Systematics and Acoustic Behavior of *Borinquenula*, a New Genus of Brachypterous Coneheaded Katydids Endemic to Puerto Rico (Orthoptera, Tettigoniidae, Copiphorinae)[1]

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ABSTRACT

BORINQUENULA, new genus, is apparently most closely related to *Eriolus*, and, although it is a copiphorine, some of its characters suggest the Agraeciinae. Three new species are described: ***martorelli*** (type-species) 485 to 975 m in the Sierra de Luquillo; ***caritensis***, 700 and 800 m in the Sierra de Cayey and 845 m in the Cordillera Central; and ***minor***, 100–1000 m in the Cordillera Central, the Sierra de Cayey, and the Sierra de Luquillo. *B. martorelli* and *caritensis* are most similar in morphology but have strikingly different calling songs. The calling song of *minor* is unusually variable in 3 parameters. The relation between calling song and characters of the stridulatory file in *Borinquenula* illustrates 3 generalizations that apply to both gryllids and tettigoniids. The characters separating Copiphorinae and Agraeciinae and the history of usage of those 2 subfamily names are discussed.

In this paper we describe a new genus of large, distinctive West Indian katydids. Endemic genera of katydids are known from Jamaica, Cuba, Hispaniola, and the Lesser Antilles, but *Borinquenula* is the 1st such genus from Puerto Rico. It has been taken chiefly in forested Puerto Rican mountains, but 1 species (*minor*), also occurs in tall grasses and at altitudes approaching sea level. The genus is of special interest because it has attributes of 2 subfamilies, Copiphorinae and Agraeciinae.

Although the discovery of *Borinquenula* is noteworthy, the occurrence on a single island of more than 1 species of a striking endemic katydid genus is not unique. Five other examples are known from the West Indies (all are Pseudophyllinae from the Greater Antilles; see Beier 1960, 1962): *Jamaicana* (Jamaica, 3 species), *Polyancistroides* (Cuba, 3), *Polyancistrus* (Hispaniola, 6), *Pseudopleminia* (Jamaica, 2), *Spelaeala* (Hispaniola, 2).

Source of Material, and Acknowledgments.—The new genus first came to our attention in 1961 when several specimens, collected as early as July 1959 by L. F. Martorell and S. Medina, University of Puerto Rico, Rio Piedras, were loaned to Gurney by Dr. Martorell. In 1964, George Drewry, Puerto Rico Nuclear Center, Caparra Heights Station, collected the first of several specimens, and later others were taken in the El Yunque area by Robert J. Lavigne, University of Wyoming, Laramie, while associated with Dr. Drewry. A larger collection, including 3 species, was made by Walker with P. C. Drummond in January 1969, when they surveyed the Puerto Rican singing Orthoptera and studied these species in the field. In June 1969, T. J. Cohn, San Diego State College and University of Michigan, visited Puerto Rico and likewise made a large collection containing all 3 species. Dr. Cohn quickly recognized the significance of his discovery, and we are especially indebted to him for generously loaning the specimens.

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Borinquenula, new genus

Head.—Fastigium acutely produced in advance of compound eyes more than distance between eyes, dorsal width at base between basal segments of antennae moderately greater than width of basal segment, in lateral view with blunt ventral tooth about opposite apex of 1st antennal segment, ventral base of fastigium meeting face with surface irregularity but no deep sulcus, and line of demarcation sometimes unclear; dorsal surface of head sometimes shallowly and irregularly furrowed, otherwise smooth, evenly

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rounded; cheeks smooth; face strongly oblique; compound eyes small, globose; lateral ocelli on basal half of fastigium about opposite ventral tooth; median ocellus opposite ventral margin of antennal scrobes. Antennae long, setaceous, greatly surpassing abdomen when extended posteriorly; palpi slender, maxillary one extending nearly to compound eye when directed anteriorly; mandibles heavily sclerotized, strongly toothed.

Thorax.—Pronotum with conspicuous posterior development of elongate dorsal disk, extending posteriorly over part of 1st abdominal tergum in male, scarcely over all of metanotum in female, anterior margin truncate with well-rounded lateral corners, posterior margin broadly rounded, lateral lobes shallow, lateral margins expanded opposite anterior coxae, no distinct lateral sulci, but rudimentary transverse sulcus just anterior to lateral expansion near lateral margin only; prosternum unarmed; mesosternal and metasternal plates with posterior lobes obliquely angled; anterior margin of metasternal plate with minute to medium-length spinelike tubercle (Fig. 31, sp) near each lateral corner. *Legs.*—All coxae with short spinelike apical tubercle ventrally, only front coxa with conspicuous elongate dorsal spine (directed anteriorly); front and middle femora with 3–4 small spines on ventroanterior margins, single genicular spine on each side; hind femur extending about to or a little exceeding apex of abdomen, length ca. 6 times maximum width, anteroventral margin with 6–7 medium-sized spines, geniculars lobe of each side with very distinct apical spine, anterior and posterior spines subequal, posterior one barely longer; hind tibia about as long as femur, with dorsal surface shallowly sulcate, ventral surface moderately convex to scarcely sulcate, dorsal margins each with 1 apical spur and 6–13 (usually 10–12) anterior and 9–13 (usually 11–12) posterior spines, ventral margins with 9–17 (usually 10–15) anterior and 7–10 (usually 8–10) posterior spurs; spurs on ventral margins include 2 closely set apical ones on each margin and several near base which are hardly distinguishable from spines. The ventral spinelike spurs of the hind tibia are comparable, although smaller, to the conspicuous spurs of *Neobarrettia* described by Cohn (1965: 22.) Second tarsal segment slightly shorter than 1st segment, 3rd segment conspicuously bilobed, 4th (with claws) about as long as other segments combined, arolium absent, each claw with ventral sensory seta at base, 1st and 2nd segments with impressed longitudinal groove laterally. Male tegmina overlapping, with well-developed stridulatory apparatus, extending about to base of 2nd or 3rd tergum; right tegmen with stridulatory vein less heavily sclerotized than left tegmen; female tegmina lateral, extending about to base of 1st tergum; wings rudimentary (male), or absent (female).

Abdomen.—Ten segments visible from above, plus rudimentary 11th partly concealed at posterior margin of 10th (epiproct, or supra-anal plate); male cerci with slender, dorsally curved, lateral tooth; female cerci unspecialized, short, tapering to acute apex; male subgenital plate deeply emarginate posteriorly, styli distinct; female subgenital plate bilobed, inconspicuous; ovipositor moderately upcurved, acute, lacking teeth; titillator of male variable.

General color varying from blackish brown to pale yellowish green.

Type-species.—Borinquenula martorelli, n. sp.

Other Species.—B. caritensis, n. sp.; *B. minor,* n. sp.

The feminine generic name *Borinquenula,* meaning a small inhabitant of Puerto Rico, is adapted from "Borinqueno" (native of Puerto Rico) and the diminutive ending "ula"; Borinquen is an old name for Puerto Rico, from the Taino Indian language.

Key to species of *Borinquenula*

1. Length of fastigium (from apex to transverse line of demarcation just anterior to median ocellus, Fig. 32, lf) less than 4 mm; color predominantly green and pale brown; V-shaped posterior emargination of male subgenital plate less than ⅓ as long as plate (Fig. 20); number of teeth in stridulatory file more than 45; song a rattle (Fig. 38–40) ..... *minor*

   Length of fastigium more than 4 mm; color predominantly dark brown; V-shaped posterior emargination of male subgenital plate from ⅓ to ½ as long as plate (Fig. 16, 18); number of teeth in stridulatory file fewer than 40; song a click or lispy buzz (Fig. 35–37) 2

2. Posterior emargination of ultimate male tergum deep (Fig. 15); emargination of male subgenital plate ca. ½ length of plate, much greater than length of stylus (Fig. 16); fastigium rarely less than 6 mm long; proximal portions of femora pale brown in fresh specimens; song a lispy buzz (Fig. 35) (Distribution: Luquillo Mountains) ..... *martorelli*

   Posterior emargination of ultimate male tergum shallow (Fig. 17); emargination of male subgenital plate not as deep as in *martorelli,* about equal to length of a stylus (Fig. 18); fastigium rarely as much as 6 mm long; proximal portions of femora pink in fresh specimens; song a click (Fig. 36, 37). (Distribution: Mountains of central Puerto Rico) ..... *caritensis*

Before presenting descriptions of the 3 species, we will describe variation in several structures that show differences among the species.

Fastigial Length.—(See Table 1.) Fig. 32, lf, represents the limits of the fastigium for purposes of measuring length. The transverse line of demarcation anterior to the median ocellus sometimes is indistinct, in which case the base of fastigium is indicated by a minutely roughened texture of the surface cuticle contrasting with a smooth cephalic surface near the ocellus.

Male Cerci.—Male cerci of the 3 species differ chiefly in the apex of the main cercal body. In ventral view (Fig. 21–23) there is no recurved apical tip, or scarcely any, in *minor,* though, it is pronounced in the other two. A ventral view of the cercus of *martorelli* shows the recurved apical margin (Fig. 21, ram) medially located, but in *caritensis* the recurved apical margin (Fig. 22) is usually located near the mesal margin; in mesal

Table 1.—Morphological variation in *Borenquenula*. When range of measurements (in mm) is given, mean and number of measurements are in parentheses. Number of spurs on each hind tibia, when different, are given separately.

Character and specimens	Species		
	martorelli	*caritensis*	*minor*
Length of fastigium			
♂ holotype	7.2	5.3	3.2
♀ allotype	6.5		3.1
♂ paratypes	5.9–8.0 (7.0, n = 18)	4.9–6.1 (5.6, n = 8)	2.5–3.6 (3.1, n = 16)
♀ paratypes	6.3, 6.4, 6.5		3.7
Length posterior apical spine of hind femur			
♂ holotype	1.4	1.0	.7
♀ allotype	1.7		.7
♂ paratypes	1.3–1.7 (1.5, n = 10)	0.8–1.2 (1.1, n = 8)	.5–0.7 (.6, n = 10)
♀ paratypes	1.4, 1.5, 1.6		.6
No. spurs on ventral anterior margins of hind tibiae			
♂ holotype	15, 14	11	10, 8
♀ allotype	15, 17		9
♂ paratypes	13–17 (14.8, n = 9)	9–12 (10.4, n = 8)	9–11 (10.1, n = 10)
♀ paratypes	14–16 (14.5, n = 3)		10, 11
Length of stridulatory file			
♂ holotype	1.41	1.49	2.16
♂ paratypes	1.41, 1.37	1.54	2.10, 2.12, 2.29
No. teeth in stridulatory file			
♂ holotype	29	33	56
♂ paratypes	32, 34	31	54, 54, 59

view the apical margin of the 2 species is somewhat different (Fig. 24, ram, 25). There is no distinct recurved apical margin in *minor* (Fig. 26). The shape and position of the mesal tooth appear to differ slightly in the 3 species, but it is difficult to utilize as a recognition character because of the widely different appearance when viewed from somewhat different directions.

Titillators.—Several males of each of the 3 species were relaxed and the structures in and near the titillator cavity were exposed in situ; those structures of other specimens were dissected, treated with caustic, and preserved in glycerine. Both *martorelli* and *minor* have a single pair of elongate, well-sclerotized titillator arms projecting posteriorly from folds dorsad from the titillator cavity, but no titillator has been found in *caritensis*. Instead, there are several longitudinal folds above the cavity in *caritensis* which are pale brown and apparently more stiffly sclerotized than membranous folds surrounding the titillator cavity in *martorelli* and *minor*. These brown folds of *caritensis* are extensively and densely covered with very delicate, short, spinelike setae; the main folded and setae-covered area of membrane, when dissected and spread out, measures ca. 1.0×2.0 mm. Setae also occur on unpigmented membrane ventrad from the titillator cavity and elsewhere surrounding it.

The titillator arms of *martorelli* are each ca. 0.7–1.0 mm long, the apices rather flattened (laterally compressed) and curved as in Fig. 27. The arms of *minor* are ca. 0.5 mm long, the apices (Fig. 29) not flattened nor produced as acutely nor in as curved a shape as in *martorelli*. Each titillator arm of *martorelli* is brown on about the apical half, and at a magnification of ca. 80×, the brown portion is seen to have elongate striations. The titillator arms of *minor* are brown on about the apical fourth and there covered with short, rodlike spicules. On membrane near the bases of those arms there are traces of spinelike setae similar to those of *caritensis*, but they have not been observed in *martorelli*.

Titillators in Tettigoniidae have been discussed by Chopard (1920: 122–40, 1949: 624–5); Ander (1970: 62); and Tuxen (1970: 344–5). Especially in Decticinae and related subfamilies, titillators have been described in detail for some genera by several authors. Following Ander (1970), we regard the 2 arms of an individual specimen as comprising 1 titillator.

Apical Spines of Hind Femur.—The length of the apical spines of the hind femur is diagnostic for species (Table 1). The posterior apical spine is generally slightly longer than the anterior one (Fig. 33).

Armature of Hind Tibia.—A survey of the spines and spurs of the hind tibia was made to determine whether species can be distinguished by counting them. All counts were broadly overlapping among the species except that *martorelli* was distinctive in the number of spurs on the ventral anterior margins (Table 1).

Male Tegmina.—*B. minor* is distinctive in both file length and the number of stridulatory teeth (Table 1). Other tegminal differences are less impressive. Fig. 30 shows a typical male tegmen of *martorelli* in dorsal view. The tegmina of *minor* usually extend farther posteriorly on the abdomen than in *martorelli* and *caritensis*, and the apical part of the *minor* tegmen (Fig. 30, ra for *martorelli*) usually has less development of large reticulated cells than the other species.

Borinquenula martorelli, n. sp.

(Fig. 1–7, 15, 16, 21, 24, 27, 28, 30–35, 41)

MALE (*Holotype*).—General appearance as in Fig. 1. Integument mainly smooth, glossy, with shallow wrinkles and pitlike irregularities on sides of pronotum, less so on central part of disk, occiput of head and most of fastigium definitely but shallowly roughened, somewhat less so than in illustrated paratype (Fig. 7).

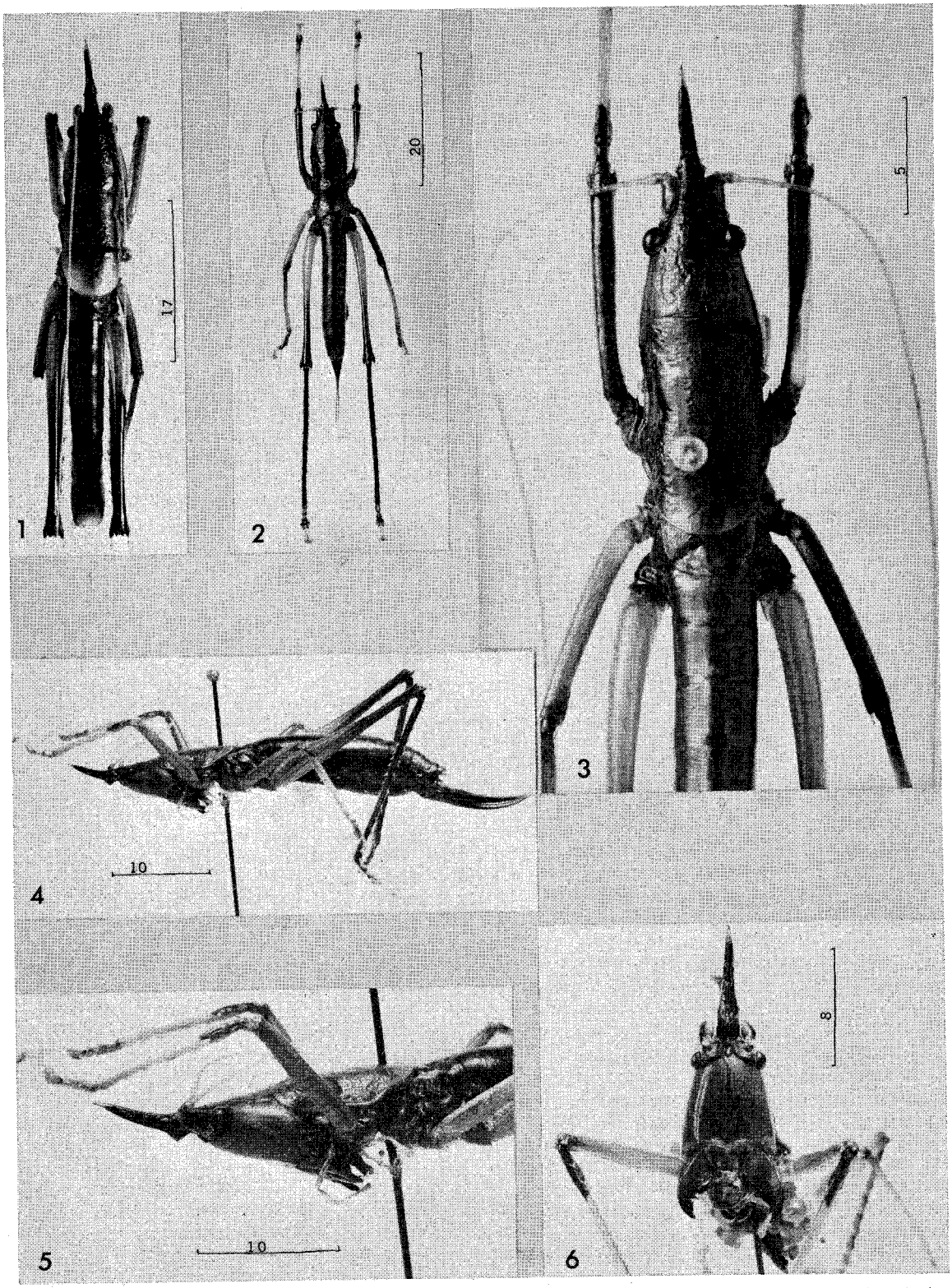

FIG. 1–6.—Specimens of *B. martorelli* from Caribbean National Forest. 1, Dorsal view of male; 2, dorsal view of female; 3, anterior portion of female, much enlarged; 4, lateral view of female (front legs set in abnormal position to display profile of head; 5, same as Fig. 4, enlargement of anterior portion; 6, male, frontal view, showing mandibles open. (Scale: lengths of lines shown in millimeters.)

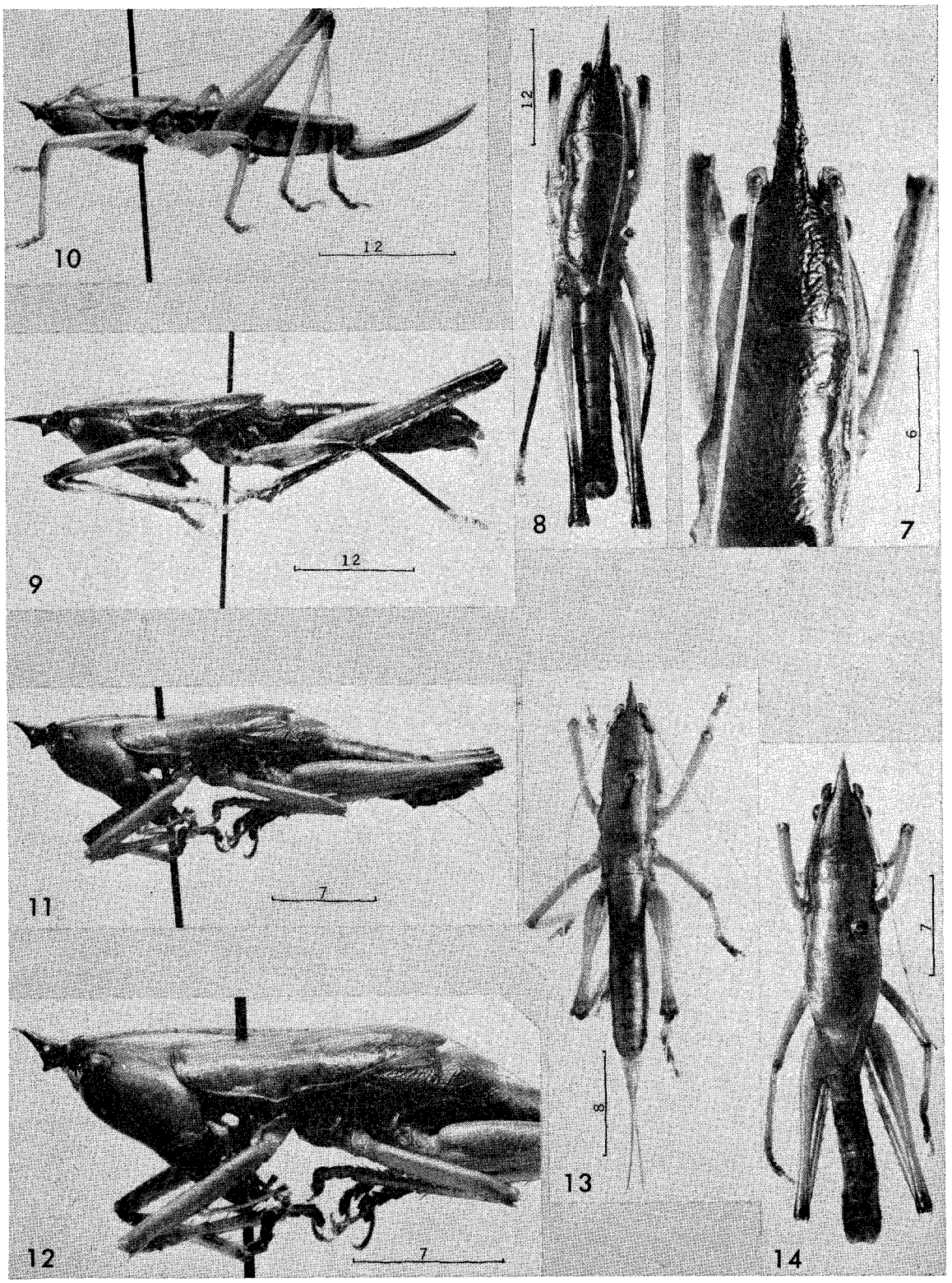

FIG. 7–14.—Specimens of *Borinquenula*. 7, *B. martorelli,* anterior portion of male from Caribbean National Forest. 8, 9, *B. caritensis,* male from Adjuntas, 8, dorsal, 9, lateral; 10–14, *B. minor,* 10, 13, female from Guayama, lateral and dorsal; 11, 12, male from Guavate Recreation Area lateral view and anterior portion of same more enlarged; 14, male from Adjuntas, dorsal view. (Scale: lengths of lines shown in millimeters.)

Head with ratio of dorsal fastigial width opposite midlength of basal antennal segment to maximum width of that segment 15:11; face and genae smooth (Fig. 6); mandibles toothed. Pronotum extending to base of tergum 1, lateral lobe with pronounced marginal protrusion above coxa 1. Thoracic sterna as in Fig. 31; metasternal plate with short spinelike tubercles near lateroanterior angles. Tegmen as in Fig. 30. Front femur with 3 short widely spaced spines on ventroanterior carina; front and middle tibiae with 7 anterior and 6 posterior spines on respective ventral carinae; middle femur with 4 short spines on ventroanterior margin; hind femur with 7 (right) or 8 (left) medium-sized spines on ventroanterior margin. Supraanal plate deeply emarginate posteriorly (Fig. 15); subgenital plate deeply emarginate, with small terminal styli; cercus with conspicuously recurved apical lobe (Fig. 21, 24).

FEMALE (*Allotype*).—General appearance as in Fig. 2–5, essentially as in male except for sexual features. Pronotum proportionally shorter than in holotype (length 1.49 times greatest width, contrasted with 1.85 times width in holotype), extending part way across metanotum; tegmen unspecialized, lateral; wings absent; ovipositor moderately curved, greatly compressed, apically acute; subgenital plate with deep, broad median emargination of posterior margin, each lateral lobe subquadrate.

Measurements (mm).—The measurements of the holotype and allotype are followed, in parentheses, by the range and mean for 18 representative adult male paratypes, then in a 2nd parentheses by measurements of each of 3 ♀ paratypes. Pronotal length, ♂ 12.2, ♀ 10.0 (10.1–13.1, 11.9) (9.7, 9.9, 9.0); pronotal width, ♂ 6.4, ♀ 6.8 (5.4–6.6, 6.1) (6.5, 6.4, 6.0); length of hind femur, ♂ 20.9, ♀ 21.1 (17.6–21.8, 19.6) (21.0, 21.3, 18.3); ovipositor, ♀ 13.8 (12.8, 13.0, 12.3).

Coloration.—Holotype generally light brown. Fastigium mostly piceous, ca. 1 mm located subapically yellow orange, tip touched with dark, dorsal base between antennal bases reddish brown; remainder of head capsule brownish orange, base of clypeus darkened; compound eyes light gray; ocelli whitish; 2 basal segments of antennae dark brown, flagellum and palpi whitish yellow; pronotum brownish orange, much paler on posterior third; most of legs and thoracic venter pale brown; femoral-tibial joints of front and middle legs, especially dorsum of tibia in basal fourth blackish brown; apical fourth of hind femur and all of hind tibia blackish, spines pale, tips reddish brown; abdomen blackish brown below and on sides, paler above with narrow longitudinal dark streak, tip of abdomen yellowish.

In the allotype, the head on occiput and cheeks, also pronotum, are darker than in holotype; otherwise essentially the same. All but 6 of the 38 adults agree with the holotype in having about the posterior third of pronotum paler than the remainder; 4 of the 6 are females. One male, probably somewhat teneral when killed, is mainly yellowish green, the yellowish tinge strong on the dorsum of the abdomen, the fastigium reddish brown except preapically, the lower face and mouth area strongly reddish; another male is mostly typical, but has the posterior third of pronotum greenish. All adults show a median dorsal longitudinal dark streak on the abdomen. There are 6 nymphs, from 13 to 34 mm long, which are variable shades of pale yellowish; some are more orange, all with numerous brown spots and streaks of pinkish and brown; the fastigium is pale.

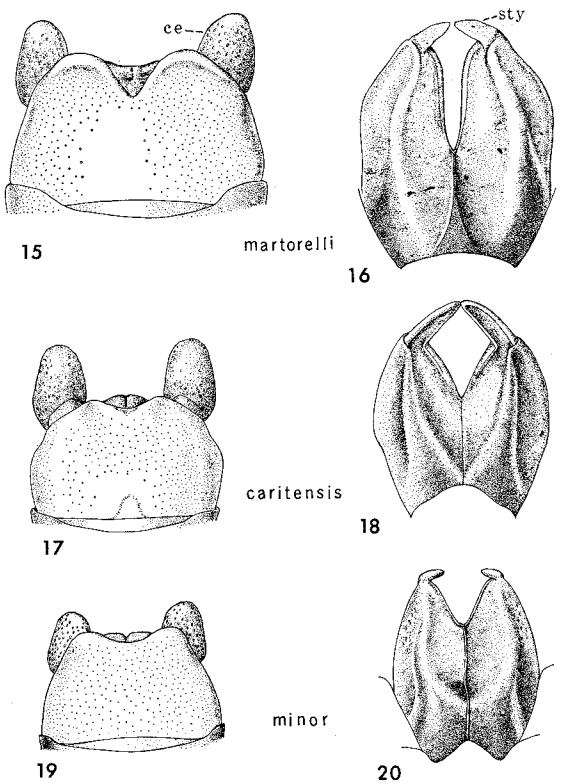

FIG. 15, 17, 19.— Supra-anal plate and cerci of male *Borinquenula*, dorsal view. FIG. 16, 18, 20.— Subgenital plate, ventral view. All drawings show posterior end uppermost. 15, 16, *B. martorelli* from Caribbean National Forest; 17, 18, *B. caritensis* from Guavate Recreation Area; 19, *B. minor* from Adjuntas; 20, same, from Las Tetas de Cerro Gordo. (ce = cercus; sty = stylus.)

Specimens Examined (34 ♂, 4 ♀, 6 nymphs)—PUERTO RICO: All in Luquillo Mountains, Caribbean National Forest. (For this species and the others, all specimens except holotype and allotype are considered paratypes. Most paratypes are in U.S. National Museum, University of Michigan Museum of Zoology, and Florida State Collection of Arthropods. Paratypes have been donated to British Museum, University of Puerto Rico at Rio Piedras, and Academy of Natural Sciences of Philadelphia. The localities are listed roughly in the order of northern and eastern localities first, followed by more western and southern localities. References, in parentheses, to Fig. 34 show location on map. Because of small size of map, all *martorelli* localities except last 2 are

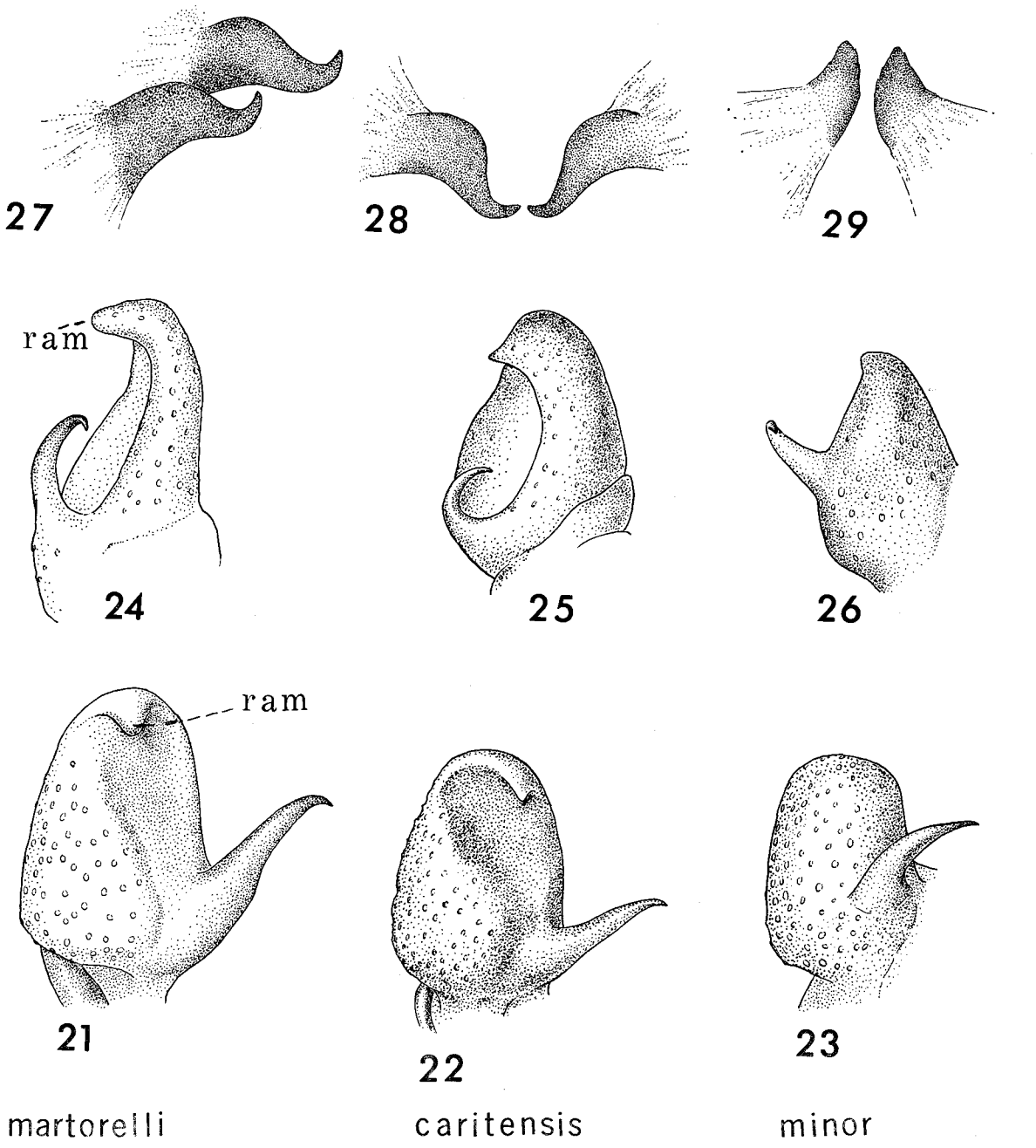

FIG. 21–29.—Details of male genitalia of *Borinquenula*. 21–23, Ventral view of left cercus; 24–26, mesal view of left cercus. 21, 24, *B. martorelli*, from Caribbean National Forest; 22, 25, *B. caritensis* from Guavate Recreation Area; 23, 26, *B. minor* from Adjuntas; 27, *B. martorelli* from Caribbean National Forest, lateral profile of titillator. 28, same, posterior view of titillator showing bases of arms artificially diverging; 29, *B. minor*, from Adjuntas, posterior view of titillator. (ram = recurved apical margin of cercus.)

represented by *10*.[4]) Near El Yunque, 485 m, km 9.7 on Hwy. 191, 19 Jan. 1969 (T. J. Walker, P. C. Drummond), no. 4 (Fig. 34, *10*) 2 ♂; near El Yunque, 600 m, km 11.6 on Hwy. 191, 17 Jan. 1969 (T.J.W., P.C.D.), no. 1, 12 ♂, 1 nymph (includes holotype, U.S. National Museum, Type no. 71,563); swimming pool at km 12, Hwy. 191, 1950 ft, 24 June 1969 (T. J. Cohn), no. 12, 3 ♂; same as previous record but 25–26 June 1969, no. 15, 3 ♂, 1 ♀; Molindero, near km 13 on Hwy. 191, 2280 ft, 25 June 1969 (T.J.C.), no. 14, 4 ♂; at El Toro

[4] Numerals in italics refer to locations on Fig. 34 identified by the same numerals.

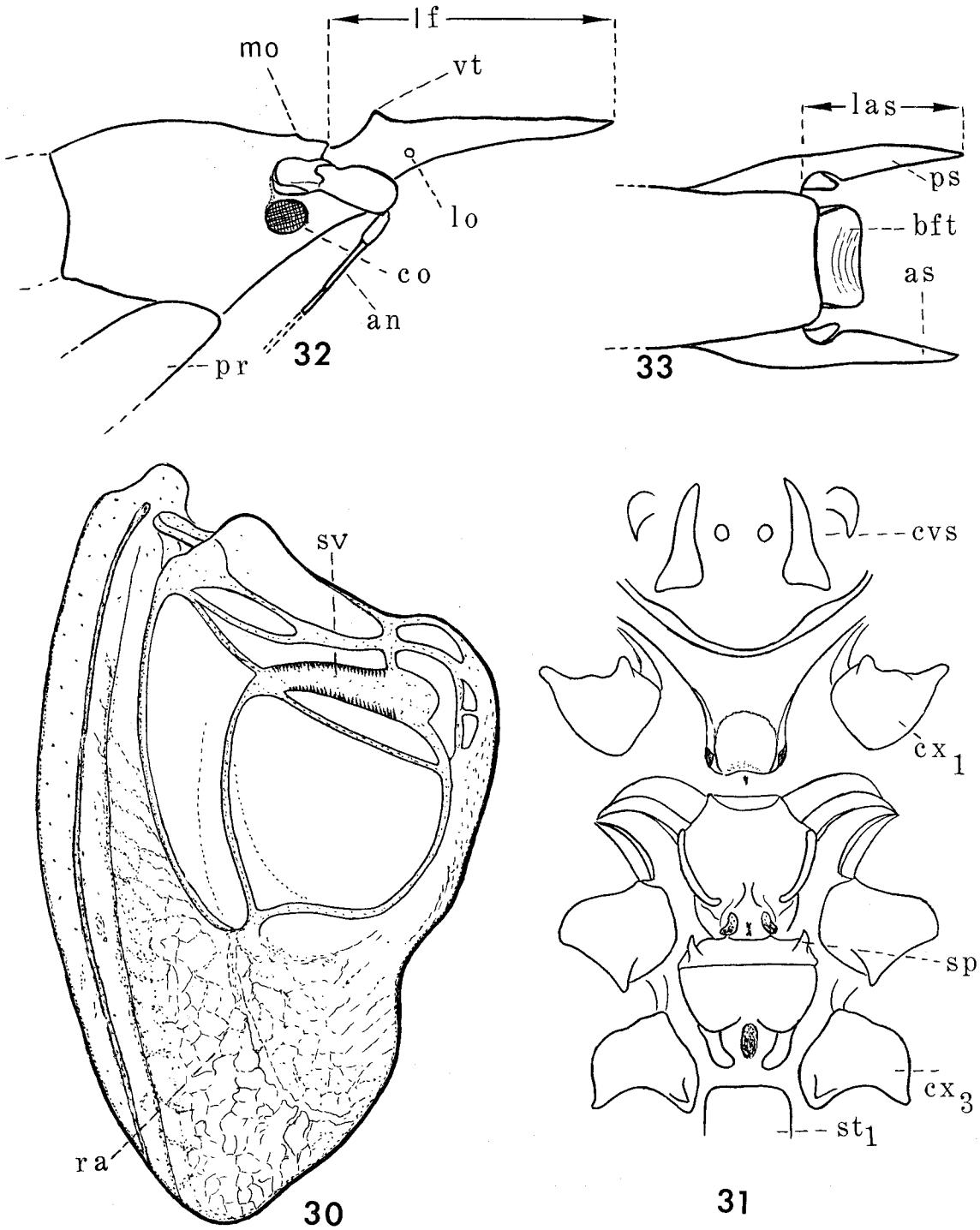

FIG. 30–33.—Structural details of *B. martorelli* males from Caribbean National Forest. 30, Dorsal view of left tegmen; 31, diagram of sternum of thorax, anterior portion uppermost; 32, diagram of head, in lateral view, *ventral surface uppermost,* mandibles not shown, to demonstrate method of measuring length of fastigium; 33, diagram of apical portion of left hind femur, dorsal view, to show method of measuring length of posterior apical spine. (an = antenna; as = anterior apical spine; bft = base of folded hind tibia; co = compound eye; cvs = cervical sclerites; cx_1 = front coxa; cx_3 = hind coxa; las = length of apical spine; lf = length of fastigium; lo = lateral ocellus; mo= median ocellus; pr = pronotum; ps = posterior apical spine; ra = reticulated apical area of tegmen; sp = spinelike tubercle; st_1 = sternum of 1st abdominal segment; sv = stridulatory vein; vt = ventral tooth of fastigium.)

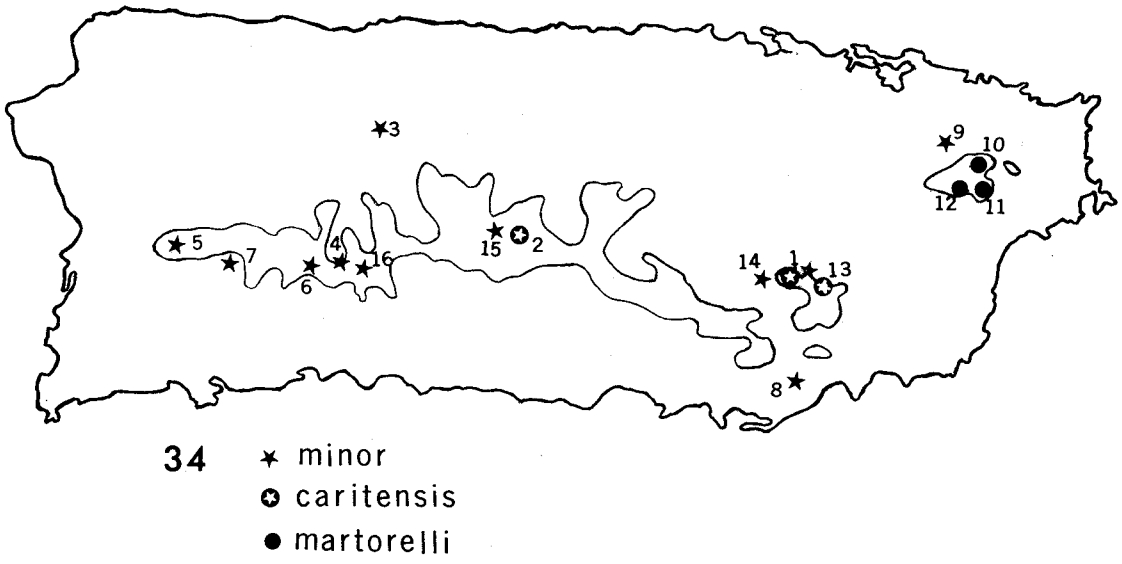

FIG. 34.—Map of Puerto Rico to show distribution of *Borinquenula*. Outlined areas on map represent approximate zones of 610 m altitude or higher. Numerals correspond to localities listed in text distribution records.

Trail, 2220 ft, at km 13.5 on Hwy. 191, 24–26 June 1969 (T.J.C.), no. 1, 1 ♂; near El Yunque Peak, ca. 3000 ft, on dead leaves of Sierra Palm, *Euterpe globosa*, 27 Oct. 1964 (Geo. Drewry), 1 ♂, 1 ♀; mossy forest, El Yunque, 3200 ft, 28 Mar. 1970 (R. Lavigne, F. Lavigne, Preston Webster), 1 ♂; El Yunque, at light, 7 Aug. 1959 (L. F. Martorell, S. Medina G.), 1 ♀; El Yunque, 2000 ft, July 1959 (Martorell and Medina), 1 ♀ (allotype, USNM); El Yunque, 30 July 1959 (Medina and Martorell), 2 ♀ nymphs, 1 ♂ nymph, Pico del Oeste (Harvard University Study Site), 3000 ft, 26 June 1969 (T.J.C.), no. 16 (Fig. 34, *11*) 2 ♂; near El Yunque, 650 m, at km 14.6 on Hwy. 191, 19 Jan. 1969 (T.J.W., P.C.D.), no. 5 (Fig. 34, *12*) 5 ♂, 2 nymphs.

Records Based on Song.—On 19 Jan. 1969, *B. martorelli* was identified by song at 25 places along Highway 191. Its lowest occurrence was at about the same elevation (ca. 485 m) on the north slope (km 9.6) and south slope (km 19.9).

Ecology.—Males were heard to sing and were collected chiefly 1–2 m up on undergrowth of the rain forest. Some were in rank weedy areas in forest clearings, and 3 were heard 6–10 m high in vines and trees. Specimens were collected on small trees, forbs, grasses, and palms. Though they bit and were prickly because of femoral spines and the fastigium, they were easily caught once seen with a headlight.

Song.—At 17°C, the calling song was a beady buzz lasting 1.0–1.5 sec and repeated every 4–6 sec. Audiospectrographic analyses of tapes indicate something of the effect of temperature on wing-stroke rate (Fig. 41). Some buzzes lack the change in duration and intensity of pulses (corresponding to wing strokes) evident in Fig. 35. The principal frequencies taped were 14 kHz and the dominant frequencies may be ultrasonic (cf. Suga 1966).

Derivation of Name.—This striking species is named for its discoverer, Luis F. Martorell, in recognition of his longtime service to Entomology, especially his sustained efforts to broaden the knowledge of the fauna of Puerto Rico.

Borinquenula caritensis, n. sp.

(Fig. 8, 9, 17, 18, 22, 25, 34, 36, 37)

MALE (*Holotype*).—General appearance as in Fig. 8 and 9; differing from *martorelli* chiefly as described in the key. Head with ratio of dorsal fastigial width opposite midlength of basal antennal segment to width of that segment 15:10. Front femur with 3 (left) or 4 (right) widely spaced spines on ventroanterior carina; front tibia with 7 anterior and 6 posterior spines on respective ventral carinae; middle femur with 4 short spines on anterior margin; middle tibia with 7 (left leg) or 8 (right) spines on ventroanterior carina, and 6 spines on ventroposterior carina; hind femur with 8 well-spaced medium-sized spines on ventroanterior margin. Supra-anal plate shallowly emarginate (Fig. 17); subgenital plate deeply emarginate, with long terminal styli (Fig. 18); cercus with recurved apical lobe on ventral surface (Fig. 22) slightly different from *martorelli*.

Measurements (mm).—Each measurement of the holotype is followed in parentheses by the range and mean for the 8 adult male paratypes. Pronotal length, 12.3 (11.9–14.2, 13.2); pronotal width, 6.0 (6.0–7.5, 7.0); length of hind femur, 19.5 (19.0–23.0, 21.7).

Other Structural Variation.—The recurved apical margin of the cercus is not always located as mesally as in Fig. 22, but the apical breadth of cercus in ventral view usually is wider than in *martorelli*

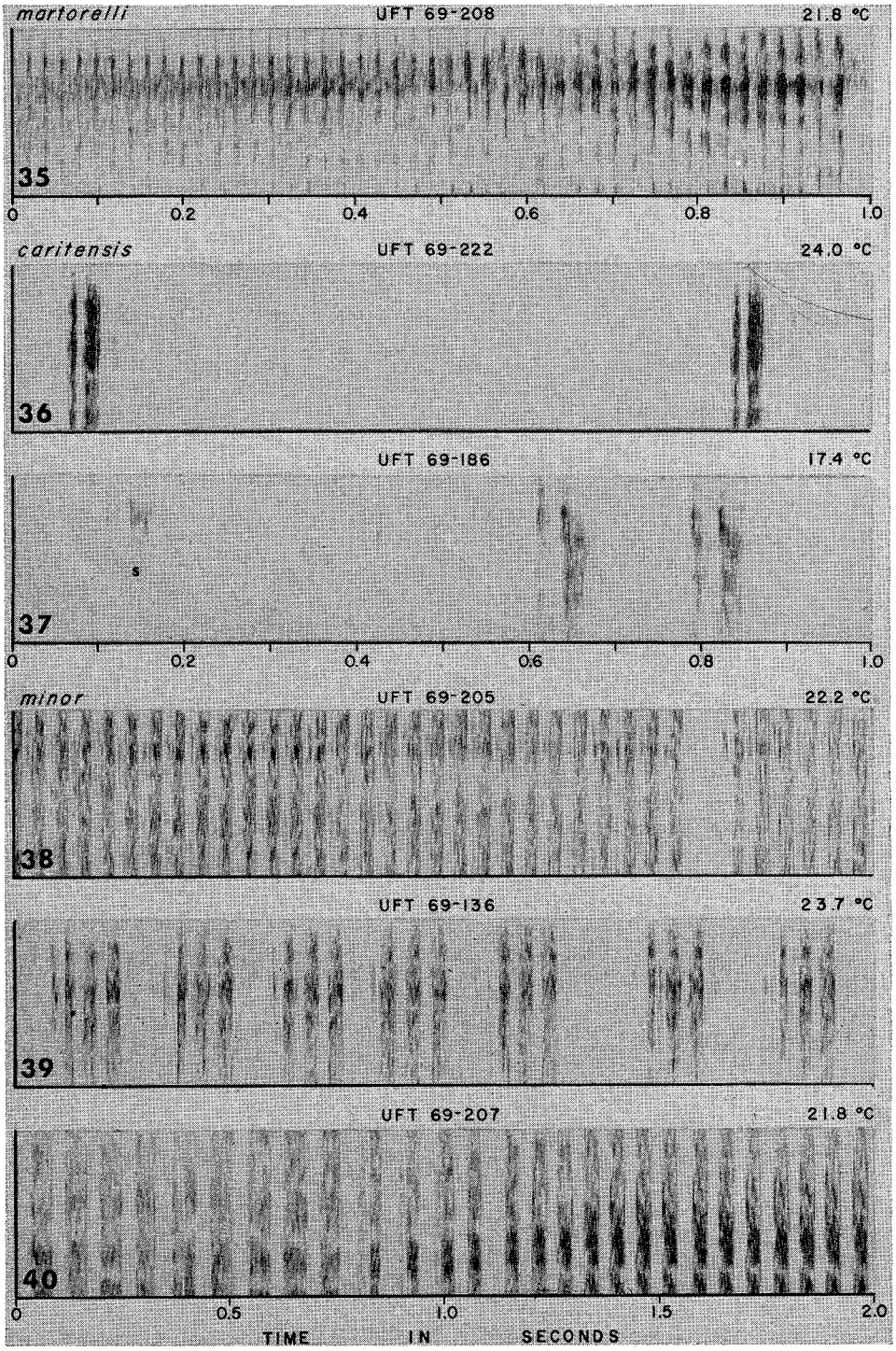

FIG. 35–40.—Audiospectrograms of calling songs of *Borinquenula*. 35, *B. martorelli* (Hwy. 191, near El Yunque); 36, 37, *B. caritensis;* 36, usual song (holotype); 37, double click, s = single click of neighboring individual (type locality); 38–40, *B. minor;* 38, usual song (holotype); 39, trios (Las Tetas de Gordo); 40, peculiarly slow sequence followed by sequence at usual rate (type locality). (All but Fig. 37 are from tapes of caged individuals.)

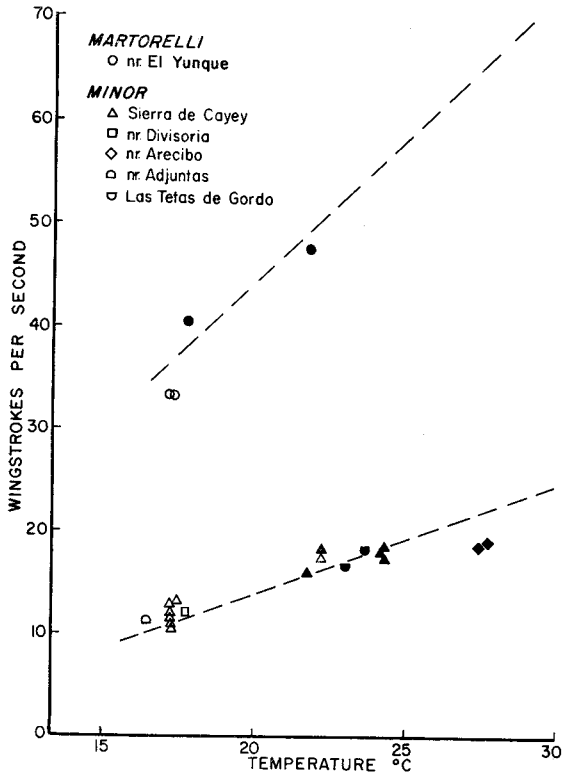

FIG. 41.—Effect of temperature on wing-stroke rates in *Borinquenula*. Open symbols indicate field recordings. Solid symbols are for laboratory recordings of caged individuals. The dashed lines are drawn by eye and their slopes are based on extensive recordings under controlled temperatures of U.S. copiphorines.

and the 2 species nearly always can be distinguished in this way.

Coloration.—Holotype much as in type of *martorelli* except for generally darker shades, plus several details. Most of head, fastigium, 2 basal segments of antenna, apical third of all femora, base and apical half (dorsal and mesal only) of front tibia, and most of middle tibia blackish brown to piceous; hind tibia black, spines and streaks at their bases pale; pronotum and most of venter reddish orange; abdomen dark reddish brown on sides, dorsum orange red, *without a median dark streak;* cerci and styli light reddish brown. Three paratypes have pale dorsum of abdomen hardly distinct, nearly all dark; otherwise, paratypes vary little from holotype.

Specimens Examined. (9 ♂).—PUERTO RICO: Near Area Recreativa Guavate (Guavate Recreation Area), 1.1 mile W junction Hwy. 184 and 179, 700 m, 20 Jan. 1969 (T. J. Walker, P. C. Drummond), no. 2 (Fig. 34, *1*), 4 ♂ (includes holotype, U.S. National Museum, type no. 71,564); 24 miles E of Adjuntas on Hwy. 143, at km 32.3 (0.5 miles W Cerro Dona Juana), 2600 ft, 23 June 1969 (T. J. Cohn), no. 9 (Fig. 34, *2*), 5 ♂.

Records Based on Song.—On 20 Jan. 1969, Walker heard *B. caritensis* at km 22.0, Highway 184, ca. 800 m (near Cerro La Santa) (Fig. 34, *13*). On the night of 21 Jan. 1969, he did *not* hear it on a slow drive from Adjuntas east to within 5 km of the westernmost record, nor did he hear it farther west during 2 other nights of field work at appropriate altitudes: 13 Jan., Cerro Gordo, and 14 Jan., Monte Guilarte.

Ecology.—Most specimens were heard ca. 1 m up in the undergrowth of a forest that included tree ferns and palms. One specimen was heard and captured on tall grass at the forest edge.

Song.—The song was a 2-pulsed click produced at a rate of ca. 1/sec. 17.4°C and 1.3/sec at 24°C (Fig. 36). One individual was taped that interspersed pairs of clicks (Fig. 37) with the single ones. Another individual produced occasional sequences of ca. 8 clicks at a rate of ca. 5/sec at 17.4°C. The most intense taped frequencies were above 10 kHz.

At the type locality, singing began at 7 PM. It was heard at a 2nd locality at 11 PM. Neighboring individuals usually alternated their clicks.

Derivation of Name.—The name *caritensis* refers to the collecting site: the Bosque Estatal de Guavate-Carite (Guavate-Carite State Forest).

Borinquenula minor, n. sp.

(Fig. 10–14, 19, 20, 23, 26, 29, 34, 38–41)

MALE (Holotype).—Smallest of the species of *Borinquenula,* with short apical spines on the hind femora and a short fastigium.

Head with ratio of dorsal fastigial width opposite midlength of basal antennal segment to width of that segment 12:8. Front femur with 2 well-spaced spines on apical half of ventroanterior carina; front and middle tibiae each with 7 anterior and 6 posterior spines on respective ventral carinae; middle femur with 3 short spines on ventroanterior margin; hind femur with 5 (left leg) and 7 (right leg) spines on ventroanterior margin. Paired apical spines on femora clearly shorter than those of *caritensis* and *martorelli* (Table 1). Supra-anal plate broadly and shallowly concave at apex (Fig. 19); subgenital plate with tiny styli and V-shaped posterior emargination (Fig. 20); cercus *without* recurved apical lobe.

FEMALE (*Allotype*).—General appearance as in Fig. 10 and 13. Pronotum with length 1.6 times greatest width; tegmina widely separated, reaching posterior margin of metanotum; wings absent; ovipositor proportionally longer and narrower than in *martorelli;* subgenital plate essentially as in *martorelli.*

Measurements (mm).—The measurements of the holotype and allotype are followed, in parentheses, by the range and mean for 16 representative adult male paratypes, then in a 2nd parentheses by measurements of 1 ♀ paratype. Pronotal length, ♂ 12.1, ♀ 7.6 (10.4–13.3, 11.6) (7.4); pronotal width, ♂ 5.3, ♀ 4.9 (4.6–5.6, 5.1) (4.9); length of hind femur,

♂ 13.9, ♀ 15.0 (12.3–14.5, 13.4) (13.5); ovipositor 12.6 (12.4).

Other Structural Variation.—The large vein (radius?) on the lateral field of the male tegmen usually branches differently from *martorelli;* on the dorsal field there seldom is such a strongly reticulated pattern as in *martorelli* (Fig. 30).

Coloration.—Holotype of various shades of tan and brown, except for pronotum. Face, ventral part of fastigium, and 2 basal segments of antenna blackish brown, pale with pinkish tinge on clypeus and mandibles; dorsum of head, most of dorsum of abdomen pale orange; pronotum yellowish green, irregularly blotched especially on anterior half with very pale orange; tegmina yellowish gray, darker near costal margin; sides and venter of abdomen mostly reddish brown, paler on prosternum and some of abdominal pleura; tarsi, bases of femora, and apex of hind femur dirty brown.

The allotype is somewhat paler than the holotype; pronotum with distinct green limited to few areas on disk; ovipositor light brown; tegmina light green tinged with pale yellow. In the 27 paratypes, the pronotum varies from uniform dull grayish orange to nearly uniform dark yellow green with only small flecks of pale orange; nearly all specimens have some green on pronotum. A few specimens have all of the abdomen pale except venter; fastigium rarely is nearly all pale.

Specimens Examined. (27 ♂, 2 ♀)—PUERTO RICO: El Verde Field Station, Luquillo Forest, 30 July 1967 (Geo. Drewry) (Fig. 34, *9*), 2 ♂; Quebrada Espiritu Santo (One-half mile S El Verde Field Station), Luquillo Forest, 7 Apr. 1970 (R. Lavigne), (Fig. 34, *9*), 6 ♂, 1 ♀; Guavate Recreation Area, 1.1 mile W junction Hwy. 184 and 179, 700 m, 20 Jan. 1969 (T. J. Walker, P. C. Drummond), no. 2 (Fig. 34, *1*), 10 ♂ (includes holotype, U.S. National Museum, Type no. 71,565); Guayama, 20 June 1969 (Geo. Drewry), (Fig. 34, *8*), 1 ♀ (allotype, U.S. National Museum); 10 km S Arecibo, on Hwy. 10, 9 Jan. 1969 (T.J.W., P.C.D.), no. 1 (Fig. 34, *3*), 1 ♂; near Adjuntas, km 30.4 on Hwy. 10, 500 m, 21 Jan. 1969 (T.J.W., P.C.D.), no. 3 (Fig. 34, *4*), 1 ♂; near Adjuntas, km 6.9 on Hwy. 131, 1000 m, 14 Jan. 1969 (T.J.W., P.C.D.), no. 2 (Fig. 34, *6*), 3 ♂; Maricao State Forest, 9 miles N Sabana Grande, at km 12, 2600 ft, 20 June 1969 (T. J. Cohn), no. 4 (Fig. 34, *7*), 2 ♂; Las Tetas de Cerro Gordo (near Maricao), ca. 880 m, 13 Jan. 1969 (T.J.W., P.C.D.), no. 1 (Fig. 34, *5*), 2 ♂.

Records Based on Song.—On 20 Jan. 1969, *B. minor* was identified by song on Hwy. 1 at points 0.7 and 6.1 miles N of the junction with Hwy. 184 and at 5 localities between km 0.9 and 7.5 on Hwy. 184 (ca. 400–700 m) (Fig. 34, *14*). On 21 Jan. 1969, *B. minor* was taped (UFT 69-198, 200) at km 27.4 (ca. 800 m) and km 0.2 Hwy. 143, and it was heard along Hwy. 10 between the junction with Hwy. 143 and Adjuntas (ca. 500 m) (Fig. 34, *15, 16, 4*).

Ecology.—*B. minor* ranges to lower altitudes and occurs in more open areas than the other 2 species. Walker found it in greatest abundance at the type-locality, where males were mostly singing ca. 1 m up on 2-m broad-bladed grass growing in open areas. However, at the same locality, a few individuals were singing from undergrowth in the edge of the forest. Elsewhere he heard *minor* in similar habitats: forest edge and densely overgrown open areas. It was never heard within closed-canopy forest. At Quebrada Espiritu Santo, *minor* was collected by R. J. Lavigne on tall grass which surrounds a parking lot, and he sent us photographs of males resting lengthwise, head down on the grass stems. Dr. Lavigne found the katydids "definitely associated with the grass although from the singing, some probably occur on the vegetation in the forest edge community."

Song.—The song of *B. minor* is a lispy rattle. It varies to an unusual degree in 3 parameters: duration and intervals of pulse sequences ("rattles"), pulse rhythm within sequences, and pulse rate (corresponding to wing-stroke rate). The duration of rattles was most often 2–6 sec and was nearly regular within a sequence of rattles. However, 3 individuals taped at the type-locality rattled without pausing for 24 sec or longer. The intervals between rattles in prolonged sequences of rattles varied from 10 to 60 sec and were fairly regular within a single sequence. The most infrequent rattles were produced by a solitary singer. The nearly continuous rattles were made by males with nearby singing neighbors. With only distant neighbors the rattles were shorter (2–6 sec) with longer intervals (10–20 sec) and were generally alternated.

The pulse rhythm within rattles was generally either continuous (Fig. 38) or with consecutive groups of 3's (Fig. 39) or more rarely 4's or 2's. The 2 contrasting pulse rhythms were first noted at the type-locality, and it was thought that 2 species might be involved. However, certain individuals collected producing each pulse rhythm in the field eventually produced the other while caged. Furthermore, individuals producing a uniform sequence often ended with a single triplet, and when individuals sang erratically, triplets were often produced. The 3 taped individuals that rattled without pause for 24 sec or more were producing their pulses in triplets. In the same locality, 2 specimens were heard to alternate 2-sec-long rattles of triplets every 10–15 sec. The significance of triplet production is not known. It occurred in individuals from near the eastern and western extremes of *minor's* range (Fig. 34, *1, 5*).

The final parameter that shows unusual variation in *minor* is pulse rate. The pulse rate within triplets and within most longer uniform sequences of pulses (Fig. 38, 39) was the same. However, an individual along Hwy. 10 just south of Adjuntas was heard to consistently start its rattles with a slow pulse rate and then shift to a higher rate. A caged individual from the type-locality was later taped producing the same shift, and audiospectrographic analy-

sis (Fig. 40) showed that the faster rate was the same as that produced in other songs. The significance of the peculiarly slow initial rate is not known. The effect of temperature on the usual pulse rate is shown in Fig. 41.

The frequency spectra of the tapes of *minor* differed from those of *martorelli* and *caritensis* in containing intense sounds as low as 2 kHz. In some instances frequencies from 2 to 17 kHz appeared about equally intense.

Derivation of Name.—The name *minor* relates to the small size in comparison to the other species.

DISCUSSION

Relation of File Structure to Song.—The species of *Borinquenula* illustrate these 3 generalizations concerning the relation of file structure and the physical characteristics of the song produced in gryllids and tettigoniids. (1) Species with very similar files may have very different songs; e.g. *martorelli* and *caritensis*. The differences in the songs are of course mainly a matter of different patterns of movements of about the same apparatus (cf. *Oecanthus fultoni* Walker and *O. rileyi,* Baker, Walker 1962). (2) Among species of the same genus there is an inverse relation between wing-stroke rate and number of teeth in the file; e.g. *martorelli* and *minor* (cf. Walker 1963, p. 788). (3) Among species in different genera, relations are unpredictable. For instance, species that have nearly identical songs may have very different files. *B. minor* and *Belocephalus subapterus* Scudder are brachypterous copiphorines with closely similar wing-stroke rates, but the file of *subapterus* is 30% longer and has 100% more teeth than that of *minor*.

Origin of Borinquenula.—The most striking differences between *Borinquenula* and its closest surviving relatives are its abbreviated tegmina and wings and its prolonged male pronotum, which is suggestive of *Atlanticus* (Decticinae). Three other West Indian endemic genera of tettigoniids are brachypterous (*Spelaeala,* Hispaniola; *Polyancistroides,* Cuba) or have brachypterous montane species (*Polyancistrus,* Hispaniola). The brachypterous copiphorine genus *Belocephalus* evidently evolved in Florida, perhaps at a time when high sea levels made Florida a group of islands. Populations adapted to mountain conditions or living on islands seem especially well suited to benefit from reduced long-range dispersal by flight. As the importance of flight becomes less, brachypterousness is more likely to prove of adaptive advantage.

The prolonged pronotum apparently protects the tegmina. This idea is supported by the sexual dimorphism of the tegmina being matched by sexual dimorphism in pronotal prolongation. Such a condition is found not only in *Borinquenula* but also in *Atlanticus* (Decticinae) and in *Cycloptilum* (Gryllidae), genera with similarly abbreviated tegmina in the male and vestigial ones in the female. *Belocephalus, Spelaeala,* and *Polyancistroides* are 3 genera with abbreviated tegmina in which the male pronotum is not prolonged over the tegmina; however, the latter 2 genera have peculiar structures that may have a similar function.

Relationships of Borinquenula.—This genus is a somewhat atypical member of the Copiphorinae; some characters also suggest the Agraeciinae. In Karny's key to Copiphorinae (1913a), which is essentially given in an English translation for American genera by Bruner (1915: 379), *Borinquenula* runs to near *Acanthacara.* We have seen the unique type of *Acanthacara acuta* Scudder, a wingless female, apparently immature, from Ecuador; the fastigium has no ventral tooth, and the sum of generic characters places the genus in the Agraeciinae.

If *Borinquenula* were long winged, it would run to *Eriolus* or near. Based on a Puerto Rican species near *E. caraibeus* Bolivar, we find that genus very suggestive of *Borinquenula,* especially in the head and thoracic sterna. The fastigium of *B. minor* is very similar in shape and size to the fastigium of our species of *Eriolus.* The principal generic differences, in addition to the fully winged condition, are (1) pronotum of *Eriolus* much shorter, with lateral lobe much deeper and greatly expanded near front coxa; (2) different specialization in *Eriolus* of male genitalia, mainly more elongate cerci with 2 terminal appendages, and structure of titillator; the latter consists of a rather elaborate shieldlike sclerite, apparently folded lengthwise when at rest, between the halves of which lie 2 fingerlike cylindrical processes that are directed posteriorly when the basal "shield" is expanded. This shield recalls a broad circular shield borne by an elongate median basal "stalk" in *Belocephalus sabalis* Davis; that shield does not fold, and there are no additional conspicuous processes. In contrast to *Borinquenula, Belocephalus* has prosternal spines and a pronounced transverse ventral sulcus at the base of the fastigium; also, the pronotum is much shorter than in *Borinquenula.*

A review of characters traditionally used to define the subfamilies Copiphorinae and Agraeciinae reveals that those differences are not entirely dependable. Furthermore, though most genera assigned to one subfamily or the other clearly belong there, some genera cannot be placed with certainty. The 5 characters listed in Table 2 are used most often to distinguish Copiphorinae from Agraeciinae.

From the 1st 2 characters in Table 2, it would appear that *Borinquenula* is agraeciine, the 3rd and 4th suggest a copiphorine affinity, and the 5th is indefinite because there are both greenish and brown species of *Borinquenula.* We are strongly influenced in the subfamily placement of *Borinquenula* by the similarity of the fastigium to that of *Eriolus.* Many genera are not clear cut in belonging to Agraeciinae or Copiphorinae; however, it appears best to recognize both subfamilies, at least until more of the genera of debatable position are critically reviewed.

The proventriculus of several genera each of Copiphorinae and Agraeciinae was examined by clearing in caustic and examining with a steroscopic microscope. No fundamental differences in proventicular

structure were noted. Representatives of both subfamilies are similar to *Neoconocephalus* as illustrated by Judd (1948: 152, Fig. 48). However, detailed examination of slide-mounted preparations by compound microscope would be necessary for dependable comparisons. Similarly, a more extensive comparative study of titillators than we have made would be necessary to determine whether any general distinction between Agraeciinae and Copiphorinae is possible on that basis.

Brief History of Usage of Agraeciinae and Copiphorinae.—In exploring the affinities of *Borenquenula,* Gurney made a review of the usage of Agraeciinae and Copiphorinae. The name Agraeciinae, based on *Agraecia* Serville, dates from the tribe Agroeciini of Redtenbacher (1891: 330, 432), raised to the subfamily Agroeciinae by Kirby (1906: 225), followed by Caudell (1911: 4) who used the spelling Agraeciinae. Because of the several spellings of Agraeciinae in literature, the principal facts relative to spelling are noteworthy. Serville (1831: 152) proposed *Agraecia,* with an *ae* ligature, the name derived from 2 Greek words, one (agros) meaning field, the other (oikos) meaning home, abode, or house. From the derivation of the 2nd part, the same as used in *Oecanthus,* an *oe* rather than *ae* ligature would appear to have been the correct spelling, and may actually have been intended by Serville. Probably for this reason, Burmeister (1838: 707) emended *Agraecia* to *Agroecia,* and he was followed by Redtenbacher (1891: 451). Kirby (1906: 259) used the *oe* and labelled Serville's original spelling an error. However, Serville's spelling of *Agraecia* is clear, the *ae* ligature being quite distinct from an *oe* ligature in *Choeradodis* (Serville 1831: 50), for example. Therefore, to preserve original spelling and to continue predominant recent usage (Zeuner 1939: 118, Ragge 1955: 154, and Beier 1955: 253, *Agraecia* should be used as the basis for the tribal or subfamily name.

The name Copiphorinae was first used by Caudell (1911: 4) for the group called Conocephalinae by Kirby (1906: 229), which was the tribe Conocephalini of Redtenbacher (1891: 328, 334). As a suprageneric group, the latter dated from Conocephalidae of Burmeister (1838: 702). The change in application of the name Conocephalinae was explained by Caudell (1910: 96) on the basis of the type-species of the genus *Conocephalus.*

A basic pioneer work in the classification of katydids of this large complex was that of Redtenbacher (1891) who recognized Agroeciini and Conocephalini as 2 of the 4 major tribes of the Conocephaliden. Brunner (1893) accepted the arrangement. Caudell (1911), who gave the 1st major key in English to the subfamilies of Tettigoniidae, followed Redtenbacher in distinguishing Agraeciinae as having the fastigium noticeably narrower than the basal antennal segment, rather than wider as in Copiphorinae. In Karny's 2 important reviews (1913a, b), long characterizations of Agraeciinae and Copiphorinae appear, but when compared critically the essential differences between the subfamily descriptions are the 5 characters listed in our Table 2. Ragge (1955: 154) is a recent author who accepted the distinctness of the 2 subfamilies.

Caudell (1918: 24) pointed out the difficulty of assigning certain genera to either of the 2 subfamilies, and Hebard (1927: 140–2) indicated the uncertainty that earlier authors had experienced. As a result of the indecisiveness of traditional separation characters, several recent orthopterists have reduced the rank of the 2 groups or otherwise modified the classification. Zeuner (1936; 1939: 118–9) regarded Salomoninae and Copiphorinae as 2 of the 5 subfamilies in the Conocephaloid Group, and he included the Agraeciinae of authors in the Salomoninae. He found the structure of prothoracic tracheae important in group placement, but he did not distinguish Salomoninae and Copiphorinae in that way. As a suprageneric group, Salomoninae dates from Salomonitae of Brongniart (1897: 2, 4) who regarded them as a group of "Agroecieae." Beier (1955: 246; 1962: 1) included Agraeciini and Copiphorini as tribes or groups within Conocephalinae when he gave keys to tettigoniid subfamilies. Chopard (1949: 663) did similarly, but with higher ranks, i.e., his Conocephalidae included Conocephalinae, Agroecinae, Copiphorinae, and Listroscelinae.

Table 2.—Characters used to distinguish Copiphorinae from Agraeciinae.

Structure	Agraeciinae	Copiphorinae
Connection of vertext with top of frons	Directly or by a thin keel (no wide transverse sulcus)	Usually separated by wide transverse sulcus (seldom a keel)
Ovipositor shape	Usually curved dorsally	Usually straight
Ventral tooth of vertex	Not present	Present
Width of fastigium compared with width of 1st antennal segment	Usually narrower	Usually wider
General color	Seldom green	Often green

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