relatively robust and measure 0.07–0.14 mm in length. Some of these have conspicuously parallel whorls of tubercles; however, others have tubercles more randomly placed on the surface of the spindle, not in clearly defined linear or parallel whorls (Figs. 7B, 8C, D). Some spindles may be slightly curved, but tuberculation is mostly symmetrical on opposite sides of any given sclerite. Most of the sclerites are uniformly rose red to deep red, while some of the larger spindles are bicolored: red-orange toward one end and yellow at the opposite end.

Color. The specimens are uniformly colored deep cherry red.

DISTRIBUTION. — *Leptogorgia gilchristi* is considered a southern African endemic and was previously known to be distributed along the coast of South Africa from Danger Point (Cape Province) to Durnford Point (Natal) (Williams 1992a:247; 1992b:394). Discovery of this new variant extends the range north along the coast of Natal to Sodwana Bay, in the vicinity of the Mozambique border (Fig. 5).

Leptogorgia bayeri sp. nov. and *L. gilchristi* are the only two species of the genus in which anastomosis has been observed or recorded (Williams 1992a:246, and present paper).

REMARKS. — Williams (1992b:383) reported on the high amount of phenotypic variability observed in several southern African octocorals, including *Leptogorgia gilchristi*. The material described above represents a hitherto unknown variant of *L. gilchristi* and is the only member of the genus known to occur in an Indo-Pacific coral-reef community (the subtidal reefs of Sodwana Bay, northern Natal).

Leptogorgia lutkeni (Wright and Studer, 1889) (Figs. 5, 9, 10A)

Lophogorgia lutkeni Wright and Studer, 1889:150, pl. 30 figs. 1 and 1a, pl. 34 fig.1.
Lophogorgia lutkeni (non Wright and Studer, 1889) J. A. Thomson and Henderson, 1905:306, pl. 3 fig. 6. J. A. Thomson and Simpson, 1909:264. J. A. Thomson and Crane, 1909:132, fig. 11. J. S. Thomson, 1917:35, pl. 1 fig. 2.
Leptogorgia lütkeni Bielschowsky, 1918:30. Kükenthal, 1924:328.

MATERIAL. — Holotype: NHM 1889.5.27.86, H.M.S. Challenger St.145a, off Prince Edward Island, 310 fathoms (567 m).

REDESCRIPTION. — **Growth form and branching.** The holotype is 245 mm in length. The colonial growth form is upright, multiply branched from a single trunk, and planar (Fig. 9). The holdfast spreads slightly and is 7–8 mm in diameter. The trunk measures 13 mm between the holdfast and the first branching node, and is 1.8–2.0 mm in diameter.

The proximal-most 20 to 25 mm of the specimen is denuded of coenenchyme. The surface of this exposed axis is covered with short longitudinal furrows, dark brown to black in color, with mottled areas that are tan or light gray. The proximal regions of the branches are somewhat flattened, resulting from the axis itself being flattened. The axis in this region is thus elliptical in transverse section. One lower branch measures 2.3 mm wide by 1.0 mm in depth. The distal most portions of the branches are mostly cylindrical or only slightly flattened. The coenenchyme is thin and of relatively equal thickness throughout. It is not differentially expanded or spreading.

The branching pattern throughout the specimen is dichotomous to somewhat lateral. The distance between branching nodes varies from 5 to 26 mm, but mostly exceeds 10 mm. The ultimate branches are mostly elongate and narrow and vary from 60 to 140 mm in length. The branches near their apices are 1.0–1.5 mm in diameter. The apices of the ultimate branches are mostly uniformly rounded. Anastomosis does not occur anywhere in the holotype.

Polyps. The polyps in the holotype are all tightly retracted into the coenenchyme, and thus details of morphology are not discernible. The retracted polyps form minute slits on the surface

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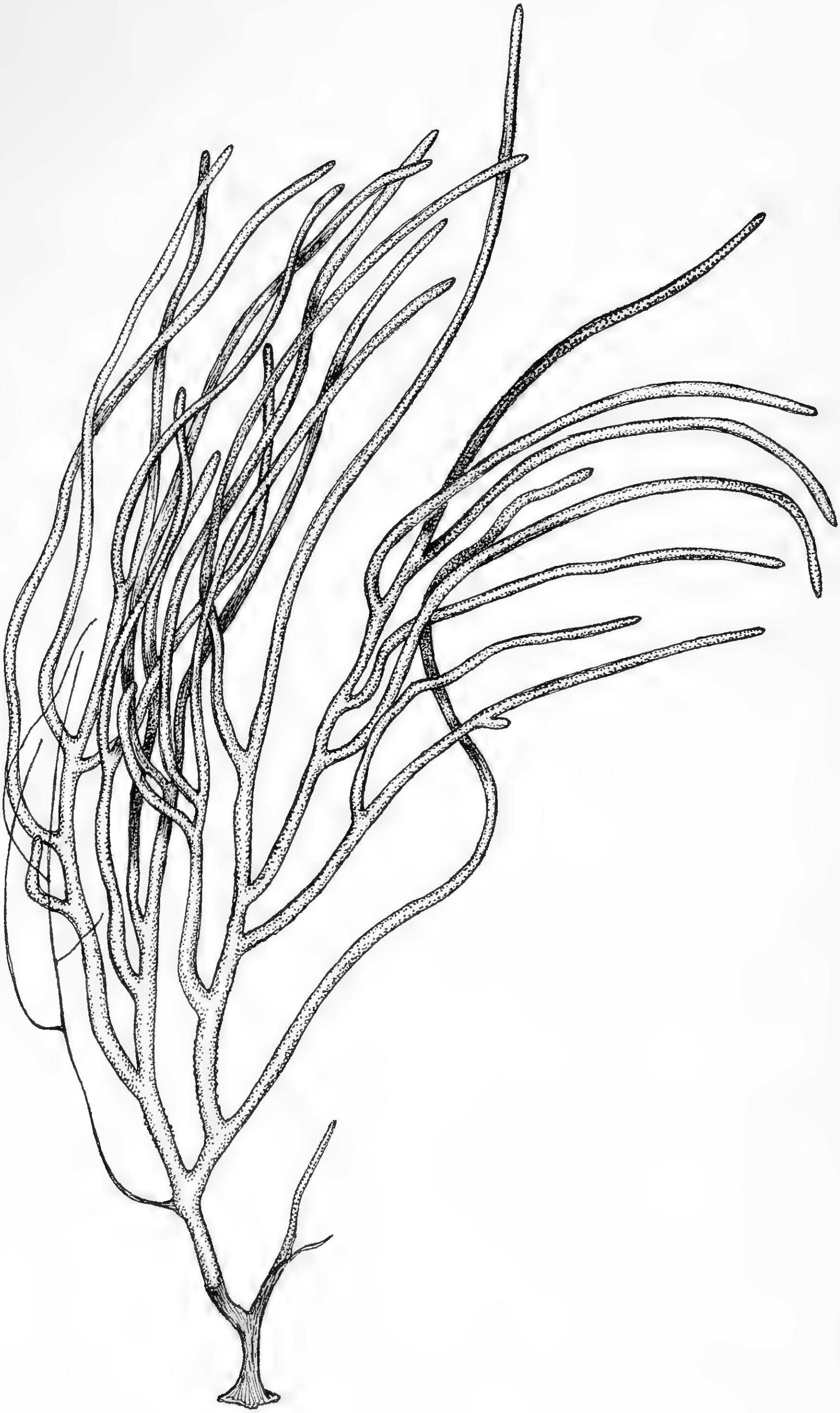
FIGURE 8. *Leptogorgia gilchristi* (SAM-H4016). Scanning electron micrographs of polyp sclerites (A-B) and coenenchymal sclerites (C-I). A. 0.070 mm. B. 0.069 mm. C. 0.090 mm. D. 0.101 mm. E. 0.074 mm. F. 0.068 mm. G. 0.035 mm. H. 0.050 mm. I. 0.040 mm.



of the branches. These slits do not exceed 0.4 mm in length. The retracted polyps form rounded protuberances on the branches approximately 1.0 mm in diameter. Polyp calyces are absent. The polyps are not biserially arranged; however, on the lower branches the polyps are arranged in two opposite series of several longitudinal rows each, along the narrow edges of the branches. The broad flattened surfaces of the branches are devoid of polyps. By contrast, in the distal-most regions of the branches, the polyps for the most part cover the entire surface area of each branch.

Sclerites. The coenenchymal sclerites are of two kinds: radiates and spindles (Fig. 10A).

The radiates are predominantly eight-radiates and are 0.04 to 0.085 mm in length. Some radiates are highly ornamented, while others are only sparsely tuberculated. The spindles are mostly 0.10 to 0.17 mm in length. These spindles are for the most part elongate and contain 3–5 parallel whorls of tubercles. Some of the spindles are somewhat curved. In some, the tuberculation is asymmetrical: the large tubercles on one side may be smooth while those of the opposite side are rough and ornamented with fine tuberculation. In such cases, the divergent tubercles are of equal size and none are highly modified or reduced.

Color. The holotype is dull orange-red to brick red throughout. The sclerites are reddish orange.

DISTRIBUTION. — The species is known only from the type locality, Prince Edward Island in the subantarctic (Fig. 5, arrow).

REMARKS. — The holotype was examined and redescribed to confirm that the specimen does indeed belong to the genus *Leptogorgia*, and that the genus is distributed in the subantarctic.

Leptogorgia lutkeni was originally described as *Lophogorgia lutkeni*, but Grasshoff (1988:97–98; 1992:77–78) has shown that *Lophogorgia* Milne Edwards and Haime, 1857:167 is a synonym of *Leptogorgia* Milne Edwards and Haime, 1857:163. The holotype of *Leptogorgia lutkeni*, is the only known specimen. Comparative examination of the holotype with the southern African species of *Leptogorgia* has shown that it most closely resembles dichotomously branched colonies of *Leptogorgia palma* (Pallas, 1766) (Fig. 11). Both *Lophogorgia lutkeni* and this variant of *L. palma* are dichotomously branched and a deep brick red or cherry red in color. This form of *L. palma* was previously named as a separate species, *Lophogorgia crista* Möbius, 1861, which Grasshoff (1992:77) and Williams (1992a:239, 242) considered to be a junior synonym of *Leptogorgia palma* (Fig. 12).

Comparison of the sclerites of *Leptogorgia lutkeni* and the "crista" variant of *L. palma*, serve to distinguish the two taxa (Fig. 10). *Leptogorgia lutkeni* has larger sclerites, up to 0.17 mm in length, and many of them are elongate spindles (Fig. 10A). In the "crista" variant of *L. palma*, the sclerites are mostly more compact eight radiates and spindles, and do not exceed 0.1 mm in length (Fig. 10B and Williams 1992a:240).

Material identified as *Lophogorgia lutkeni* by J. A. Thomson and Henderson, 1905, from Cheval Paar, Gulf of Manaar, Sri Lanka; J. A. Thomson and Simpson, 1909, from the Andaman Islands, Bay of Bengal; J. A.Thomson and Crane,1909, from Okhamandal, Arabian Sea, India; and J. S. Thomson, 1917, from Gordon's Bay, Cape Province, South Africa, should not in my view be considered conspecific with Wright and Studer's subantarctic species. Stuart Thomson's material appears to be synonymous with *Leptogorgia palma* (compare pl. 1, fig. 2, of J. S. Thomson, 1917 with fig. 41, page 241, of Williams, 1992a), while all of J. A. Thomson's specimens from the Indian Ocean are more likely assignable to the genus *Pseudopterogorgia* (see Fig. 5).

DISCUSSION

GORGONIIDS WITH EXPANDED COENENCHYME. — Alderslade (1986:81) observed that only a few species of holaxonian gorgonians have an expanded or spreading coenenchyme and these are restricted to the Gorgoniidae. These include *Phycogorgia fucata* (Valenciennes, 1846) from Chile; *Phyllogorgia dilatata* (Esper, 1806) from Brazil; three tropical western Atlantic species of *Pterogorgia*: *P. anceps* (Pallas,

←

FIGURE 9. *Leptogorgia lutkeni* (holotype); 240 mm in height.

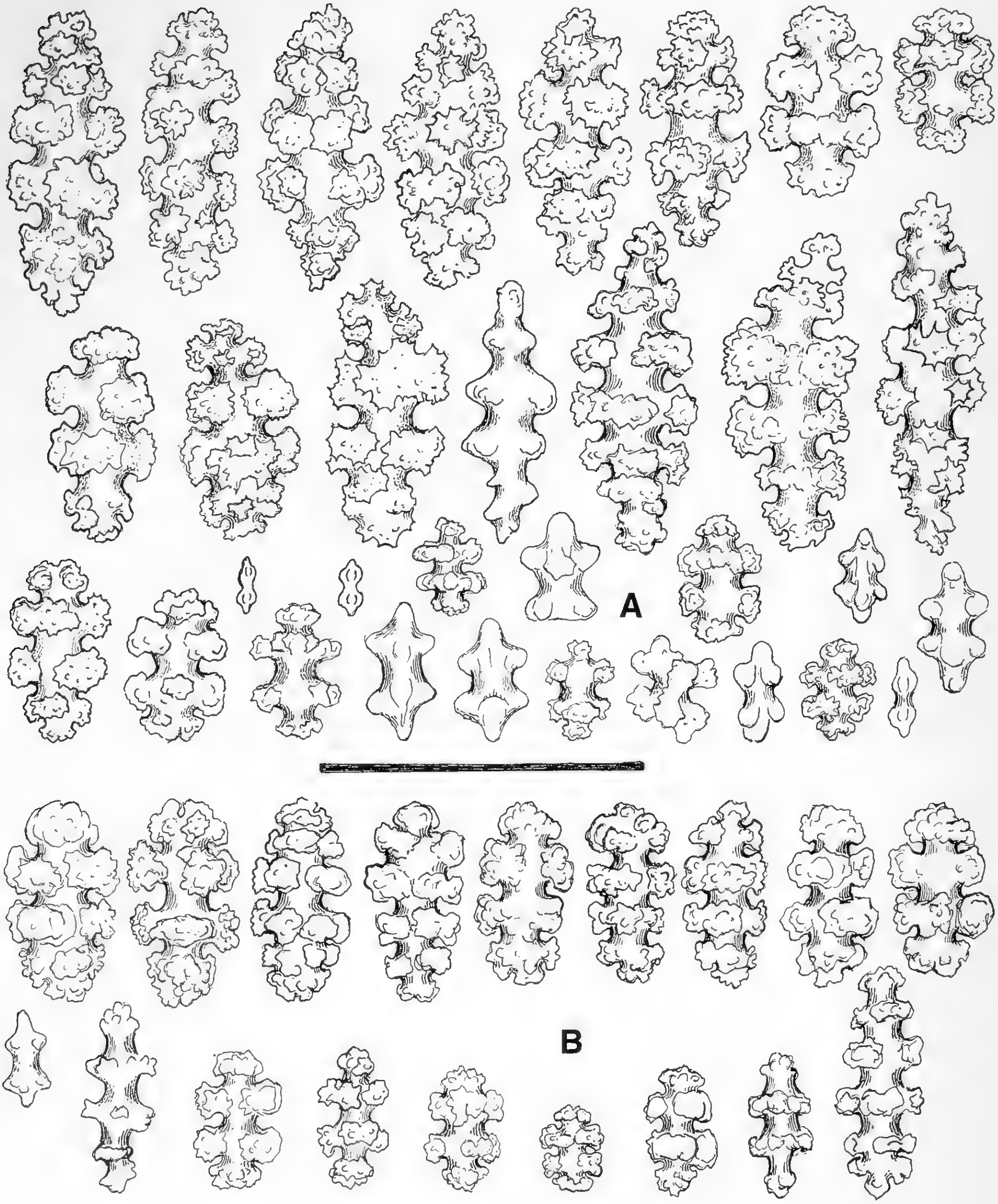


FIGURE 10. Coenenchymal sclerites. A. *Leptogorgia lutkeni* from Prince Edward Island (holotype). B. *Leptogorgia palma* (var. "*crista*") from South Africa (CAS 108321). Scale bar = 0.15 mm.

1766), *P. citrina* (Esper, 1792), and *P. guadalupensis* Duchassaing and Michelin, 1846; *Hicksonella expansa* Alderslade, 1986 from the Great Barrier Reef; *Leptogorgia bayeri* sp. nov. from Natal; and to a lesser extent some tropical western Atlantic species of *Pseudopterogorgia*, such as *P. americana* (Gmelin, 1791) and *P. acerosa* (Pallas, 1766). Table 1 provides a summary of differentiating characteristics for these taxa.

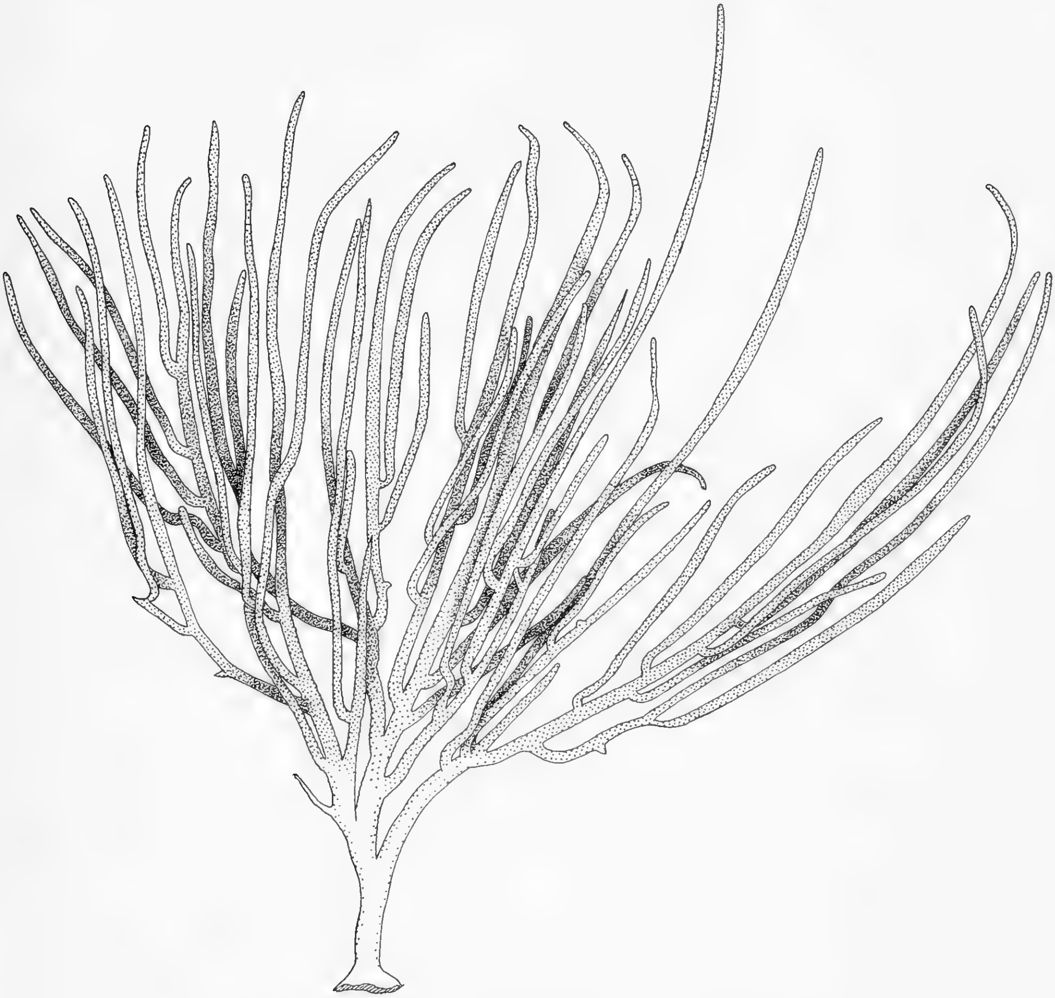


FIGURE 11. A variant of *Leptogorgia palma* (formerly *Lophogorgia crista*) (SAM-H3344) from South Africa; 210 mm in height.

THE GENUS *LEPTOGORGIA* IN THE INDIAN OCEAN. — Of the approximately 54 species in the genus *Leptogorgia*, perhaps 12 are found in the Panamic Province of the eastern Pacific, 36 are distributed in the Atlantic Ocean, five are endemic to southern Africa, and one is known from the subantarctic/Southern Oceans. Thus, the Atlantic has the highest diversity with outliers of lesser diversity in the eastern Pacific, southern Africa, and the subantarctic.

Williams (1992b) described the biogeographic aspects of the Cape Endemic Province with regard to the octocoral fauna. The five species considered endemic to southern Africa are *Leptogorgia barnardi* Stiasny, 1940, *L. bayeri* sp. nov., *L. capensis* (Hickson, 1900), *L. gilchristi* (Hickson, 1904), and *L. palma* (Pallas, 1766). Although the ranges of *Leptogorgia barnardi* and *L. capensis* extend eastward along the south coast of South Africa into the eastern Cape Province, only *L. bayeri*, *L. gilchristi*, and *L. palma* extend northward along the coast of Natal and well into the Indian Ocean (Williams 1992b:394, fig. 24E-H). It is therefore evident that of the 54 species of *Leptogorgia*, three extend into the southwestern fringe of the Indo-Pacific Province (Fig. 5).

TABLE 1. Comparison of gorgoniid taxa with expanded coenenchyme.

	Type of branching	Axis	Branch shape	Expanded coenenchyme	Anastomosis	Sclerites	Distribution
Hicksonella expansa	irregularly pinnate	cylindrical	strongly flattened	strong and leaflike	occasional	wart clubs and spindles	Great Britain, Australia
Phyllogorgia dilatata	pinnate	cylindrical	strongly flattened	strong and leaflike	common	scaphoids and spindles	Brazil
Phycogorgia fucata	—	flat	flattened	—	—	—	Chile
Pterogorgia spp.	lateral or dichotomous	cylindrical	weakly to strongly flattened	strong	absent	scaphoids and spindles	W Atlantic
Pseudopterogorgia spp.	pinnate	cylindrical	cylindrical to weakly flattened	weak	absent	scaphoids and spindles	W Atlantic, Indo-West Pacific
Leptogorgia bayeri	dichotomous	cylindrical	strongly flattened	strong	occasional	spindles only	Natal
Leptogorgia spp.	variable	cylindrical or flattened	cylindrical to flattened	absent	absent	spindles only	E Pacific, Atlantic, SW Indian Ocean, subantarctic

TABLE 2. Comparative features for the gorgoniid genera *Leptogorgia* and *Pseudopterogorgia*.

	Leptogorgia	*Pseudopterogorgia* (Indo-Pacific)	*Pseudopterogorgia* (Caribbean)
Type of branching	variable	lateral or pinnate	pinnate-plumose
Amount of branching	variable	sparse to abundant	abundant
Anastomosis	occasional to absent	absent	absent
Scaphoids	absent	weakly developed	well developed
Largest tubercles on C-shaped sclerites	convex side	concave side	concave side
Distribution	Panamic/Atlantic/ southern Africa	Indo-West Pacific (Mozambique to Torres Strait)	Tropical western Atlantic

COMPARISON BETWEEN *LEPTOGORGIA* AND *PSEUDOPTEROGORGIA* — Table 2 compares three groups of related gorgoniid taxa: *Leptogorgia*, the Indo-Pacific *Pseudopterogorgia*, and tropical western Atlantic species presently allocated to the genus *Pseudopterogorgia*. It is not clear if the western Atlantic taxa are congeneric with the Indo-Pacific taxa. Kükenthal (1919:854) proposed the name *Pseudopterogorgia* for several Indo-Pacific taxa with scaphoids, originally described in the genera *Gorgonia* and *Leptogorgia*. Kükenthal (1924:355) recognized four species of *Pseudopterogorgia*: *P. australiensis* (Ridley, 1884), *P. oppositipinna* (Ridley, 1888), *P. pinnata* (Nutting, 1910), and *P. luzonica* Kükenthal, 1919. Bayer (1951:97) established the genus *Antillogorgia* to accommodate the West Indian plumose gorgoniids with scaphoids that were differentiated from *Pterogorgia* Ehrenberg, 1834 (restricted to non-plumose forms with broad and flattened branches). Bayer (1961:224) subsequently considered the Indo-Pacific and tropical western Atlantic taxa to be generically inseparable, and thus relegated *Antillogorgia* to the synonymy of *Pseudopterogorgia*. It is possible that the two geographically disparate groups may represent separate genera, but we here retain the existing classification of *Pseudopterogorgia* and *Leptogorgia* in the Indo-Pacific, as a detailed comparative examination of more material will have to be made first before the problem can be satisfactorily resolved.

If the two geographically distinct groups of taxas do indeed represent two distinct genera, then the generic name *Antillogorgia* would have priority for the western Atlantic species. However, a good argument can be made for the continued application of the name *Pseudopterogorgia* for the western Atlantic taxa. A substantial body of literature outside the field of pure taxonomy is adequate justification for action by the International Commission of Zoological Nomenclature to conserve a threatened name (F. M. Bayer, pers. comm.). This is certainly the case with *Pseudopterogorgia* where a large body of literature has been produced in the past two decades, particularly in the fields of chemical ecology and natural products chemistry (e.g., McEnroe and Fenical 1978; Look et al. 1986; Fenical 1987; Harvis et al. 1988; Harvell and Fenical 1989; Roussis et al. 1990; Tinto et al. 1991; and Haiyin et al. 1995). A reasonable argument in favor of conservation could therefore be brought before the ICZN for consideration.

Table 2 and Fig. 12A–C shows differences between the genera *Leptogorgia* and the two groups of *Pseudopterogorgia*. A detailed comparison of scaphoids and curved spindles of these groups reveal that the sclerite differences be-

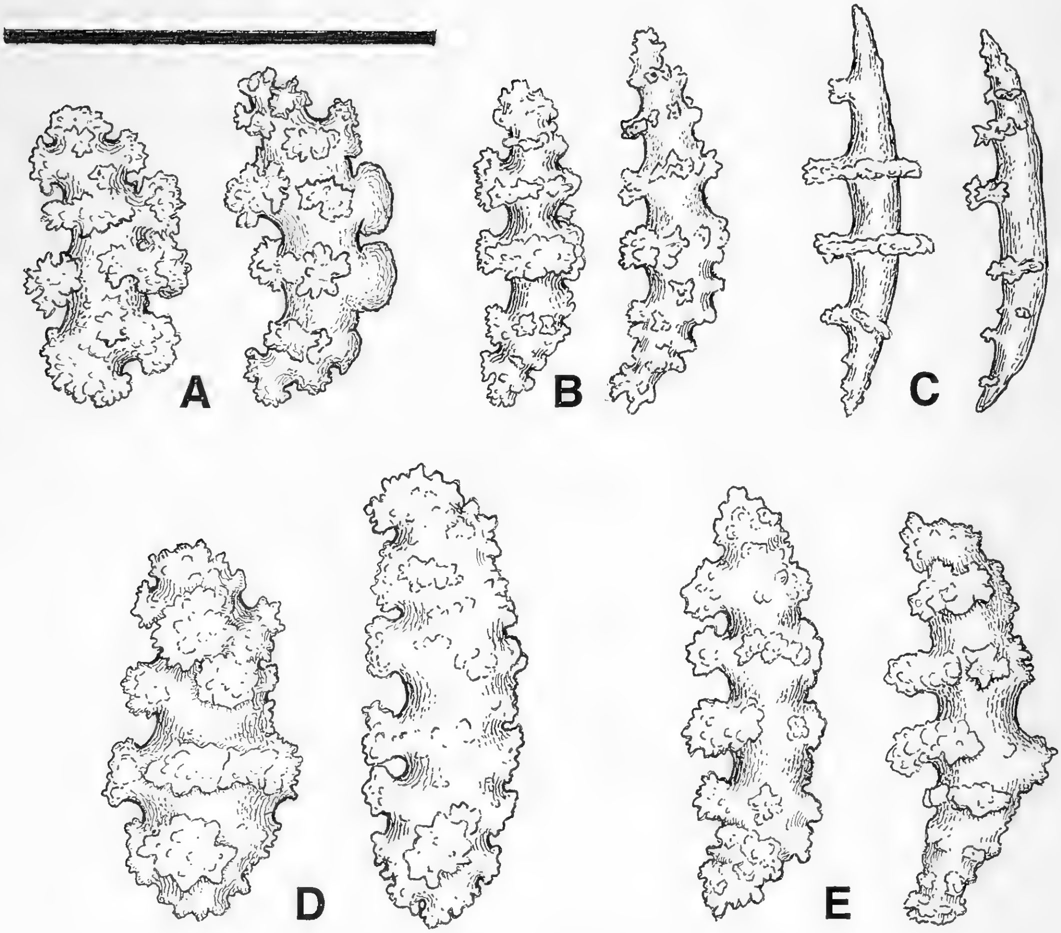


FIGURE 12. Comparison of C-shaped sclerites in the genera *Leptogorgia*, *Pseudopterogorgia*, and *Pterogorgia*. A. Curved spindles in *Leptogorgia capensis* from South Africa (NHM 1901. 7. 6. 3). B. Scaphoids in *Pseudopterogorgia* sp. from Darwin, Australia (MTM C.11 117). C. Scaphoid with transverse crests and smooth scaphoid in *Pseudopterogorgia acerosa* from Florida, U. S. A. (CAS 097785). D. Scaphoids in *Pterogorgia citrina* from Florida (CAS 098024). E. Scaphoids in *Pterogorgia anceps* from Florida (CAS 097934).

tween some species of *Leptogorgia*, such as *L. capensis* and some specimens of Indo-Pacific *Pseudopterogorgia*, are very subtle (Fig. 12A vs. 12B). Bayer, Grasshoff, and Verseveldt (1983:21) define a scaphoid as a "spindle more or less distinctly curved in the form of a 'C' and with the warts of the convex side suppressed or modified." In *L. capensis*, the warts on the convex side of curved spindles are modified but not suppressed. In a specimen of *Pseudopterogorgia* sp. from Darwin, Australia, the warts on the convex side of curved sclerites are only slightly modified and reduced. As a matter of comparison, the warts on the convex side of curved sclerites (scaphoids) in the West Indian species *P. acerosa* are highly reduced and/or modified (Fig. 12C). In many species of *Leptogorgia*, such as *L. bayeri* and *L. lutkeni*, the warts on the convex side of curved spindles are neither markedly reduced or modified (Fig. 2B and 10A).

Examination of Indo-Pacific loan material from the Natural History Museum (London) and the Northern Territory Museum (Darwin), as well as the holdings of the California Academy of Sciences, has revealed that the genus *Pseudopterogorgia* has a widespread distribution in the

Indian Ocean with collecting sites in Mozambique, India, Sri Lanka, and Myanmar, as well as Madagascar (Tixier-Durivault 1972:47) (Fig. 5). The known distribution of *Leptogorgia*, on the other hand, includes the eastern Pacific (California to Chile) and western Atlantic (Carolinas to Brazil); and from the Iberian Peninsula and Mediterranean Sea extends down the west coast of Africa to Angola, and then in southern Africa from the Cape Peninsula to the vicinity of the Natal/Mozambique border (Fig. 5).

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(Compiled by Juliet Knowles)

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Bactris panamensis
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