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**NEW SPECIES OF
AMERICAN BARK BEETLES
(SCOLYTIDAE: COLEOPTERA)**

by

Stephen L. Wood

**BIOLOGICAL SERIES — VOLUME XIX, NUMBER 1
JANUARY 1974 / ISSN 0068-1024**

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NEW SPECIES OF AMERICAN BARK BEETLES (SCOLYTIDAE: COLEOPTERA)¹

by

Stephen L. Wood²

ABSTRACT

The following 156 species of American Scolytidae are described as new to science: *Cnesinus reticulatus* (Venezuela), *C. beaveri* (Brazil), *C. teretis* (Venezuela), *C. alienus* (Venezuela), *C. deperditus* (Colombia), *C. fulgens* (Venezuela), *C. fulgidus* (Colombia), *C. lucaris* (Venezuela), *C. triangularis* (Colombia), *C. brighti* (Mexico), *C. coracinus* (Mexico), *Bothrosternus lucidus* (Brazil), *Hylastes niger* (Mexico), *Xylechinus mexicanus* (Mexico), *Phloeotribus nanus* (Brazil), *Chramesus corniger* (Mexico), *Ch. disparilis* (Mexico), *Ch. variabilis* (Mexico), *Ch. microporosus* (Mexico), *Ch. aquilus* (Mexico), *Ch. wisteriae* (Mississippi), *Ch. marginatus* (Mexico), *Carphoborus piceae* (Oregon), *Carphobius cupressi* (Guatemala), *Cladoconus atrocis* (Brazil), *Scolytodes canalis* (Mexico), *S. costabilis* (Mexico), *Pseudothysanoes contrarius* (Mexico), *P. recavus* (Mexico), *Thysanoes granulifer* (Mexico), *Micracisella mimetica* (Mexico), *M. ocellata* (Mexico), *Hyllocurus rivalis* (Mexico), *H. binodatus* (Mississippi), *Cryphalomorphus parvatus* (Honduras, Costa Rica), *Cr. setifer* (Guatemala), *Cr. hirtus* (Mexico), *Cr. rusticus* (Mexico), *Cr. turtus* (Mexico), *Hypothenus apicalis* (Mexico), *Hyl. indigenus* (Mexico), *Hyl. trivialis* (Costa Rica, Panama, Venezuela), *Hyl. dolosus* (Costa Rica), *Hyl. solocis* (Mexico), *Hyl. vesculus* (Mexico), *Hyl. suspectus* (Costa Rica, Panama, Venezuela), *Pericryphalus sobrinus* (Brazil), *Dendrocranulus limatus* (Venezuela), *D. reditus* (Venezuela), *D. conditus* (Venezuela), *D. consimilis* (Mexico), *D. vinealis* (Honduras), *D. vicinalis* (Costa Rica), *D. securus* (Costa Rica), *D. fulgidus* (Panama), *D. vicinus* (Honduras), *D. rudis* (Mexico), *D. confinis* (Panama), *Gnathophthorus artus* (Brazil), *Dryocoetoides verrucosus* (Venezuela), *Dr. pilcatus* (Venezuela), *Dr. velutinus* (Venezuela), *Dr. rusticus* (Venezuela), *Dr. severus* (Venezuela), *Dr. insculptus* (Colombia), *Dr. indolatus* (Venezuela), *Sampsonius expulsus* (Colombia), *Sam. detractus*

(Panama), *Sam. usurpatus* (Costa Rica), *Xyleborus pristis* (Costa Rica), *X. micarius* (Costa Rica), *X. bicornutus* (Venezuela), *X. crinitulus* (Venezuela), *X. pandulus* (Costa Rica, Panama), *X. varulus* (Venezuela), *X. palatus* (Mexico), *X. exutus* (Costa Rica), *X. rusticus* (Mexico), *X. ocellatus* (Colombia), *X. opimus* (Florida), *X. lacunatus* (Costa Rica), *X. meridensis* (Venezuela), *X. aclinis* (Panama), *X. dissimulatus* (Costa Rica), *X. concentus* (Costa Rica, Venezuela), *X. tribulatus* (Costa Rica), *X. vismiae* (Costa Rica), *X. demissus* (Costa Rica), *X. meritus* (Costa Rica), *X. prolatus* (Costa Rica), *X. dissidens* (Mexico), *Xyleborinus dirus* (Costa Rica), *Xy. tribulosus* (Panama), *Xy. protinus* (Costa Rica), *Xy. celatus* (Colombia), *Araptus insinuatus* (Guatemala), *A. interjectus* (Guatemala), *A. accinctus* (Mexico), *A. delicatus* (Mexico), *A. genialis* (Guatemala), *A. dentifrons* (Mexico), *A. facetus* (Costa Rica), *A. cuspidus* (Mexico), *A. placatus* (Mexico), *A. decorus* (Costa Rica), *A. blanditus* (Mexico), *A. medialis* (Costa Rica), *A. conditus* (Costa Rica), *A. frugalis* (Costa Rica), *A. laudatus* (Costa Rica), *A. vesculus* (Costa Rica), *A. exigialis* (Panama), *A. refertus* (Guatemala), *A. trepidus* (Guatemala), *A. frontalis* (Guatemala), *A. nigrellus* (Costa Rica), *A. vinnulus* (Costa Rica), *A. furvus* (Panama), *A. furvescens* (Guatemala), *A. lepidus* (Costa Rica), *A. mendicus* (Costa Rica), *A. nanulus* (Mexico), *A. festivus* (Mexico), *Pseudopityophthorus festivus* (Mexico), *Gnathotrichus obscurus* (Mexico), *G. omisus* (Costa Rica), *Gnathotrupes dilutus* (Costa Rica), *Gp. concentus* (Costa Rica), *Tricolus simplicis* (Guatemala), *T. inornatus* (Costa Rica), *T. inaffectus* (Costa Rica), *T. cecropii* (Costa Rica), *T. intrusus* (Venezuela), *T. ardis* (Costa Rica, Panama), *T. parsus* (Costa Rica), *T. rufithorax* (Costa Rica), *T. badius* (Costa Rica, Panama), *T. partilis* (Costa Rica), *T. fenoris* (Costa Rica), *T. frontalis* (Mexico), *T. capitalis* (Panama), *T. naevus* (Costa Rica), *T.*

¹Most of the field work that led to the discovery of these insects was sponsored by the National Science Foundation

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scitulus (Costa Rica, Panama), *T. peltatus* (Panama, Costa Rica), *T. aciculatus* (Mexico), *T. bicolor* (Costa Rica), *T. amplus* (Mexico), *Amphicranus mirandus* (Costa Rica), *Am. tornatilis* (Costa Rica), *Am. macellus* (Costa Rica), *Am. spinescens* (Costa Rica), *Am. spinosus* (Costa

Rica), *Am. mucronatus* (Panama), *Am. acus* (Venezuela), *Paracorthylus mutilus* (Panama), and *Par. concisus* (Costa Rica). New subspecies include *Ips borealis lanieri* (Colorado, South Dakota), and *X. sharpi lenis* (Mexico).

INTRODUCTION

A large number of species new to science were discovered during the preparation of a monograph of the Scolytidae of North and Central America. Since it will be several years before the monograph is concluded, the new names are being published in order to stabilize nomenclature and to facilitate identification. On the following pages 157 species and 2 subspecies are described as new to science. The new species represent the following genera: *Cnesinus* (11), *Bothrosternus* (1), *Hylastes* (1), *Xylechinus* (1), *Phloeotribus* (1), *Chramesus* (7), *Carphoborus* (1), *Carphobius* (1), *Cladoctonus* (1), *Scolytodes* (2), *Pseudothysanoes* (2), *Thysanoes* (1), *Micracisella* (2), *Hyllocurus* (2), *Cryphalomorphus* (5), *Hypothenemus* (7), *Pericryphalus* (1), *Dendrocranulus* (11), *Gnathophtorus* (1), *Dryocoetoides* (7), *Sampsonius* (3),

Xyleborus (22), *Xyleborinus* (4), *Araptus* (28), *Pseudopityophthorus* (1), *Gnathotrichus* (2), *Gnathotrupes* (2), *Tricolus* (19), *Amphicranus* (7), and *Paracorthylus* (2). One new subspecies in *Ips* and one in *Xyleborus* are also named.

The new species are from the following areas: United States (4), Mexico (42), Guatemala (10), Honduras (2), Costa Rica (45), Panama (10), Colombia (7), Venezuela (20), and Brazil (6). In addition, one species each also occurred in the following combinations of countries: Honduras/Costa Rica, Costa Rica/Venezuela. Two species are from Costa Rica/Panama/Venezuela; four are from Costa Rica/Panama.

Illustrations, keys, and supplemental taxonomic notes useful in identifying these species will be presented in the monograph.

SYSTEMATIC SECTION

Cnesinus reticulatus, n. sp.

This species is distinguished from the very closely related *retifer* Wood by the slightly larger size, by the much more coarsely punctured pronotal disc, and by the slightly shorter declivital setae.

FEMALE.—Length 2.0 mm (paratype 1.9 mm), 2.5 times as long as wide; color very dark brown.

As in *retifer* except punctures on posterior third of pronotum at least twice as wide, interspaces between punctures less than half as wide as a puncture, punctures reduced in size anteriorly but in all areas much larger than in *retifer*. Interstitial setae on declivity slightly finer and shorter than in *retifer*.

TYPE LOCALITY.—Thirty km E Palmar, Bolivar, Venezuela.

TYPE MATERIAL.—The female holotype and one female paratype were collected at the type locality on 12-VI-70, 200 m, No. 529, from *Vismia cayennensis*, by S. L. Wood.

The holotype and paratype are in my collection.

Cnesinus beaveri, n. sp.

This species is distinguished from the allied *blackmani* Schedl by the smaller size, by the more widely separated eyes and more broadly convex frons, by the much more elongate, strigose pronotal punctures, and by the finer, more widely spaced elytral vestiture.

FEMALE.—Length 1.4 mm (paratypes 1.35-1.45 mm), 2.7 times as long as wide; color dark brown.

Frons evenly convex above shallow, transverse impression at level of antennal bases; surface strongly reticulate, with very fine, moderately sparse, somewhat obscure punctures; vestiture of sparse, short hair; eyes separated by 2.0 times width of an eye.

Pronotum 1.1 times as long as wide; outline as in *blackmani*; surface smooth, shining, punctures fine and longitudinally striate, striations

about 2-8 or more times as long as wide, often longitudinally confluent. Vestiture confined to anterior third, of course, short, rather sparse setae.

Elytra 1.8 times as long as wide, 1.9 times as long as pronotum; sides almost straight and parallel on slightly less than basal three-fourths, rather narrowly rounded behind; anterior margins narrowly elevated, crest shallowly marked into separate crenulations, no submarginal crenulations; striae 1 moderately, others weakly impressed, punctures rather coarse, distinctly impressed; interstriae distinctly wider than striae, shining, almost smooth, but with short, obscure, subtransverse lines indicated, punctures fine, shallow, uniseriate, close. Declivity steep, convex; striae 1 moderately, others weakly impressed, impression narrower than punctures; interstriae 1 distinctly, others weakly convex. Vestiture largely confined to declivity; consisting of slender interstitial bristles, each with its apical third apparently flattened; bristles two-thirds as long as distance between rows, spaced within a row by length of a bristle.

TYPE LOCALITY.—About 260 km N Xavantina, Mato Grosso, Brazil (12°49' S 51°46' W).

TYPE MATERIAL.—The female holotype and three female paratypes were taken at the type locality on 1-XII-68, No. F40, by R. A. Beaver; one female paratype bears the same data except 13-X-68, No. B105; and one female paratype the same data except 26-XI-68, No. D71G.

The holotype and one paratype are in the British Museum (Natural History), two paratypes are in the Museu de Zoologia, Universidade de São Paulo, and two paratypes are in my collection.

Cnesinus teretis, n. sp.

This species is distinguished from the allied *blackmani* Schedl by the smaller size, by the larger eyes, by the different frontal sculpture in both sexes, and by the less strongly impressed striae with smaller striae punctures.

FEMALE.—Length 1.5 mm (paratypes 1.3-1.5 mm), 2.7 times as long as wide; color dark brown, pronotum almost black.

Frons very narrow, weakly convex from vertex to epistoma, median two-thirds on lower half a slightly elevated plateau, this area to vertex smooth, polished and entirely devoid of punctures or setae; lateral areas below obscurely reticulate, with moderately abundant, coarse, short setae, a row of setae continued along me-

dian margin of eye almost to narrowest point between eyes; eyes separated by less than half greatest width of eye, eyes very large, coarsely faceted.

Pronotum 1.15 times as long as wide; as in *blackmani* except sides more strongly constricted on basal half, punctures slightly smaller and more elongate. Vestiture confined to anterior third, of fine, short, recumbent hair.

Elytra 1.6 times as long as wide, 1.6 times as long as pronotum; outline as in *blackmani*; striae 1 moderately, others feebly impressed, punctures small, shallow; interstriae twice as wide as striae, almost flat, smooth, shining, punctures minute, uniseriate, those bearing setae usually minutely granulate. Declivity steep, convex; striae 1 impressed; interstriae 1 narrowly convex; interstitial punctures replaced by small, rounded, setiferous granules. Vestiture confined to declivity, discal interstriae and posterior half of 3, 5, and 7; consisting of coarse bristles up to slightly less than twice as long as distance between rows, only slightly longer than distance between bristles within a row.

MALE.—Similar to female except frons weakly, transversely impressed on lower half more strongly convex on upper half, surface reticulate and finely, sparsely punctured, vestiture more generally distributed; disc with rows of very small, fine interstitial setae.

TYPE LOCALITY.—Seven km NW Socopo, Barinas, Venezuela.

TYPE MATERIAL.—The female holotype, male allotype, and 35 paratypes were taken at the type locality on 13-II-70, 200 m, No. 322, from *Nectandra* twigs, by S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Cnesinus alienus, n. sp.

This species is distinguished from the distantly allied *nitidus* Eggers by the very differently sculptured frons, by the larger, shallow pronotal punctures, by the very shallow, smaller striae punctures, and by the much more deeply sulcate elytral declivity.

MALE.—Length 2.3 mm (allotype 2.5 mm), 2.7 times as long as wide; color dark brown, almost black.

Frons basically convex with central third rather deeply concave, lower margin of concavity at level just above antennal insertion armed by a pair of small, pointed, rather widely separated denticles; upper margin of concavity with a median prominence; surface reticulate, almost

rugose, a few small granules in lateral and lower areas, punctures minute, obscure; vestiture of fine, sparse hair.

Pronotum 1.2 times as long as wide; outline as in *nitidus*; surface mostly dull, obscurely reticulate to minutely, longitudinally etched, punctures rather small, two to three times as long as wide, larger than in *nitidus*. Glabrous except for a very few setae on anterior fourth.

Elytra 1.7 times as long as wide, 1.6 times as long as pronotum; outline as in *nitidus*; striae feebly impressed, punctures small, shallow; interstriae about three times as wide as striae, almost smooth, subshining, punctures obsolete. Declivity steep, rather broadly sulcate; striae punctures minute, distinct; sutural interstriae moderately elevated, 2 strongly, broadly impressed, 3 abruptly, moderately elevated on median side, devoid of granules, fine, uniseriate punctures distinct except on 2. Vestiture confined to declivity consisting of interstitial rows of rather short bristles.

FEMALE.—Similar to male except frontal depression less well developed, callus at upper margin of concavity not evident; minute, confused interstitial punctures indicated on disc.

TYPE LOCALITY.—Forty km SE Socopo, Barinas, Venezuela.

TYPE MATERIAL.—The male holotype and female allotype were taken at the type locality on 25-I-70, 150 m, No. 273, from a liana known locally as bejuco blanco, by S. L. Wood.

The holotype and allotype are in my collection.

Cnesinus deperditus, n. sp.

This species is distinguished from the allied *reticulatus* Chapuis by the smaller size, by the different frontal sculpture, by the very much more finely, obscurely punctured discal interstriae, and by the shorter, much less strongly impressed elytral declivity.

FEMALE.—Length 2.7 mm (paratype 2.5 mm), 2.6 times as long as wide; color very dark reddish brown.

Frons as in *reticulatus* except upper half much more strongly convex; transverse elevation just above epistoma unarmed, triangular patch of erect setae rather large, extending to deepest point in impression; lateral margins of frons abrupt but not acutely elevated.

Pronotum 1.1 times as long as wide; widest just behind middle, sides rather strongly arcuate, rather narrowly rounded in front; surface subshining, sculpture similar to but slightly

finer than in *reticulatus*, punctures rather shallow, moderately coarse, many or most at least partly, longitudinally confluent. Vestiture of moderately abundant, coarse, short setae.

Elytra 1.9 times as long as wide, 2.1 times as long as pronotum; sides almost straight and parallel on slightly less than basal three-fourths, rather broadly rounded behind; striae deeply, abruptly impressed, punctures rather obscurely indicated; interstriae about twice as wide as striae, evidently finely rugose, punctures fine, obscure, confused, rather abundant. Declivity steep, convex; striae narrower and less strongly impressed than on disc except 1 on right side wider, interstriae 1 on right side flattened; interstitial punctures largely replaced by fine granules.

TYPE LOCALITY.—Piedras Blancas, 10 km E Medellin, Antioquia, Colombia.

TYPE MATERIAL.—The female holotype and one female paratype were taken at the type locality on 15-VII-70, 2500 m, No. 685, *Quercus humboldti*, S. L. Wood.

The holotype and paratype are in my collection.

Cnesinus fulgens, n. sp.

This species is distinguished from the very closely related *niger* Wood by the larger size, by the slightly wider male epistomal elevation with much shorter setae, by the more finely punctured pronotum, by the slightly smaller, less deeply impressed striae punctures, and by the more deeply impressed declivital striae.

MALE.—Length 2.7 mm (paratypes 2.6-2.9 mm), 2.7 times as long as wide; color dark reddish brown.

Frons as in *niger* except epistomal elevation wider, nonpubescent area distinctly wider, setae on its upper portion about half as long.

Pronotum as in *niger* except punctures much smaller, more numerous, less strigose.

Elytra as in *niger* except striae punctures smaller, not as deep; interstriae more than twice as wide as striae, punctures confused; declivital interstriae 2 and 3 more strongly convex.

FEMALE.—Similar to male except epistomal elevation reduced to a transverse callus with one row of finer, longer setae on its upper margin.

TYPE LOCALITY.—La Carbonera Experimental Forest, 50 km (airline) NW Merida, Merida, Venezuela.

TYPE MATERIAL.—The male holotype, female allotype, and 25 paratypes were collected at the

type locality on 14-XI-69, 2500 m, No. 136, from *Rubus* sp., by S. L. Wood. Thirty-two paratypes are from La Mucuy Experimental Forest, 20 km NE Merida, Merida, Venezuela, 22-XII-69, 2500 m, No. 205, from *Rubus* sp., by S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Cnesinus fulgidus, n. sp.

This species is distinguished from the closely allied *fulgens* Wood by the smaller size, by the sculpture of the male epistomal elevation, by the weakly impressed elytral striae, and by the feebly convex declivital striae.

MALE.—Length 1.2 mm (paratypes 2.1-2.4 mm), 2.6 times as long as wide; color dark reddish brown, pronotum often black.

Frons as in *fulgens* except median longitudinal axis of epistomal elevation half as great as transverse axis, its upper margin bearing a narrow band of very short setae similar to those in *fulgens*, glabrous area triangular, its surface strongly reticulate.

Pronotum as in *fulgens* except punctures more nearly oval, deeper.

Elytra as in *fulgens* except striae 1 moderately, others very weakly impressed, punctures small, moderately deep; interstriae flat, smooth, shining, twice as wide as striae, punctures minute, confused; declivity as in *fulgens* except striae 2 and 3 not impressed, interstriae feebly or not at all convex, 3 with a row of small, rounded granules; declivital vestiture distinctly longer.

FEMALE.—Similar to male except epistomal elevation reduced to a transverse callus with one row of longer setae on its upper margin.

TYPE LOCALITY.—Piedras Blancas, 10 km E Medellin, Antioquia, Colombia.

TYPE MATERIAL.—The male holotype, female allotype, and 57 paratypes were taken at the type locality on 15-VII-70, 2500 m, No. 654 and 685, from *Quercus humboldtii* twigs, by S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Cnesinus lucaris, n. sp.

This species is distinguished from the closely allied *perplexus* Wood by the much less extensive male epistomal elevation and smaller brush of epistomal setae, by the less coarsely sculptured pronotum, and by the much more slender elytral vestiture.

MALE.—Length 2.3 mm (paratypes 2.2-2.5 mm), 2.8 times as long as wide; color dark brown, elytra sometimes reddish brown, pronotum often almost black.

Frons essentially as in *perplexus* except epistomal elevation much smaller, occupying slightly more than median third, its longitudinal axis about equal in length to width of pedicel, its upper slope ornamented by about three rows of compressed bristles, these bristles covering a smaller area and finer than in *perplexus*.

Pronotum as in *perplexus* except grooves slightly narrower and longer, ridges not as strongly convex, finer. Vestiture finer than in *perplexus*.

Elytra as in *perplexus* except both ground cover and erect bristles much more slender, slightly longer on declivity.

FEMALE.—Similar to male except epistomal elevation smaller, its bristles finer, reduced to one row.

TYPE LOCALITY.—Merida, Merida, Venezuela.

TYPE MATERIAL.—The male holotype and five paratypes were taken at the type locality on 29-XII-69, 1700 m, No. 210, from a small liana, by S. L. Wood. The female allotype and 14 paratypes bear the same data except 22-XI-69, and either No. 7 from a twig, or No. 6 from *Vismia*; one paratype bears the same data except 8-XI-69, No. 119 from *Rubus*.

The holotype, allotype, and paratypes are in my collection.

Cnesinus triangularis, n. sp.

This species is distinguished from the closely related *gibbulus* Wood by the smaller average size, by the smaller female epistomal elevation with its setae less numerous and longer, by the less deeply impressed striae, by the much smaller interstitial punctures, and by the shorter, stouter declivital pubescence.

FEMALE.—Length 2.2 mm (paratypes 2.1-2.4 mm), 2.7 times as long as wide; color black.

Frons as in *gibbulus* except epistomal elevation smaller, triangular, epistomal margin of triangle almost straight, median angle of triangle about 60 degrees, bristles more slender, much longer; frons sparsely pubescent, particularly in lateral areas.

Pronotum as in *gibbulus*.

Elytra 1.9 times as long as wide; as in *gibbulus* except striae very weakly impressed, punctures small, deep; interstriae three times as wide as striae, shining, with a few very shallow, ob-

scure, transverse lines, punctures very fine, moderately confused on 2 and 3, almost uniseriate on others. Vestiture confined to declivity, consisting of stout bristles, each bristle very slightly longer than distance between rows.

MALE.—Similar to female except frontal elevation replaced by a small, low, transverse, epistomal callus, specialized bristles absent.

TYPE LOCALITY.—Piedras Blancas, 10 km E Medellin, Antioquia, Colombia.

TYPE MATERIAL.—The female holotype, male allotype, and 12 paratypes were taken at the type locality on 15-VII-70, 2500 m, No. 656, from a twig of a shrub known locally as Uvo de Monte, by S. L. Wood. Eighty-eight paratypes bear the same data except No. 658, taken from a twig of a small tree known locally as Graptero, by S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Cnesinus brighti, n. sp.

This species is distinguished from *elegantis* Wood by the smaller size, by the smaller female epistomal tubercles, by the coarser frontal vestiture, by the coarser pronotal striations, by the fine hair covering the pronotum, by the less strongly impressed striae, and by the discal pubescence.

FEMALE.—Length 2.5 mm (paratypes 2.2-2.6 mm), 2.7 times as long as wide; color rather dark reddish brown.

Frons as in *elegantis* but with epistomal denticles much smaller and basally contiguous, vestiture stouter and slightly more abundant.

Pronotum 1.1 times as long as wide; striations coarser and wider than either *elegantis* or *coracinus*, punctures not evident. Vestiture of rather abundant, fine, short hair on disc, longer and coarser anteriorly.

Elytra 1.9 times as long as wide; as in *elegantis* except vestiture extends to base of disc, consisting of rather abundant, short, coarse, confused setae of about uniform length, not longer on declivity, each seta about equal in length to width of an interstriae.

MALE.—Similar to female except epistomal tubercles absent.

TYPE LOCALITY.—Nine miles (14 km) SE Teopisca on highway 24, Chiapas, Mexico.

TYPE MATERIAL.—The female holotype, male allotype and 65 paratypes were taken at the type locality on 14-V-69, by D. E. Bright. Three para-

types have identical data except they are 30-V-69; three paratypes are from Lagos des Colores, 17-V-69, D. E. Bright.

The holotype, allotype, and most paratypes are in the Canadian National Collection, some paratypes are in my collection.

Cnesinus coracinus, n. sp.

This species is distinguished from *elegantis* Wood by the smaller size, by the stouter body, by the finer, closer female epistomal tubercles, by the finer frontal vestiture, by the slightly coarser pronotal striation, by the coarser striae punctures, and by the shorter, stouter declivital setae.

FEMALE.—Length 2.2 mm (paratypes 2.1-2.3 mm), 2.5 times as long as wide; color black.

Frons as in *elegantis* except epistomal tubercles smaller, much closer, concavity not quite as deep, extending slightly nearer upper level of frons, surface obscurely punctured, vestiture finer, less abundant.

Pronotum 1.04 times as long as wide; much as in *elegantis* but with striations more distinctly punctured and wider.

Elytra 1.6 times as long as wide; striae punctures slightly larger and deeper than in *elegantis*, interstriae feebly convex; declivity less strongly impressed, interstriae each with a row of granules. Vestiture confined to declivity, consisting of sparse, short, ground vestiture of rather fine hair, and rows of interstitial bristles; each bristle about as long as distance between rows, more closely spaced within a row.

TYPE LOCALITY.—Five miles (8 km) S Simohovel, Chiapas, Mexico.

TYPE MATERIAL.—The female holotype and four female paratypes were taken at the type locality on 4-VII-69, by D. E. Bright.

The holotype and two paratypes are in the Canadian National Collection; two paratypes are in my collection.

Bothrosternus lucidus, n. sp.

The elytral declivity of this species has moderately long, uniseriate interstitial setae as described for *truncatus* Eichhoff; it differs, however, by the absence of a median frontal tubercle, by the pronotum being wider than long, by the smoother, more regularly punctured pronotum, and probably by other characters.

MALE.—Length 2.3 mm (paratypes 2.3-2.5 mm), 2.2 times as long as wide; color reddish brown.

Frons as in male *brevis* Eggers except upper area slightly more strongly convex, lower area less strongly, less extensively impressed, with no indication of a transverse callus, punctures smaller, less conspicuous; vestiture similar but coarser.

Pronotum 0.92 times as long as wide; outline as in *brevis* except more distinctly constricted on basal third; surface almost smooth, shining, feebly reticulate at base and in lateral areas; punctures small, close, moderately deep, round to oval; lateral margin with a fine, acutely elevated line. Glabrous. Lower three-fourths of anterior propleural area excavated and filled by a dense brush of white hair.

Elytra 1.4 times as long as wide, 1.6 times as long as pronotum; sides almost straight and parallel on basal three-fourths, abruptly rounded, somewhat narrowly rounded at apex; basal margins almost smooth, more distinctly elevated than in *brevis*; striae narrowly, distinctly impressed, punctures clearly, shallowly indicated; interstriae twice as wide as striae, almost flat, smooth except a few wrinkles on basal half, punctures fine, distinct, confused. Declivity steep, broadly convex; striae reticulate, distinctly wider than on disc, punctures larger, deeper; interstriae as wide as striae, reticulate, punctures replaced by small, shining, uniseriate granules. Vestiture abraded on disc; on declivity consisting of uniseriate interstitial rows of moderately long, rather stout bristles, each bristle as long as distance between rows, very slightly closer within a row.

FEMALE.—Similar to male except frontal impression not quite as deep or as extensive, a feeble, transverse, elevated line indicated on one specimen.

TYPE LOCALITY.—About 260 km N Xavantina, Mato Grosso, Brazil (12°49' S 51°46' W).

TYPE MATERIAL.—The male holotype, female allotype, and six paratypes were taken at the type locality, in 1968, by R. A. Beaver; the holotype and five paratypes were taken 18-XI-68, No. D06, the allotype on 24-IX-68, No. 173, and one paratype on 30-XI-68, No. D98.

The holotype, allotype, and one paratype are in the British Museum (Natural History), two paratypes are in the Museu de Zoologia, Universidade de São Paulo, and three paratypes are in my collection.

Hylastes niger, n. sp.

This species is distinguished from *mexicanus* Wood by the narrowly impressed declivital striae with the punctures much smaller, and by the

much more closely spaced granules on the declivital interstriae.

MALE.—Length 4.3 mm, 2.7 times as long as wide; color black.

Frons and pronotum as in *mexicanus* except frons less distinctly reticulate, pronotum with punctures distinctly smaller.

Elytra as in *mexicanus* except striae punctures much smaller, interstriae twice as wide as striae on disc, almost three times as wide on declivity; declivity not as steep; interstitial granules on declivity much more closely spaced, spaced by distances equal to less than half width of an interstriae.

FEMALE.—Similar to male except frons more finely punctured; anterior discal area of pronotum with punctures reduced to almost obsolete.

TYPE LOCALITY.—Thirty-one km (19 mi) E Tulancingo, Hidalgo, Mexico.

TYPE MATERIAL.—The male holotype and female allotype (damaged) were taken at the type locality on 10-VII-67, 2100 m, No. 185, from the same tunnel in a *Pinus* log 60 cm in diameter, by S. L. Wood.

The holotype and allotype are in my collection.

Xylechinus mexicanus, n. sp.

This species is distinguished from *marmoratus* Blandford by the more slender, more irregularly sculptured pronotum which lacks scalelike setae, by the slightly coarser striae punctures, and by the much more slender interstitial bristles.

MALE.—Length 1.9 mm (paratypes 1.6-1.9 mm), 2.7 times as long as wide; color brown, vestiture pale.

Frons as in *marmoratus* but broader, vestiture finer, without scales.

Pronotum 1.0 times as long as wide; about as in *marmoratus* but anterior constriction not as strong; surface shining, irregular throughout, punctures fine, shallow, most subvulcaute. Vestiture of short, coarse hair of moderate abundance; scales absent.

Elytra 1.7 times as long as wide; as in *marmoratus* except bases of interstriae 2-5 each bearing 1-4 submarginal crenulations, striae punctures very slightly larger. Ground vestiture shorter than in *marmoratus*, apparently less abundant, much more slender on sutural interstriae than elsewhere; erect bristles slender, blunt or pointed, their length and spacing as in *marmoratus*.

FEMALE.—Similar to male except submarginal crenulations at bases of elytra mostly absent.

TYPE LOCALITY.—Yerba Buena, 20 mi (32 km) N Bochil, Chiapas, Mexico.

TYPE MATERIAL.—The male holotype, female allotype and nine paratypes were taken at the type locality on 21-V-69, 8000 feet elevation, by D. E. Bright.

The holotype, allotype, and five paratypes are in the Canadian National Collection, four paratypes are in my collection.

Phlocotribus nanus, n. sp.

This species superficially resembles *hystrix* Wood, although the relationship is remote. It differs from *hystrix* by the smaller size, by the subobsolete stria punctures, by the more abundant interstitial scales, and by the absence of spines and elevated areas on the elytral declivity.

MALE.—Length 1.4 mm (paratypes 1.4-1.6 mm), 1.8 times as long as wide; color yellowish brown.

Frons as in *hystrix* except surface sculpture finer, less regular. Antennae as in *hystrix*.

Pronotum 0.81 times as long as wide; outline about as in *hystrix*; surface shining, very densely, rather coarsely, deeply punctured, each puncture bearing a short, stout, subscalelike seta; anterolateral margin armed by about three small crenulations.

Elytra 1.1 times as long as wide, 1.5 times as long as pronotum; sides almost straight and parallel on basal half, broadly rounded behind; striae strongly impressed, their margins slightly beaded indicating positions of punctures, but punctures obsolete; interstriae twice as wide as striae, surface shining, finely punctate-granulate and with a median row of slightly larger granules. Declivity rather steep, broadly convex; interstriae slightly narrower and more convex than on disc; devoid of tubercles or other elevations. Vestiture confined to interstriae, consisting of a dense ground cover of very short, stout, subscalelike, pointed setae, each slightly longer than wide, and interstitial rows of slightly longer, similar setae; longer setae less than twice as long as ground cover, about four to six times as long as wide.

FEMALE.—Similar to male except broadly convex, more coarsely granulate-punctate, devoid of denticles; anterolateral areas of pronotum with about 20 small crenulations on each side.

TYPE LOCALITY.—About 260 km N Xavantina, Mato Grosso, Brazil (12°49' S 51°46' W).

TYPE MATERIAL.—The male holotype, female allotype, and eight paratypes were taken at the type locality, in 1968, by R. A. Beaver. The holotype was taken I-XII-68, No. C20, the allotype and one paratype I-XII-68, No. F27, two paratypes I-XI-68, No. F19, four paratypes I-XII-68, No. F26, and one paratype 28-IX-68, No. A07.

The holotype, allotype, and two paratypes are in the British Museum (Natural History), two paratypes are in Museu de Zoologia, Universidade de São Paulo, and four paratypes are in my collection.

Chramesus corniger, n. sp.

This species is unique in the genus. The male frons is very weakly impressed, the lateral margins are not elevated at all, the lower frons in the male bears a pair of large denticles near but not on the epistomal margin. The elytral ground vestiture is absent.

MALE.—Length 1.4 mm (paratypes 1.3-1.4 mm), 1.7 times as long as wide; color very dark brown, almost black, vestiture pale.

Frons very shallowly concave from epistoma almost to upper level of eyes, lateral margins rounded, not elevated; a pair of rather large tubercles just above epistomal margin; their bases separated by about one-third width of frons; surface subshining, finely rugulose, a few small, indistinct granules on upper half; vestiture of sparse, fine, inconspicuous hair. Antennal club moderately large.

Pronotum 0.80 times as long as wide; widest near base, sides arcuately converging to rather weak constriction just before rather narrowly rounded anterior margin; entire surface strongly reticulate; punctures small, widely spaced, those on anterior half granulate to very finely asperate. Vestiture of short, stout bristles of moderate abundance.

Elytra 1.1 times as long as wide; sides almost straight and parallel on slightly more than basal half, broadly rounded behind; basal margins of elytra each armed by about 15 crenulations, one submarginal crenulation on interstriae 2; striae feebly impressed, punctures moderately coarse, close; interstriae slightly wider than striae, uniseriately, finely granulate except slightly confused on 2, punctures not evident. Declivity rather steep, convex; sculpture about as on disc. Vestiture of interstitial rows of stout bristles, each 8-10 times as long as

wide, slightly shorter than distance between rows, slightly confused on discal interstriae 2.

FEMALE.—Similar to male except frons weakly convex, unarmed; pronotal granules smaller in median area, two or three of those on antero-lateral angles crenulate.

TYPE LOCALITY.—Lago Catemaco, Veracruz, Mexico.

TYPE MATERIAL.—The male holotype, female allotype, and six paratypes were taken at the type locality on 16-20-VI-69, by D. E. Bright.

The holotype, allotype, and three paratypes are in the Canadian National Collection; three paratypes are in my collection.

Chramesus disparilis, n. sp.

This species superficially resembles *acacicolens* Wood, but the male frons is entirely different; the elytral ground vestiture and erect bristles are broad. It is not closely related to any species from North or Central America.

MALE.—Length 1.6 mm (paratypes 1.4-1.7 mm), 1.9 times as long as wide; color dark brown, vestiture pale.

Frons very deeply, broadly concave from epistoma to slightly above eyes; lateral margins subacutely elevated, armed just above level of antennal insertion by a pair of low, blunt, subquadrate denticles having bases displaced mesad from crest of lateral margins; surface finely rugose-reticulate, shining; vestiture of sparse, minute hair in concavity, of a few stout setae of moderate length on margins. Antennal club small for this genus, apex narrowly rounded.

Pronotum 0.76 times as long as wide; widest at base, sides and anterior margin almost forming a semicircular arc, anterior constriction almost obsolete; surface finely reticulate, shining, small granules of moderate abundance extending from anterior margin to base. Vestiture rather abundant, short, scalelike, each scale about two to three times as long as wide.

Elytra 1.3 times as long as wide; sides almost straight and parallel on slightly more than basal half, rather broadly rounded behind; basal margins each armed by 13 crenulations, about six submarginal crenulations scattered from interstriae 2-4; striae distinctly, weakly impressed, punctures rather coarse, deep; interstriae slightly wider than striae, each with a uniseriate row of fine granules and minute, obscure punctures. Declivity rather steep, convex; as on disc except interstriae 2 on lower half devoid of granules and feebly impressed. Vestiture con-

sisting of ground cover of short, recumbent, interstitial scales, each scale about twice as long as wide; and interstitial rows of erect, scalelike bristles, each about six times as long as wide, each slightly more than half as long as distance between rows or between bristles within a row.

FEMALE.—Similar to male except frons feebly convex, lateral margins rounded and unarmed; scales in elytral ground cover only slightly longer than wide.

TYPE LOCALITY.—Lagos de Colorcs, Chiapas, Mexico.

TYPE MATERIAL.—The male holotype and 22 paratypes were taken at the type locality on 14-VI-69, from *Acacia*, by D. E. Bright. The female allotype and 25 paratypes are from seven miles (11 km) SE Teopisca, on highway 24, Chiapas, Mexico, 31-V-69, from *Acacia*, by D. E. Bright.

The holotype, allotype, and most of the paratypes are in the Canadian National Collection; the other paratypes are in my collection.

Chramesus variabilis, n. sp.

This species is distinguished from *vincalis* Wood by the more extensive, more deeply impressed male frons, with lateral armature higher, by the smaller pronotal punctures, by the larger scales in the elytral ground vestiture, and by the much stouter erect interstitial bristles.

MALE.—Length 1.9 mm (paratypes 1.8-2.3 mm), 1.6 times as long as wide; color dark brown, vestiture forming a slightly variegated pattern in most specimens.

Frons broadly, deeply concave from epistoma to slightly above eyes, lateral margins acutely rather strongly elevated, armed just above level of antennal insertion by a large triangular dentition; surface reticulate, epistoma and large pre-mandibular lobe smooth, shining; vestiture of sparse, minute hair. Antennal club large.

Pronotum 0.74 times as long as wide; outline as in *disparilis*; surface finely reticulate, punctures small, shallow, close, spaced by distances equal to diameter of a puncture, devoid of granules. Vestiture of short hair and equal numbers of scales, each scale four to six times as long as wide; central and anterior setae darker.

Elytra 1.05 times as long as wide; sides almost straight and parallel on basal half, broadly rounded behind; twelve pairs of crenulations on basal margins, six submarginal crenulations scattered on bases of interstriae 2-4; striae distinctly impressed, punctures small, rather

shallow; interstriae three times as wide as striae, smooth, bristle-bearing punctures small, almost uniseriate, punctures bearing ground scales minute. Declivity rather steep, convex; sculpture as on disc. Vestiture of ground cover of small scales, each scale one to two times as long as wide; and rows of erect bristles, each bristle about twice as long as ground cover, half as long as distance between rows, as long as distance between bristles within a row, each bristle about six times as long as wide; in an obscure variegated pattern.

FEMALE.—Similar to male except frons weakly convex, lateral margins rounded, unarmed, surface rugose-reticulate; anterolateral areas of pronotum sparsely asperate.

TYPE LOCALITY.—Lago Catemaco, Veracruz, Mexico.

TYPE MATERIAL.—The male holotype, female allotype, and 24 paratypes were taken at the type locality on 16-20-VI-69, by D. E. Bright.

The holotype, allotype, and 15 paratypes are in the Canadian National Collection; nine paratypes are in my collection.

Chramesus microporosus, n. sp.

This species is distinguished from *periosus* Wood by the deeper male frontal concavity which extends slightly above the upper level of the eyes, by the finer pronotal punctures and granules, by fewer submarginal crenulations on the elytral bases, by the minute stria punctures, and by the more slender, nonsubplumose scales of the elytral ground vestiture.

MALE.—Length 2.2 mm (paratypes 1.8-2.4 mm), 1.6 times as long as wide; color very dark reddish brown.

Frons as in *periosus* except concavity extending slightly above eyes, much deeper on upper half. Pronotum as in *periosus* except punctures less than one-third as large, granules much smaller and less numerous.

Elytra as in *periosus* except submarginal crenulations near base of elytra about half as numerous, stria puncture very minute to entirely obsolete, striae smooth, shining, interstitial punctures also minute; scales in ground cover about four times as long as wide, not subplumose; bristles about three times as long as ground cover, scalelike, each about six to eight times as long as wide.

FEMALE.—Similar to male except frons convex, foveate at center; lateral areas of pronotum asperate; stria puncture very small, but dis-

tinctly larger; interstriae each with a row of moderately large, pointed tubercles.

TYPE LOCALITY.—El Sumidera, 15 miles (24 km) N Tuxtla Gutierrez, Chiapas, Mexico.

TYPE MATERIAL.—The male holotype, female allotype, and 15 paratypes were taken at the type locality on 7-VI-69, by D. E. Bright.

The holotype, allotype, and nine paratypes are in the Canadian National Collection; six paratypes are in my collection.

Chramesus aquilus, n. sp.

Among Central American forms, this species is most nearly allied to *demissus* Wood, but it is distinguished by the more deeply concave male frons with the lateral margins more strongly elevated, by the more distinctly punctured pronotal disc, by the more rounded interstitial tubercles, and by the different elytral vestiture.

MALE.—Length 1.8 mm (paratypes 1.5-1.8 mm), 1.5 times as long as wide; color black, vestiture pale.

Frons broadly, rather deeply concave from epistoma to slightly below upper level of eyes, lateral margins acutely, rather strongly elevated with highest point just below level of antennal insertion, devoid of denticles; surface strongly reticulate, smooth on epistoma, minute, obscure punctures on upper half of concavity; vestiture inconspicuous. Antennal club large.

Pronotum as in *demissus* except granules smaller, posterior fourth in median area with sparse, shallow, moderately large punctures. Vestiture slightly more slender than in *demissus*.

Elytra 1.02 times as long as wide; sides almost straight and parallel on slightly more than basal half, broadly rounded behind; basal margins each armed by 11 crenulations, one or more submarginal crenulations on interstriae 2-5; striae strongly impressed, punctures moderately coarse, deep; interstriae about one and one-half times as wide as striae, moderately convex, smooth, with rows of rather large, narrowly rounded tubercles, tubercles somewhat confused on 2 and 3. Declivity rather steep, convex; sculpture about as on disc. Vestiture of ground cover of rows of scales on both margins of each interstriae, each scale up to twice as long as wide; and erect bristles in interstitial rows except moderately confused on 2 and 3 on disc, each bristle two-thirds as long as distance between rows, spaced within a row by length of a bristle, each about eight times as long as wide, equal in width to scales in ground cover.

FEMALE.—Similar to male except frons weakly convex, lateral margins rounded; pronotal granules absent, entire surface with shallow, sparse punctures of moderate size.

TYPE LOCALITY.—Eight miles (13 km) N Ocasingo, Chiapas, Mexico.

TYPE MATERIAL.—The male holotype, female allotype, and 19 paratypes were taken at the type locality on 2-VI-69, by D. E. Bright.

The holotype, allotype, and ten paratypes are in the Canadian National Collection; nine paratypes are in my collection.

Chramesus wisteriae, n. sp.

This species is distinguished from *acacicolens* Wood by the more coarsely, more deeply punctured pronotum, by the more deeply impressed striae and smaller strial punctures, and by the slightly more slender, erect interstitial bristles.

MALE.—Length 1.8 mm (paratypes 1.6-1.8 mm), 1.6 times as long as wide; color very dark brown, vestiture pale.

Frons as in *acacicolens* except surface with sparse, minutely granulate, small, obscure punctures. Pronotum as in *acacicolens* except granules evidently smaller, less conspicuous, punctures much larger, deeper, closer, punctures discernible from base to anterior fourth; vestiture slightly more abundant.

Elytra 1.2 times as long as wide; as in *acacicolens* except striae weakly impressed, punctures larger, more distinctly impressed; interstriae slightly less than twice as wide as striae; erect interstitial bristles very slightly shorter and more slender than in *acacicolens*, each bristle six to eight times as long as wide, half as long as distance between rows.

FEMALE.—Similar to male except frons weakly convex, lateral margins not elevated or armed, foveate at center; pronotal asperities in lateral areas larger; interstitial tubercles distinctly larger.

TYPE LOCALITY.—Bay St. Louis, Mississippi.

TYPE MATERIAL.—The male holotype, female allotype, and three paratypes were taken at the type locality on 12-V-45, in dead *Wisteria* stems, No. 45-9773, presumably by W. H. Anderson.

The holotype, allotype, and one paratype are in the U.S. National Museum; two paratypes are in my collection.

Chramesus marginatus, n. sp.

This species is distinguished from *setosus* Wood by the larger size, by the much more finely sculptured pronotum, and by the more nearly hairlike elytral setae.

MALE.—Length 2.5 mm (paratype 2.5 mm), 1.65 times as long as wide; color dark brown, vestiture pale.

Frons similar to *setosus* but not as deeply concave on upper half, punctures on upper half slightly larger. Pronotum outline as in *setosus*; surface reticulate, a few asperities in lateral areas, a few minute granules on median part of anterior third, punctures small, moderately close, very shallow on anterior half, somewhat deeper in posterior area. Vestiture of short, slender bristles of moderate abundance.

Elytra outline and basal armature as in *setosus*; striae distinctly impressed, punctures very small, moderately deep; interstriae at least four times as wide as striae, weakly convex, smooth, with a central row of fine granules and a row of minute punctures on each margin. Declivity rather steep, broadly convex; sculpture as on disc. Vestiture of sparse, short, erect, slender, bristlelike ground cover in approximate rows on margins of interstriae, and rows of interstitial bristles arising from granules, each bristle twice as long as ground cover, two-thirds as long as distance between rows, as long as distance between setae within a row.

TYPE LOCALITY.—Mexico.

TYPE MATERIAL.—The male holotype, female allotype, and one male paratype were intercepted at Brownsville, Texas, on 26-I-49, No. 67333, in dead wood 49-2948, by D. J. Smith, in material coming from Mexico.

The holotype and allotype are in the U.S. National Museum; the paratype is in my collection.

Carphoborus piceae, n. sp.

This species is distinguished from the closely allied *perplexus* Wood by the absence of granules on discal interstriae 3, by the less strongly elevated, more finely dentate alternate declivital interstriae, and by the smaller, flattened area on the female frons.

MALE.—Length 1.7 mm, 2.2 times as long as wide; color almost black.

Frons as in *perplexus*. Antennal club 1.3 times as long as wide. Pronotum and elytral disc as in *perplexus* except discal interstriae 3 devoid of granules; elytral declivity as in *per-*

plexus except alternate interstriae less strongly elevated and more finely dentate, interstriae 2 wider.

FEMALE.—Similar to male except frons flattened on little more than median half from epistoma to very slightly above eyes, epistomal margin distinctly elevated.

TYPE LOCALITY.—Dixie Pass, Malheur National Forest, Oregon.

TYPE MATERIAL.—The male holotype, damaged female allotype, and one damaged female paratype were taken at the type locality on 23-VI-61, from an unthrifty branch of a recently fallen *Picea engelmanni*, by S. L. Wood. The elytral declivity is missing from both females.

The holotype, allotype, and paratype are in my collection.

Carphobius cupressi, n. sp.

This is the second species assigned to this genus. It is distinguished from *arizonicus* Blackman by the larger size, by the more finely punctured frons, by the convex elytral declivity, by the absence of denticles on the declivity, by the brightly polished appearance, by the finer vestiture, and by many other characters.

MALE.—Length 2.8 mm (paratypes 2.2-3.2 mm), 2.3 times as long as wide; color very dark brown, almost black, elytra dark reddish brown.

Frons strongly, transversely impressed just below middle, impression extending to upper level of eyes, epistoma strongly raised and bearing a broad premandibular lobe, a small median tubercle at base of lobe; surface of impressed area very smooth, brightly shining, very finely punctured on lower third, punctures slightly larger above; vertex reticulate, dull. Eye shallowly emarginate, finely granulate. Antennal scape elongate; funicle 6-segmented, longer than scape; club as long as scape, 1.5 times as long as wide, with three straight, transverse sutures.

Pronotum 0.90 times as long as wide; widest near base, sides rather weakly arcuate and converging slightly on basal half, rather strongly constricted laterally just before broadly rounded anterior margin; surface smooth, brightly shining, punctures coarse, deep, close. Vestiture of fine, moderately long, rather abundant hair.

Elytra 1.6 times as long as wide, 2.1 times as long as pronotum; scutellum not exposed; sides almost straight and parallel on basal two-thirds, rather narrowly rounded behind; each basal margin strongly arcuate and armed by

about 16 crenulations, submarginal crenulations poorly developed; striae not impressed, punctures coarse, deep; interstriae smooth, shining, as wide as striae, punctures fine, deep, confused, rather numerous. Declivity rather steep, convex; sculpture about as on declivity except striae punctures slightly smaller; interstitial punctures devoid of granules. Vestiture of fine, rather short, abundant striae and interstitial hair, and interstitial rows of similar but slightly longer hair. Third tarsal segments broad, bilobed.

FEMALE.—Similar to male except frons convex, with a slight central impression.

TYPE LOCALITY.—Eleven km N San Marcos, San Marcos, Guatemala.

TYPE MATERIAL.—The male holotype, female allotype, and 17 paratypes were taken on 23-II-72, from *Cupressus lucitanica* branches, by E. W. Clark.

The holotype, allotype, and paratypes are in my collection.

Cladoctonus atrocis, n. sp.

This species is distinguished from the rather closely allied *sentus* (Wood) by the smaller size, by the stouter body form, by the coarser, more irregular pronotal and striae punctures, by the irregular interstriae, and by the presence of denticles on declivital interstriae 6 and 8.

MALE.—Length 1.6 mm (paratypes 1.5-1.8 mm), 2.1 times as long as wide; color reddish brown.

Frons as in *sentus* except slightly narrower, punctures larger, less numerous; impression on lower area slightly stronger; eye larger, more coarsely faceted.

Pronotum 0.84 times as long as wide; outline as in *sentus*; surface smooth, shining, punctures averaging larger than in *sentus*, of irregular size and shape. Vestiture consisting of a very few, very widely spaced bristles.

Elytra 1.4 times as long as wide, 1.7 times as long as pronotum; essentially as in *sentus* except striae punctures averaging larger, subquadrate; interstriae narrower than striae, punctures fine, uniseriate, surface strongly undulating, particularly near declivity. Declivity very steep, convex; punctures smaller than on disc, confused, positions of interstriae determined from positions of tubercles, each interstriae with up to 10 tubercles, except 2 entirely unarmed, largest tubercles near base, 9 acutely, not strongly elevated, its crest curved toward

and joining lateral margin at position in line with interstriae 3 (as in *seutus*). Vestiture confined to declivital area, consisting of rather widely spaced interstitial bristles, each slightly longer and stouter than in *seutus*.

FEMALE.—Similar to male except frons broadly convex, with large central area (two-thirds of area between eyes) smooth, shining, impunctate, remaining areas bearing several long hairlike setae; pronotum less deeply punctured, interstriae less irregular, declivital tubercles slightly smaller.

TYPE LOCALITY.—About 260 km N Xavantia, Mato Grosso, Brazil, at 12°49' South 51°46' West.

TYPE MATERIAL.—The male holotype, female allotype, and two paratypes were taken at the type locality on 19-X-68, No. B47/8, by R. A. Beaver. One paratype bears identical data except 18-X-68, No. B38c; four paratypes bear the same data except 25-X-68, No. B94/3; and one paratype bears the same data except 24-XI-68, D51/1.

The holotype, allotype, and two paratypes are in the British Museum (Natural History), two paratypes are in the Museu de Zoologia, Universidade de São Paulo, and four paratypes are in my collection.

Scolytodes canalis, n. sp.

This species is not closely related to any described species, although it is placed in the genus near *clusiae* Wood and *parvulus* Wood. Distinguishing characters include the slightly protuberant, lower female frons which has a narrow, shallow, median sulcus, with the frontal vestiture confined to the upper margins; the discal interstitial punctures are obsolete; and the pronotal and striae punctures are moderately coarse.

FEMALE.—Length 1.7 mm (paratypes 1.4-1.7 mm), 2.5 times as long as wide; color black.

Frons rather broadly convex, slightly protuberant on lower half, median fourth just below upper level of eyes shallowly concave, impression continued on median sixth as a shallow sulcus to epistoma; surface of upper half almost smooth, rather finely, deeply punctured, becoming finely granulate on lower half except reticulate in impressed area; vestiture apparently restricted to margins of upper half, tips of some long, yellow, hairlike setae arising on vertex reaching to epistoma.

Pronotum 1.1 times as long as wide; sides almost straight on more than basal two-thirds,

converging slightly to anterolateral angles, broadly rounded in front; anterior third weakly declivous; surface reticulate, subshining, punctures on posterior half moderately coarse, deep, not close, decreasing in size on anterior half, most of them replaced by minute granules on anterior sixth or obsolete. Glabrous.

Elytra 1.6 times as long as wide; sides straight on basal two-thirds, very slightly wider at base of declivity, rather narrowly rounded behind; striae not impressed, punctures moderately deep; interstriae as wide as striae, smooth, shining, punctures obsolete, some with one to three minute granules. Declivity steep, convex; striae punctures smaller than on disc; a few minute interstitial punctures usually present. Vestiture of fine sparse, erect, interstitial hair of moderate length on odd-numbered interstriae, much shorter to obsolete on even-numbered interstriae.

MALE.—Similar to female except frons evenly, more strongly convex, surface reticulate, with scattered punctures, subglabrous.

TYPE LOCALITY.—Mt. Tzontehultz, Chiapas, Mexico.

TYPE MATERIAL.—The female holotype, male allotype, and 20 paratypes were taken at the type locality on 26 and 29-V-69 and 12-VI-69, 9500 ft (3100 m) elevation, by D. E. Bright.

The holotype, allotype, and 14 paratypes are in the Canadian National Collection; six paratypes are in my collection.

Scolytodes costabilis, n. sp.

This species is distinguished from *melanocephalus* Blandford by the different female frontal sculpture, by the very fine punctures on the pronotal disc, and by the very small striae punctures.

FEMALE.—Length 1.8 mm (paratypes 1.8-2.0 mm), 2.6 times as long as wide; color brown.

Frons rather broadly flattened from epistoma to vertex; a pair of low, subparallel, longitudinal carinae from level of antennal insertion to epistomal margin; surface smooth and shining above level of antennal insertion, a row of punctures around margin; feebly bisulcate between carinae, finely reticulate-punctate in sulci, smooth and shining between; vestiture of long, yellow hair on margins above, tips of longest setae reach level of antennal insertion, sulci on lower third with fine, short hair.

Pronotum 1.1 times as long as wide; sides straight on basal two-thirds, converging very slightly to anterolateral angles, broadly rounded

in front; surface reticulate, anterior fourth rather strongly declivous and finely asperate, fine, almost obsolete punctures behind each asperity; punctures on posterior areas very small, shallow, moderately close. Glabrous.

Elytra 1.4 times as long as wide, 1.2 times as long as pronotum; sides almost straight and parallel on basal two-thirds, rather broadly rounded behind; basal margins not carinate, abrupt; striae not impressed, punctures very fine, distinctly impressed, spaced within a row by about twice diameter of a puncture; interstriae smooth, shining, punctures very fine, three or more times as wide as striae, uniseriate except moderately confused in some specimens. Declivity steep, convex; sculpture essentially as on disc.

TYPE LOCALITY.—Lago Catemaco, Veraacruz, Mexico.

TYPE MATERIAL.—The female holotype and four female paratypes were taken at the type locality on 16-20-VI-69 (holotype) and 1-3-V-69 (paratypes) by D. E. Bright.

The holotype and two paratypes are in the Canadian National Collection; the other two paratypes are in my collection.

Pseudothysanoes contrarius, n. sp.

This species is distinguished from *bartoni* Bruck by the more slender, recurved spines on the male declivital interstriae 2, 3, 5, and 7, by the coarser striae punctures, by the broader interstitial scales, and by the more broadly rounded anterior margin of the pronotum.

MALE.—Length 1.0 mm (paratypes 1.0-1.2 mm), 2.1 times as long as wide; color black.

Frons convex, a weak transverse impression on lower half, subfoveate at center; surface rugose-reticulate, punctures not evident; vestiture confined to epistomal brush.

Pronotum 0.89 times as long as wide; widest near base, sides moderately arcuate, converging toward rather broadly rounded anterior margin; anterior margin armed by ten small denticles. Vestiture of sparse, short, stout bristles, a few small scales in lateral area.

Elytra 1.3 times as long as wide; sides almost straight and parallel on basal two-thirds, rather broadly rounded behind; striae not impressed, punctures coarse, deep; interstriae as wide as striae, smooth, shining, with uniseriate rows of small granules. Declivity convex, gradual, beginning at middle of elytra; striae punctures gradually reduced in size until minute near apex; granules on interstriae 1 smaller than

on disc, obsolete on 2 except one or two near base enlarged into slender, sharply pointed, recurved spines, 3 with seven to nine similar spines, 5 with three, and 7 with about five spines; spines on 3 slightly recurved, longest spines equal in length to width of an interstriae, slightly shorter than interstitial scales. Vestiture of rows of minute, fine, interstitial hair, and rows of erect, interstitial scales; each scale about two-thirds as long as distance between rows, about three to four times as long as wide, those arising from posterior surface of spines often slightly larger.

TYPE LOCALITY.—Lagos des Colores, Chiapas, Mexico.

TYPE MATERIAL.—The male holotype and three male paratypes were taken at the type locality on 14-VI-69, from *Acacia*, by D. E. Bright.

The holotype and two paratypes are in the Canadian National Collection; one paratype is in my collection.

Pseudothysanoes recavus, n. sp.

This species is closely allied to *dimorphus* (Schedl), but it is distinguished by the larger, deeper, striae punctures, by the more deeply excavated female frons, by the impression extending only slightly above the eyes, by the presence of a dense fringe of short setae on the upper margin of the female frontal concavity, and by the stouter elytral scales.

FEMALE.—Length 1.3 mm (paratypes: males 1.2 mm; females 1.2-1.4 mm), 2.2 times as long as wide; color very dark brown, almost black.

Frons deeply, rather broadly concave from epistoma to slightly above eyes; premandibular epistomal lobe rather well developed; surface of concavity reticulate on upper two-thirds, smooth below; upper margin of concavity bearing a dense fringe scalelike setae on median two-thirds; epistoma with a few long, subplumose setae in lateral areas. Antennal scape strongly triangular, two and one-half times as wide as long, bearing a dense brush of long hair somewhat more elaborate than in *dimorphus*; club moderately large, elongate-oval, minutely pubescent, entirely devoid of sutures.

Pronotum 0.91 times as long as wide; as in *dimorphus* except posterior areas more finely reticulate, and granules between summit and basal margin slightly larger.

Elytra 1.4 times as long as wide; outline as in *dimorphus*; striae not impressed, punctures rather fine, distinctly impressed; interstriae

rather smooth, shining, almost twice as wide as striae, punctures very fine, uniseriate. Declivity steep, convex; interstitial punctures replaced by rounded granules of similar size and appearance to those of *dimorphus*, but more widely spaced. Vestiture of rows of minute, fine, recumbent, strial hair, and rows of erect, interstitial scales; each white scale about five times as long as wide, almost as long as distance between rows, slightly longer than distance between scales within a row.

MALE.—Similar to female except body 1.9 times as long as wide; frons rather weakly convex, rugose-reticulate, vestiture sparse, less conspicuous; anterior margin of pronotum armed by eight small teeth; interstitial punctures on disc finely granulate; interstitial scales less than one and one-half times as long as wide.

TYPE LOCALITY.—Five miles (8 km) S Simojovel, Chiapas, Mexico.

TYPE MATERIAL.—The female holotype, male allotype, and 62 paratypes were taken at the type locality on 4-VII-69, by D. E. Bright.

The holotype, allotype, and most of the paratypes are in the Canadian National Collection; the remaining paratypes are in my collection.

Thysanoes granulifer, n. sp.

This species is distinguished from *berschemiae* Blackman by the larger size, by the smaller discal interstitial tubercles, by the much larger declivital interstitial tubercles, and by the much larger declivital scales.

MALE.—Length 2.2 mm, 2.9 times as long as wide; color dark reddish brown.

Frons largely concealed by pronotum, evidently as in *berschemiae*. Pronotum as in *berschemiae*.

Elytra 1.8 times as long as wide; outline as in *berschemiae*; striae not impressed, punctures moderately coarse, deep; interstriae smooth, shining, slightly narrower than striae, punctures fine, slightly granulate, uniseriate, granules coarse near declivity. Declivity steep, convex; strial punctures slightly smaller than on disc, deep; interstitial tubercles as wide as diameter of a strial puncture, as high as wide, on interstriae 1-7, very slightly smaller on lower half of declivity. Vestiture of rows of minute, fine strial hair, and rows of erect interstitial scales; scales on disc about three times as long as wide, shorter than distance between rows, on declivity four to eight times as long as wide, one to one

and one-half times as long as distance between rows.

TYPE LOCALITY.—San Cristobal de las Casas, Chiapas, Mexico.

TYPE MATERIAL.—The unique male holotype was taken at the type locality on 7-V-69, by J. E. H. Martin.

The holotype is in the Canadian National Collection.

Micracisella mimetica, n. sp.

This species is distinguished from *knulli* Blackman by the larger size, by the frontal granules, by the shorter, broader elytral scales, and by the smaller denticles on the elevated declivital interstriae 3.

MALE.—Length 2.3 mm (paratypes 2.3-2.4 mm), 2.9 times as long as wide; color dark reddish brown.

Frons moderately convex except rather abruptly, strongly, transversely impressed on lower fourth; surface rugose-reticulate in marginal areas, more finely, rather obscurely rugose-reticulate in central area; upper two-thirds with about 30 small, high, isolated granules, two near center much larger; vestiture of uniformly distributed, short, coarse setae of moderate abundance. Eye oval, shallowly emarginate; twice as long as wide. Antennal club 1.0 times as long as wide; suture 1 reaching middle of club.

Pronotum 1.1 times as long as wide; outline and asperities as in *knulli*; anterior margin armed by six teeth, lateral pair much smaller; posterior areas rugose-reticulate, dull, with small, low, shining granules of moderate abundance. Vestiture on disc of recumbent scales, each scale about four times as long as wide; a few bristles in asperate area.

Elytra 1.9 times as long as wide; outline as in *knulli*; disc as *knulli* except surface irregular, with numerous transverse lines or wrinkles. Declivity as in *knulli* except interstriae 1 and 9 slightly more strongly convex but with denticles on summit much smaller. Vestiture recumbent, of interstitial scales except declivital interstriae 2, 4, and 8 glabrous; scales evidently slightly confused on odd-numbered interstriae, uniseriate on even-numbered interstriae; each scale two to three times as long as wide.

FEMALE.—Similar to male in all respects; distinguished externally only by terminal terga of abdomen.

TYPE LOCALITY.—Three miles (5 km) N Suchixtepec on Highway 175, Oaxaca, Mexico.

TYPE MATERIAL.—The male holotype, female allotype, and three paratypes were taken at the type locality on 4-VI-71, 9500 ft elevation, in mistletoe on oak, by D. E. Bright.

The holotype, allotype, and one paratype are in the Canadian National Collection; two paratypes are in my collection.

Micracisella ocellata, n. sp.

This species is remotely allied to *nitidula* Wood, but it is distinguished by the very deeply impressed declivital striae and by the moderately large punctures on the discal striae, each of which has a small, elevated, central point giving the appearance of an eye.

MALE.—Length 2.2 mm (paratypes 1.9-2.3 mm), 3.5 times as long as wide; color dark reddish brown, pronotum usually darker.

Frons broadly convex, a slight, transverse impression immediately above epistoma; surface finely rugose-reticulate, a few fine punctures in lateral areas, a few small granules in median area of upper half; vestiture of very short, stout, subplumose setae laterally and on upper half, a few longer setae along epistoma. Eye feebly emarginate; twice as long as wide. Antennal club as in allied species.

Pronotum 1.18 times as long as wide; essentially as in *nitidula* except scales on disc distinctly wider.

Elytra 2.4 times as long as wide; outline about as in *nitidula*; striae not impressed, punctures large, distinctly impressed, each with a small, central, elevated granule giving appearance of an eye; interstriae as wide as striae, shining, almost smooth, punctures fine, uniseriate, rather close. Declivity rather steep, convex, with apex slightly produced; striae deeply impressed, punctures small, obscure; interstriae 1, 2, and 3 equally convex, almost half as high as wide, each bearing a row of low, rounded nodules on its lateral half, granules more obscure and smaller on 3; surface on lower half somewhat rugose-reticulate. Vestiture of rows of fine, short, strial hair, and interstitial rows of recumbent scales; each scale on disc eight or more times as long as wide, about four times as long as wide on declivity.

FEMALE.—Similar in all respects to male; presumably those specimens with a few more setae on scape are females.

TYPE LOCALITY.—Three miles (5 km) N Suchixtepec on Highway 175, Oaxaca, Mexico.

TYPE MATERIAL.—The male holotype, female allotype, and 34 paratypes were taken on 4-VI-

71, 9500 ft elevation, from *Arbutus*, by D. E. Bright. Two paratypes bear identical data to the type but were taken from mistletoe on oak. Nine paratypes are from 20.5 km N Oaxaca, 31-V-71, 9000 ft, *Arbutus*, D. E. Bright. Eighteen paratypes are from 37 miles (59 km) S Valle Nacional, 24-V-71, 8500 ft, from *Arbutus*, by D. E. Bright; one paratype is from 15 mi S (24 km) Valle Nacional, 20-V-71, 4000 ft, from *Arbutus*, by D. E. Bright.

The holotype, allotype, and most of the paratypes are in the Canadian National Collection; the remaining paratypes are in my collection.

Hylocurus rivalis, n. sp.

This species is distinguished from *schwarzi* Blackman by the serrate male declivital interstriae 9, with the nodules on all interstriae higher and slightly closer, by the numerous, strong, irregularly transverse, interstitial lines, and by the more strongly rugose-reticulate pronotal disc. It is probably more closely related to *effeminatus* Wood.

MALE.—Length 2.6 mm (paratypes 2.1-2.7 mm), 2.8 times as long as wide; color very dark reddish brown, some specimens almost black.

Frons as in *effeminatus*, including transverse elevation. Antennal club distinctly larger than in *effeminatus*. Pronotum as in *effeminatus*.

Elytra 1.8 times as long as wide; outline similar to *effeminatus*; striae not impressed, punctures moderately large, deep; interstriae slightly wider than striae, shining, with numerous, irregular, coarse, transverse lines giving interstriae a suberemulate appearance, some of low, transverse ridges continuing across striae; moderately high, rounded nodules near declivity on all interstriae. Declivity steep, convex, contours about as in *schwarzi*; striae 1 and 2 continuing to base of mucro; base of each interstriae with three to five rounded nodules, largest as high as wide, 1, 3, and 7 with small, pointed tubercles to middle of declivity, tubercles on 2 and 4 extending to upper third, those on 5, 6, and 8 ending on upper fourth, 9 moderately elevated about as in *schwarzi* but with small nodules to apex of elevation. Vestiture more abundant than in *schwarzi*, of rows of minute strial hair, and rows of delicate, coarse, pointed bristles of same texture as *schwarzi*; bristles longest near base of declivity, each of longest bristles longer than distance between rows, more closely spaced within a row.

FEMALE.—Similar to male except frons devoid of transverse elevation; transverse lines

and subcrenulate ridges on elytral disc poorly developed; interstitial nodules much less than half as high, extending almost to middle of disc; declivital tubercles smaller; vestiture finer.

TYPE LOCALITY.—Three miles (5 km) N Suchixtepec on Highway 175, Oaxaca, Mexico.

TYPE MATERIAL.—The male holotype, female allotype, and 52 paratypes were taken at the type locality on 4-VI-71, 9500 ft elevation, from *Pinus*, presumably by D. E. Bright.

The holotype, allotype, and most of the paratypes are in the Canadian National Collection; the remaining paratypes are in my collection.

Hyloeurus binodatus, n. sp.

This species has the impressed frontal area with a pair of raised spongy patches somewhat reminiscent of the *rudis* group of species, but with the elytral declivity similar to female *harnedi* Blackman.

FEMALE.—Length 2.1 mm (paratypes 1.8-2.0 mm), 2.7 times as long as wide; color very dark brown, almost black.

Frons with a large, transversely reniform concavity from halfway between epistoma and upper level of eyes to vertex, widest point at upper level of eyes, occupying three-fourths of area between eyes; concavity rather abruptly impressed, moderately deep; central area of each half of concavity occupied by a protuberant, oval, spongy area, occupying about half of concave area; spongy areas rather narrowly separated from one another; general sculpture as in *rudis*; subglabrous.

Pronotum as in *rudis* except granules on disc smaller. Elytral disc as in *rudis*. Declivity as in *rudis* except tubercles distinctly larger; interstriae 1 with a moderately large protuberance at middle of declivity, slightly displaced from suture, almost as high as wide, similar to but smaller than female *harnedi*; interstriae 9 not more strongly elevated than in *rudis*. Vestiture as in *rudis*.

TYPE LOCALITY.—Nicholson, Mississippi.

TYPE MATERIAL.—The female holotype and one female paratype were taken at the type locality on 15-I-45, No. 45-2357, under hickory bark, apparently by W. H. Anderson. One female paratype is from Algiers, Louisiana, 18-IV-45, No. 45-8751, on pecan, by Rau. Slide mounts of genitalia parts designated by Anderson Scolytidae Slide No. 367 (holotype) and No. 453 (Algiers paratype) are in the U.S. National Museum.

The holotype and one paratype are in the U.S. National Museum; the other paratype is in my collection.

Cryphalomorphus parvatis, n. sp.

This unique species is characterized by the small size, by the unarmed anterior margin of the pronotum, and by the uniseriate rows of striae and interstitial scales. It is much more likely to be confused with species of *Hypothenemus* than with other *Cryphalomorphus* species.

FEMALE.—Length 0.8 mm (paratypes 0.8 mm), 2.6 times as long as wide; color very dark brown with pale scales.

Frons moderately convex, almost smooth, with rather abundant, very small punctures; vestiture inconspicuous. Eye elongate, very shallowly, broadly emarginate. Antennal scape short; club subcircular, septum poorly developed, almost transverse.

Pronotum 1.0 times as long as wide; widest slightly behind middle, sides moderately arcuate but converging only slightly to anterolateral angles then rather abruptly converging to form subangulate, broadly rounded anterior margin; anterior margin unarmed; summit distinct, in front of middle; anterior slope rather finely asperate; posterior areas obscurely subreticulate, with rather fine, isolated granules of moderate abundance in lateral and dorsal areas. Vestiture of equally abundant short hair and scales in posterior areas, hair only on anterior half.

Elytra 1.6 times as long as wide, 1.6 times as long as pronotum; sides almost straight and parallel on basal two thirds, rather narrowly rounded behind; striae not impressed, punctures uniseriate, small, rather shallow; interstriae as wide as striae, rather smooth, punctures slightly smaller than those of striae, not clearly defined. Declivity narrowly convex, rather steep; punctures slightly smaller than on disc. Vestiture of uniseriate rows of fine, short, recumbent striae hair, and uniseriate rows of erect interstitial scales; each scale about four times as long as wide, widest at its apex, spaced within a row and between rows by distances slightly shorter than length of a scale.

TYPE LOCALITY.—La Lima, Cortez, Honduras.

TYPE MATERIAL.—The female holotype and one damaged female paratype were taken at the type locality on 5-V-64, at 100 m elevation, No. 581, from *Cestrum scandens*, by S. L. Wood. One female paratype is from Guapiles, Limon, Costa Rica, 22-VIII-66, 100 m, No. 103, leguminose vine, S. L. Wood.

The holotype and paratypes are in my collection.

Cryphalomorphus setifer, n. sp.

This species is distinguished from *hirtus* Wood by the smaller size, by the presence of four to eight teeth on the anterior margin of the pronotum, by the less strongly impressed striae, and by the more slender interstitial scales.

FEMALE.—Length 1.7 mm (paratypes 1.4-1.7 mm), 2.5 times as long as wide; color very dark brown, with pale vestiture.

Frons broadly convex above, somewhat flattened below, a weak transverse impression just above epistoma; surface strongly reticulate, punctures fine, rather obscure, moderately close; vestiture inconspicuous. Eye entire, not at all sinuate. Antennal scape elongate; club rather large, ovate, suture 1 septate on lateral half, its procurved groove extending to median margin.

Pronotum 1.0 times as long as wide; widest just behind middle, sides weakly arcuate on posterior two-thirds, broadly rounded in front; anterior margin armed by four to eight small teeth; summit very slightly in front of middle; posterior areas coarsely, very closely punctured. Vestiture of short, stout, abundant hair.

Elytra 1.6 times as long as wide, 1.7 times as long as pronotum; outline as in *parvatus*; striae very feebly impressed, punctures rather coarse, moderately deep; interstriae very slightly wider than striae, smooth, punctures fine, deep, close, strongly confused. Declivity rather narrowly convex, steep; striae punctures slightly smaller, deeper; interstriae each with a uniseriate row of very fine granules. Vestiture of abundant, short ground cover, setae hairlike at base becoming scalelike on declivity, and rows of erect interstitial bristles; each erect bristle as long as distance between rows and between scales within a row, those on declivity, stouter, almost scalelike, about eight times as long as wide.

TYPE LOCALITY.—Volean Pacaya, Esquintla, Guatemala.

TYPE MATERIAL.—The female holotype, male allotype, and 24 paratypes were taken at the type locality on 1-VI-64, 1300 m elevation, No. 665, from a cut liana, by S. L. Wood. Thirty-seven additional paratypes are from Guatemala City, 30-V-64, 1300 m, No. 641, cut liana, S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Cryphalomorphus hirtus, n. sp.

This species is distinguished from *setifer* Wood by the larger size, by the presence of only two teeth on the anterior margin of the pronotum, by the more strongly impressed interstriae, and by the stouter interstitial scales.

FEMALE.—Length 1.8 mm (paratypes 1.7-1.9 mm), 2.3 times as long as wide; color dark brown, almost black.

Frons as in *setifer* except transverse impression on lower half much stronger, and punctures much coarser but shallow. Antennal club as in *setifer* but slightly wider. Pronotum as in *setifer* but anterior margin armed by only two teeth and punctures in posterior area not as deep; a few scales sometimes present on margin in front of scutellum.

Elytra 1.4 times as long as wide; sides almost straight and parallel on basal three-fourths, broadly rounded behind; striae moderately impressed on posterior half of disc, punctures rather coarse, deep; interstriae slightly wider than striae, moderately convex toward declivity, punctures on disc small, close, confused, armed near declivity by median rows of small granules. Declivity very broadly convex, steep; sculpture as on posterior part of disc except interstriae slightly narrower, granules much larger. Vestiture of abundant ground cover of short scales and median interstitial rows of erect scales; erect scales little longer than ground cover on basal half of disc, more than twice as long on declivity, each scale almost as long as distance between rows and between scales within a row, each about four to five times as long as wide.

MALE.—Similar to female except transverse frontal impression slightly deeper.

TYPE LOCALITY.—Sixteen km (10 mi) south of Oaxaca, Oaxaca, Mexico.

TYPE MATERIAL.—The female holotype, male allotype, and five paratypes were taken at the type locality on 6-VII-53, by S. L. Wood. One paratype is from 6 km S Atlixco, Puebla, Mexico, 14-VI-67, 2300 m, S. L. Wood. All specimens were taken from cut branches of a small tree having a loosely layered structure of woody tissues, rather than uniformly hard wood.

The holotype, allotype, and paratypes are in my collection.

Cryphalomorphus rusticus, n. sp.

Distinguished from *knabi* Hopkins by the two teeth arming the anterior margin of the pro-

notum, by the much wider, scalelike ground vestiture on the anterior half of the elytral disc, and by the absence of interstrial granules on the disc.

FEMALE.—Length 1.5 mm (paratypes 1.2-1.5 mm), 2.6 times as long as wide; color dark brown, almost black.

Frons as in *knabi* except transverse impression much less strongly developed, punctures coarser, deeper. Eye, antenna, and pronotum as in *knabi* except anterior margin of pronotum armed by two coarse teeth and punctures on pronotal disc distinctly larger.

Elytra as in *knabi* except discal interstriae larger, deeper; declivital striae greatly reduced; interstrial ground vestiture at base of elytra of slender scales, each scale as wide as those in erect rows, on declivity each scale as wide as long; erect scales on declivity slightly longer than in *knabi*.

MALE.—Similar to female in all respects.

TYPE LOCALITY.—Thirty-three km (21 mi) north of Juchitlan, Jalisco, Mexico.

TYPE MATERIAL.—The female holotype, male allotype, and 19 paratypes were taken at the type locality on 3-VII-65, 1300 m, No. 184, by S. L. Wood, from the same host as *hirtus* Wood (described above). Six paratypes were labeled Lagos, Guanajuato, Mexico, 11-VI-65, 2000 m, No. 44, S. L. Wood, from the same host. A series not included in the type series is from 11 km SE Tuxpan, Michoacan, Mexico, 16-VII-53, 2000 m, S. L. Wood, also from the same host.

The holotype, allotype, and paratypes are in my collection.

Cryphalomorphus trucis, n. sp.

This species is distinguished from *rusticus* Wood by the coarser, strial punctures on the elytral declivity, by the more slender discal interstrial ground vestiture, and by the different armature on the anterior margin of the pronotum.

FEMALE.—Length 1.6 mm (paratypes 1.3-1.5 mm), 2.6 times as long as wide; color very dark brown, almost black, vestiture pale.

Frons, eye, and antenna as in *rusticus* except frontal punctures larger, deeper. Pronotum as in *rusticus* except posterior areas reticulate, and anterior margin armed by about four to eight irregularly placed teeth.

Elytra as in *rusticus* except strial punctures slightly larger, deeper, interstrial punctures minute but evident; discal ground vestiture

near base of elytra proportionately much narrower than adjacent erect scales; strial punctures on declivity average much larger.

MALE.—Similar to female.

TYPE LOCALITY.—Sixteen km (10 mi) S Oaxaca, Oaxaca, Mexico.

TYPE MATERIAL.—The female holotype, male allotype, and two paratypes were taken at the type locality on 6-VII-53, 1700 m elevation, S. L. Wood. Seventeen paratypes are from 11 km (7 mi) S Atlixco, 13-VII-53, S. L. Wood; eight paratypes are from 6 km (4 mi) S Atlixco, 14-VI-67, 2300 m, No. 31, S. L. Wood; and eight paratypes are from 19 km (12 mi) SE Matamoros, Puebla, 3-VII-53, S. L. Wood. All are from the same host as *hirtus* Wood (above).

The holotype, allotype, and paratypes are in my collection.

Hypothenemus apicalis, n. sp.

This species is distinguished from *rotundicollis* Eichhoff and *erectus* LcConte by the much more slender, erect, interstrial bristles and by the strongly elevated interstriae 9 at the elytral apex.

FEMALE.—Length 1.8 mm (paratypes 1.6-2.0 mm), 2.3 times as long as wide; color dark brown, vestiture pale.

Frons essentially as in *rotundicollis*. Pronotum as in *rotundicollis*, with 10 to 14 asperities on anterior slope, posterior area more strongly reticulate, anterior margin armed by four teeth, lateral pair usually smaller.

Elytra as in *rotundicollis* except declivity not as steep, its outline with a distinct lateral constriction near middle; declivital striae more strongly impressed, punctures shallow, larger, interstriae 1-3 distinctly convex, 9 distinctly convex to junction with 3 then strongly elevated from there to apex. Vestiture of short, confused ground setae, almost hairlike on disc, becoming scalelike on declivity, and rows of erect interstrial bristles; each bristle longer on declivity, on declivity each as long as distance between rows or between bristles within a row, each about eight times as long as wide.

TYPE LOCALITY.—Three km (2 mi) E Armeria, Colima, Mexico.

TYPE MATERIAL.—The female holotype and seven female paratypes were taken at the type locality on 28-VI-65, 70 m elevation, No. 130, and on 21-VI-67, 100 m elevation, No. 72, from an unidentified liana, by S. L. Wood.

The holotype and paratypes are in my collection.

Hypothenemus indigenus, n. sp.

This species is distinguished from *rotundicollis* Eichhoff by the minutely granulate elytral surface and by the much more slender, more widely spaced, erect, interstitial bristles.

FEMALE.—Length 1.7 mm (paratypes 1.4-1.7 mm), 2.4 times as long as wide; color dark brown.

Head and pronotum as in *rotundicollis* except pronotal asperities slightly smaller, narrower, posterior areas more strongly reticulate.

Elytra 1.6 times as long as wide, as in *rotundicollis*, except surface minutely granulate, bristle-bearing interstitial punctures on disc granulate, declivital ground vestiture more nearly scalelike, and erect interstitial bristles much more slender and more widely spaced within a row; each bristle about eight times as long as wide; spaced within a row by distances slightly greater than length of a bristle.

MALE.—Similar to female except 1.2 mm long; eye reduced in size; antennal club more slender; most characters less sharply formed; vestiture longer.

TYPE LOCALITY.—Nine km (6 mi) S Huajuapán, Oaxaca, Mexico.

TYPE MATERIAL.—The female holotype, male allotype, and one male paratype were taken at the type locality on 16-VI-67, No. 45, from *Serjania*, by S. L. Wood. Two paratypes are from 17 km (11 mi) N Huajuapán, 15-VI-67, No. 43, *Psittacanthus*; 4 paratypes from 13 km (8 mi) SE Cameron, 21-VI-67, No. 76, shrub; 3 paratypes from 5 km (3 mi) S Matamoros, Puebla, 14-VI-67, 2000 m, No. 33, *Toxicodendron*; 6 paratypes from Volcan Cebornico, Nayarit, 5-VII-65, 1000 m, No. 189, *Serjania*; and one paratype from Volcan Colima, Jalisco, 23-VI-65, 500 m, No. 103, shrub; all by S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Hypothenemus trivialis, n. sp.

This species is distinguished from *bolivianus* Eggers by the smooth, shining elytral disc and smoother pronotal disc, by the more slender, slightly longer interstitial bristles, and by the much more strongly confused punctures and bristles on interstriae 2 and 3 on the basal half of the disc.

FEMALE.—Length 1.8 mm (paratypes 1.5-1.8 mm) 2.2 times as long as wide; color black.

Frons convex; a small median impression at upper level of eyes; surface rather finely rugose-reticulate, except smooth and shining in median area from epistoma to impression.

Pronotum 0.90 times as long as wide; widest on basal third, sides rather strongly, arcuately converging to rather narrowly rounded anterior margin; anterior margin armed by four teeth, lateral pair smaller; anterior slope armed by more than 35 moderately large asperities; posterior areas subreticulate, shining, granulate behind summit, granules sparse and intermixed with fine, shallow punctures laterally. Vestiture of hair, intermixed in posterior areas with slender scales.

Elytra 1.4 times as long as wide; outline as in related species; striae not impressed, punctures moderately large, shallow, their inner surfaces reticulate-granulate; interstriae smooth, shining, twice as wide as striae, punctures fine, uniseriate on 1 and 4-10, confused on 2 and 3 except near declivity. Declivity commencing near middle of elytra, rather gradual, convex; striae weakly impressed, punctures smaller, deeper; interstriae weakly convex, punctures uniseriate, finely granulate. Vestiture of rows of minute, fine, strial hair and rows of erect interstitial bristles; each bristle slightly longer than distance between rows or between bristles within a row; each bristle on disc slightly flattened, usually not flattened on declivity.

TYPE LOCALITY.—Santa Ana, San José, Costa Rica.

TYPE MATERIAL.—The female holotype and four female paratypes were taken at the type locality on 1-VIII-63, 1300 m elevation, No. 92, from *Cuparia guatemalensis*, by S. L. Wood. Other female paratypes were taken in Costa Rica as follows: 17 same locality as type, 30-VIII-63, 1300 m, No. 152, unidentified tree branches; one at Rio Damitas in the Dota Mts., San José, 22-VIII-63, 250 m, No. 129, *Vismia guianensis*; seven at Beverley, Limon, 26-VIII-63, 7 m, No. 154, vine; 14 at Pandora, Limon, 23-VIII-63, 50 m, Nos. 141 and 149, tree branches; two at Finca Cromaco on Rio Coto Brus, Puntarenas, 14-VII-63, 500 m, No. 76, seedling; one at Rincon de Osa, Puntarenas, 11-VIII-66, 50 m, No. 25; one at Cañas, Guanacaste, 13-VII-66, 30 m, No. 92, *Ochroma*. Three paratypes are from Barro Colorado Island, Canal Zone, Panama, 27-XII-63, 70 m, No. 342, tree branch; three are from Ft. Clayton, Canal Zone, Panama, 22-XII-63, 30 m, Nos. 319 and 330, *Serjania*; nine are from 10 km SE Miri, Barinas, Venezuela, 8-II-70, No. 305, *Serjania*; three are from 8 km S Colonia (near Buenaventura),

Valle de Cauca, Colombia, 9-VII-70, Nos. 617 and 620, *Ficus*; and three are from 37 km N Matías Romero, Veracruz, Mexico, 29-VI-67, 100 m, No. 125, tree branch. All were taken by me.

The holotype and paratypes are in my collection.

Hypothenemus dolosus, n. sp.

This species is distinguished from *opacus* (Eichhoff) by the absence of pits behind the asperities on the pronotal summit, by the more coarsely, deeply punctured pronotal disc, by the smooth, shining elytral surface, and by the absence of scalelike setae on the pronotum.

FEMALE.—Length 1.6 mm (paratypes 1.6-1.7 mm), 2.3 times as long as wide; color dark brown to black.

Head and pronotum as in *opacus* except asperities at pronotal summit not associated with deep pits, some punctures between summit and base form deep pits but without associated asperities; posterolateral areas subshining, deeply, closely, coarsely punctured. Vestiture all hairlike.

Elytra as in *opacus* except surface of interstriae smooth, shining; punctures on discal interstriae 2 usually uniseriate; declivital surface minutely granulate.

TYPE LOCALITY.—Pandora, Limón, Costa Rica.

TYPE MATERIAL.—The female holotype and seven female paratypes were taken at the type locality 23-VIII-63, 50 m elevation, No. 140, from *Mimosa*, by S. L. Wood; two other paratypes bear identical data except they are No. 142, from an unidentified branch; and one paratype No. 154 is from an unidentified liana. Two paratypes are from La Lima, Cortez, Honduras, 5-V-64, 200 m, No. 575, *Sweitenia* plantation, S. L. Wood.

The holotype and paratypes are in my collection.

Hypothenemus solocis, n. sp.

This species is distinguished from *squamosus* Hopkins by the more strongly impressed discal striae, by the slightly larger interstitial tubercles on both disc and declivity, by the more narrowly convex declivity with the costal margin near the apex much more strongly elevated, and by the reduction of tubercles toward the apices of interstriae 2, 4, 5, 6, and 8.

FEMALE.—Length 1.3 mm (paratypes 1.3-1.5 mm), 2.3 times as long as wide; color dark reddish brown.

Head and pronotum as in *squamosus* except surface of posterior areas more coarsely granulate.

Elytra 1.5 times as long as wide; sides almost straight and parallel on basal two-thirds, distinctly constricted near middle of declivity, rather narrowly rounded behind; striae distinctly impressed, punctures moderately large, shallow, indistinct; interstriae as wide as striae, distinctly impressed, punctures moderately large, shallow, indistinct; interstriae as wide as striae, distinctly convex, entire surface granulate, punctures uniseriate, granulate. Declivity rather narrowly convex, steep; interstriae more narrowly convex, particularly 1 and 3, granules larger except obsolete toward apices of 2, 4, 5, 6, and 8, posterior part of 9 with costal margin rather strongly elevated. Vestiture of rows of minute, fine, strial hair, and rows of erect, interstitial scales; each scale on declivity slightly shorter than distance between rows, slightly longer than distance between scales within a row, each about two to three times as long as wide.

TYPE LOCALITY.—Three km (2 mi) west of Armeria, Colima, Mexico.

TYPE MATERIAL.—The female holotype was taken at the type locality on 28-VI-65, 70 m elevation, No. 135, from a *Phoradendron* twig, by S. L. Wood. Paratypes were taken in Mexico as follows: two from Concha, Sinaloa, 20-VII-53, 15 m, S. L. Wood; three from 27 km (17 mi) E San Blas, Nayarit, 25-VII-53, 10 m, S. L. Wood; one from 8 km S Rio Santiago Ferry, 27-XI-48; two from 48 km (30 miles) N Tepic, 11-VII-65, 500 m, No. 226 in *Inga* (one specimen), No. 228 in *Serjania* (one specimen), S. L. Wood; and one from Los Corchos, Nayarit, 10-VII-65, 7 m, No. 206, tree branch, S. L. Wood.

The holotype and paratypes are in my collection.

Hypothenemus vesculus, n. sp.

This species is distinguished from *nanellus* Wood by the smooth, shining posterolateral areas of the pronotum, with the punctures entirely devoid of granulation, by the unimpressed striae, with small, shallow, strial punctures, by flat, smooth interstriae, and by the much more slender interstitial scales.

FEMALE.—Length 1.0 mm, 2.2 times as long as wide; color dark brown.

Frons as in *nanellus* but surface below upper level of eyes smooth, shining, punctures more distinct. Pronotum as in *nanellus* except

surface smooth, shining, no trace of reticulation, punctures larger, deeper, devoid of granules; scales in posterior area more slender.

Elytra about 1.5 times as long as wide; outline as in *nanellus*; striae not at all impressed, punctures small, shallow, distinct; interstriae flat, smooth, shining, two to three times as wide as striae, punctures very fine, uniseriate. Declivity rather steep, convex; essentially as on disc. Vestiture of rows of fine, short, strial hair on disc with similar supplemental interstitial hair on lower declivity, and rows of erect interstitial scales; each scale as long as distance between rows, more closely spaced within a row, each about four to six times as long as wide.

TYPE LOCALITY.—Ocosingo Valley, Chiapas, Mexico.

TYPE MATERIAL.—The unique female holotype was taken at the type locality on 7-VII-50, by L. J. Stannard.

The holotype is in my collection.

Hypothenemus suspectus, n. sp.

This species is distinguished from the closely allied *cylindricus* Hopkins by the less extensive frontal impression, and by the much more slender interstitial scales. It could easily be confused with *arecae* (Hornung) but it is smaller, and the frontal impression is much less extensive and more shallow.

FEMALE.—Length 1.2 mm (paratypes 1.1-1.3 mm), 2.4 times as long as wide; color almost black.

Frons as in *cylindricus* except lower frons shallowly, transversely impressed, not concave. Pronotum and elytra as in *cylindricus* except interstitial supplemental hairlike setae in ground vestiture more abundant on and near declivity, and erect interstitial scales much more slender, each scale about eight times as long as wide.

TYPE LOCALITY.—Pandora, Limon Prov., Costa Rica.

TYPE MATERIAL.—The female holotype was taken at the type locality on 23-VIII-63, 50 m elevation, No. 148, from a cucurbit vine, by S. L. Wood. Paratypes were taken as follows: Seven bear data identical to the type except for collection No. 144, No. 147, or No. 149, unknown tree branch; one from Finca Taboga near Cañas, Guanacaste, Costa Rica, 8-II-67, *Cecropia* petiole; two from Finca La Lola, Limon, Costa Rica, 10-I-63, *Theobroma cacao*, J. L. Saunders; one from Rincon de Osa, Puntarenas, Costa Rica, 11-VII-66, 50 m, No. 58

Cecropia petiole, S. L. Wood; one from 8 miles (13 km) S El Hato del Volean, 7-I-64, 1000 m, No. 371, tree seedling, S. L. Wood; two from 20 km SW El Vigia, Merida, Venezuela, 10-XII-69, 50 m, No. 188 vine, S. L. Wood; one from 17 km SE Miri, Barinas, Venezuela, 17-XII-69, 150 m, No. 196, *Albizzia caribaea*, S. L. Wood; one from 3 km NE Creole, Barinas, Venezuela, 18-XII-69, 150 m, No. 203, *Inga*, S. L. Wood.

The holotype and paratypes are in my collection.

Perioecryphalus sobrinus, n. sp.

This species is distinguished from *pullus* Wood by the larger size, by the more strongly reticulate pronotal disc, by the more strongly, more narrowly produced costal margin of the elytra at and near the suture, and by the more widely spaced, uniseriate, declivital interstriae.

FEMALE.—Length 1.25 mm (paratype 1.2 mm), 2.3 times as long as wide; color black.

Frons and pronotum as in *pullus* except pronotal disc much more strongly reticulate.

Elytra as in *pullus* except apical margin slightly more strongly, more narrowly produced; minute strial hair, in rows, indicate positions of obsolete strial punctures (similar setae present on *pullus* but supplemented by a few similar interstitial setae); erect interstitial scales in uniseriate rows, each slightly shorter than in *pullus* and much more widely spaced, spacing within a row slightly greater than length of scale on both disc and declivity (scales on declivital interstriae 2 in *pullus* confused, almost forming a double row).

TYPE LOCALITY.—About 260 km N Xavantina, Mato Grosso, Brazil.

TYPE MATERIAL.—The female holotype was taken at the type locality on 13-X-68, No. B07, by R. A. Beaver. One female paratype bears the same data except 7-XI-68, No. F03.

The holotype is in the British Museum (Natural History); the paratype is in my collection.

Dendrocranulus limatus, n. sp.

This species is very closely related to *limus* Wood, but it is distinguished by the smaller size, by the more strongly granulate pronotal disc, and by the more densely pubescent female frons.

MALE.—Length 1.6 mm (paratypes 1.5-1.8 mm), 2.6 times as long as wide; color dark reddish brown.

Frons as in *limus* except more coarsely, closely granulate-punctate, not at all reticulate; vesti-

ture less abundant, shorter. Pronotum as in *limus* except declivital striae with punctures slightly larger, interstriae 1 weakly elevated, 2 weakly depressed; vestiture slightly stouter.

FEMALE.—Similar to male except frons slightly flattened, rather finely, closely punctured, including central area, ornamented by abundant, long, yellow hair uniformly distributed from epistoma to well above upper level of eyes.

TYPE LOCALITY.—Bumbum Forest Station, Barinas, Venezuela.

TYPE MATERIAL.—The male holotype, female allotype, and 75 paratypes were taken at the type locality on 29-I-70, 150 m elevation, No. 276, cucurbit vine, by S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Dendrocranulus reditus, n. sp.

This species is distinguished from *vinealis* Wood by the slightly larger size, by the much stronger frontal impression of the male, with the tubercle on the summit much more strongly developed, by the finer declivital punctures, and by the more slender interstitial setae.

MALE.—Length 1.5 mm (paratypes 1.3-1.7 mm), 2.8 times as long as wide; color very dark brown.

Frons as in *vinealis* except more extensively, slightly more deeply impressed, median summit on vertex much more strongly developed, forming a rather narrowly rounded elevation. Pronotum as in *vinealis* except granules in median area of disc much smaller, almost obsolete, obscure reticulation present in some specimens. Elytra as in *vinealis* except declivital punctures smaller, interstriae 2 not as strongly impressed; interstitial bristles more slender, very slightly longer.

FEMALE.—Similar to male except frons convex, feebly impressed on lower half, summit on vertex feebly elevated, surface more coarsely, more uniformly punctured, vestiture sparse; pronotal reticulation more commonly present.

TYPE LOCALITY.—Nine km S Barraneas, Barinas, Venezuela.

TYPE MATERIAL.—The male holotype, female allotype, and 42 paratypes were taken at the type locality on 1-X-69, 150 m elevation, No. 34 (some paratypes No. 35), cucurbit vine, S. L. Wood. Other paratypes were taken in Venezuela as follows: 12 from 8 km SW Bumbum, Barinas, 11-II-70, 150 m, No. 311; 20 from 20 km SW El

Vigia, Merida, 10-XII-69, 50 m, No. 185; and 24 from 5 km W El Pino (near shore of Lake Maricao), Merida, 20-XI-69, 10 m, No. 142; all from the same host and collector.

The holotype, allotype, and paratypes are in my collection.

Dendrocranulus conditus, n. sp.

This species is distinguished from the very closely allied *consimilis* Wood by the more finely punctured, subreticulate frons, by the much less strongly granulate, reticulate pronotal disc, by the larger striae punctures, and by the slightly depressed declivital interstriae 2 which is entirely without granules.

MALE.—Length 1.4 mm (allotype 1.3 mm), 2.6 times as long as wide; color reddish brown.

Frons as in *consimilis* except surface obscurely reticulate, punctures slightly smaller and less granulate. Pronotum as in *consimilis* except surface of disc reticulate, distinctly, rather coarsely punctured, each puncture with a small, transversely elongate granule lateral to each puncture. Elytra as in *consimilis* except striae punctures larger; interstriae as wide as striae, impunctate; declivity with interstriae 2 slightly depressed, interstriae with uniseriate, fine punctures, devoid of granules; acute ventrolateral margin of declivity less well developed.

FEMALE.—Similar to male except elytral declivity very slightly more convex.

TYPE LOCALITY.—Bumbum Forest Station, Barinas, Venezuela.

TYPE MATERIAL.—The male holotype, female allotype, and one callow, male paratype with collapsed frons were taken at the type locality on 29-I-70, 150 m, No. 276, from a cucurbit vine, by S. L. Wood.

The holotype, allotype, and paratype are in my collection.

Dendrocranulus consimilis, n. sp.

This species is allied to *limbus* Wood, but it is distinguished by the smaller size, by the more slender form and by the shorter setae on the declivity.

MALE.—Length 1.4 mm (paratypes 1.2-1.5 mm), 2.5 times as long as wide; color yellowish brown.

Frons convex, with a slight transverse impression on lower half; surface shining, closely, deeply, rather coarsely punctured at sides and above, becoming almost impunctate on median

fourth of lower half; vestiture of fine, sparse, long hair uniformly distributed.

Pronotum 1.2 times as long as wide, sides on more than posterior two-thirds subparallel, feebly arcuate, anterior margin broadly rounded; anterior third moderately declivous, fine asperate, asperities decreasing in size but attaining base in lateral areas; disc shining, rather coarsely punctured, most punctures partly granulate; surface on posterior half very slightly subreticulate. Vestiture of sparse hair.

Elytra 1.6 times as long as wide, 1.4 times as long as pronotum; sides almost straight and parallel on more than basal two-thirds, abruptly, very broadly rounded behind; striae not impressed, punctures rather small; interstriae almost smooth, twice as wide as striae, punctures uniseriate, almost as large as those of striae. Declivity very steep, transversely flattened between interstriae 3, longitudinally slightly convex; posterolateral margin from suture to about interstriae 3 subacutely elevated; striae 1 and 2 distinctly impressed; interstriae 1 weakly elevated, 2 very slightly depressed, punctures of 2 and 3 finely granulate, obscurely granulate in lateral areas. Vestiture of rows of minute, obscure, recumbent, strial hair and rows of erect interstitial bristles; each bristle about one and one-third times as long as distance between rows or within a row, except shorter, slightly more than half as long on declivital interstriae 1 and 2.

FEMALE.—Similar to male except frons more broadly, evenly convex, with frontal pubescence about twice as abundant.

TYPE LOCALITY.—Los Corchos, Nayarit, Mexico.

TYPE MATERIAL.—The male holotype, female allotype, and 40 paratypes were taken at the type locality on 10-VII-65, 7 m elevation, No. 207, from an unidentified, climbing cucurbitaceous vine, by S. L. Wood. Other specimens, not included in the type series, are from Honduras.

The holotype, allotype, and paratypes are in my collection.

Dendrocranulus vinealis, n. sp.

This species is distinguished from the closely allied *pumilus* Wood by the shining pronotal disc, by the subrenulate granules accompanying each puncture on the pronotal disc, and by the much more strongly impressed male frons.

MALE.—Length 1.3 mm (paratype 1.2 mm),

2.7 times as long as wide; color very dark brown.

Frons convex above upper level of eyes, strongly, transversely impressed below that level; surface smooth and shining, with moderately fine, subgranulate punctures in convex area, almost impunctate in impressed area, vestiture of sparse hair.

Pronotum outline as in *pumilus*, anterior area more coarsely asperate; surface shining, punctures moderately coarse, deep, rather close, each with a low, lateral, subrenulate, transverse granule. Vestiture confined to margins, sparse, hairlike.

Elytral outline about as in *pumilus*; striae not impressed, punctures small, moderately deep; interstriae smooth, twice as wide as striae, punctures slightly smaller than those of striae, rather widely spaced. Declivity steep, rather broadly flattened; strial punctures deeper, slightly larger than on disc; interstriae 1 weakly elevated, 2 weakly depressed, punctures not at all granulate; ventrolateral margin rounded. Vestiture of interstitial rows of flattened bristles, each bristle slightly longer than distance between rows or within a row.

TYPE LOCALITY.—La Lima, Cortez, Honduras.

TYPE MATERIAL.—The male holotype and one male paratype were taken at the type locality on 5-V-64, 200 m elevation, No. 579, in *Cayaponia microdonta*, by S. L. Wood.

The holotype and paratype are in my collection.

Dendrocranulus vicinalis, n. sp.

This species is distinguished from *vicinalis* Wood by the much smaller strial and interstitial punctures, by the more gradual elytral declivity, and by the interstitial granules on the declivity.

MALE.—Length 1.5 mm (paratypes 1.6-1.7 mm), 2.9 times as long as wide; color yellowish brown.

Frons as in *vicinalis* except impression not as abrupt, impunctate area much smaller, small granules more conspicuous in lateral areas. Pronotum as in *vicinalis* except discal punctures slightly smaller, granules not as slender. Elytra as in *vicinalis* except strial and interstitial punctures smaller, very shallow; punctures on declivital interstriae 1-3 replaced by small granules.

FEMALE.—Similar to male except frontal impression not as strong, sculpture finer, vestiture finer, more abundant but not conspicuous.

TYPE LOCALITY.—Rio Damitas in the Dota Mountains, San José, Costa Rica.

TYPE MATERIAL.—The male holotype, female allotype, and one male paratype were taken at the type locality on 18-II-64, 250 m elevation, No. 441 (paratype 440), in an unidentified climbing vine, by S. L. Wood.

The holotype, allotype, and paratype are in my collection.

Dendrocranulus securus, n. sp.

This species is distinguished from *maurus* (Blandford) by the partly reticulate postero-lateral areas of the pronotum, by the reticulate, more finely punctured frons, and by the shorter, stout setae on declivital interstriae 1 and 2.

MALE.—Length 1.8 mm (paratypes 1.7-2.1 mm), 2.5 times as long as wide; color reddish brown.

Frons convex, a shallow, transverse impression from epistoma to upper level of eyes; surface reticulate, punctures moderately fine, deep, close, not at all granulate, less abundant near median line on lower half; vestiture sparse, hairlike.

Pronotum 1.1 times as long as wide; widest well behind middle, sides moderately arcuate on posterior half, feebly constricted one-third length from anterior margin, anterior margin rather narrowly rounded; asperities small, abundant; surface of disc and lateral areas subreticulate, punctures rather small, deep, a low, transverse, rounded granule lateral to each puncture. Vestiture fine, sparse, hairlike.

Elytra 1.5 times as long as wide, 1.4 times as long as pronotum; sides almost straight and parallel on less than basal two-thirds, posterior margin straight on median half; striae not impressed, punctures rather small, deep, close; interstriae almost smooth, twice as wide as striae, punctures fine, uniseriate, rather widely regularly spaced. Declivity steep; striae 1 weakly impressed; interstriae 1 weakly elevated; interstitial punctures minutely granulate; central half flattened, broadly convex in all marginal areas as in *maurus*. Vestiture of rows of minute, recumbent strial hair, and rows of erect, interstitial bristles; each bristle almost as long as distance between rows and between bristles within a row, slightly shorter and coarser than in *maurus*.

FEMALE.—Similar to male except frontal impression less distinct, vestiture very slightly more abundant.

TYPE LOCALITY.—Rio Damitas in the Dota Mountains, San José, Costa Rica.

TYPE MATERIAL.—The male holotype, female allotype, and 19 paratypes were taken at the type locality on 18-II-64, 250 m elevation, No. 446, from an unidentified climbing vine, by S. L. Wood. Four paratypes are from Playon, Puntarenas, Costa Rica, 22-II-64, 50 m, Nos. 454 and 455, and three paratypes are from Turrialba, Cartago, 9-III-64, 700 m, Nos. 460, 458, same host and collector.

The holotype, allotype, and paratypes are in my collection.

Dendrocranulus fulgidus, n. sp.

This species is distinguished from the closely allied *maurus* (Blandford) by the discal granules on the pronotum, by the narrower elytral declivity, by the more strongly impressed male frons, and by the more coarsely punctured female frons, with less abundant vestiture.

MALE.—Length 2.0 mm (paratypes 1.8-2.3 mm), 2.8 times as long as wide; color dark reddish brown, elytra lighter.

Frons as in *maurus* except transverse impression distinctly deeper, median summit on vertex slightly higher. Pronotum as in *maurus* except granules extend to impunctate median line; posterolateral areas reticulate. Elytra as in *maurus* except more slender, declivity narrower, strial punctures much smaller, not as deep, interstriae 2 more distinctly impressed, surface brightly shining; granules as in *maurus*; declivital setae on interstriae 1 and 2 very short, less than half as long as on 3 or on disc.

FEMALE.—Similar to male except frons planoconvex, more coarsely punctured on lateral thirds than in female *maurus*, vestiture fine, long, slightly less abundant than in female *maurus*.

TYPE LOCALITY.—Volcan de Chiriqui, near Cerro Punta, Chiriqui, Panama.

TYPE MATERIAL.—The male holotype, female allotype, and 97 paratypes were taken at the type locality on 11-I-64, 1800 m elevation, Nos. 378 (holotype and allotype), 408, and 418, from a cucurbit vine, by S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Dendrocranulus vicinus, n. sp.

This species is distinguished from the very closely related *shedli* Wood by the less strongly impressed male frons, by the more coarsely

punctured, nongranulate female frons, with a tuft of abundant, fine, long, yellow hair, and by the larger granules in the median area of the pronotal disc.

MALE (allotype).—Length 1.5 mm (paratypes 1.4-1.7 mm), 3.0 times as long as wide; color yellowish to reddish brown.

Frons as in female *schedli*. Pronotum as in *schedli* except granules in median area of disc slightly larger and evidently never associated with punctures. Elytra as in *schedli* except striae 1 and 2 and interstriae 2 usually less strongly impressed.

FEMALE (holotype).—Similar to male except frons more broadly convex, more closely punctured, punctures not at all granulate, ornamented by a tuft of long, fine, abundant, yellow hair.

TYPE LOCALITY.—La Lima, Cortez, Honduras.

TYPE MATERIAL.—The female holotype, male allotype, and 20 paratypes were taken at the type locality on 5-V-64, 200 m elevation, No. 579, from *Cayaponia microdonta*, by S. L. Wood. Four paratypes are from La Ceiba, Atlantida, Honduras, 20, 29-V-49, at light, E. C. Becker.

The holotype, allotype, and paratypes are in my collection.

Dendrocranulus rudis, n. sp.

This species is allied to *cucurbitae* (LeConte), but it is distinguished by the slightly larger rugae on the pronotal disc, with the punctures obscure to obsolete, and by the less deeply excavated male frons with the median elevation on the vertex less well developed.

MALE.—Length 1.8 mm (paratypes 1.6-1.9 mm), 2.8 times as long as wide; color very dark brown.

Frons somewhat flattened, transversely impressed from epistoma to upper level of eyes, weakly ascending above; median elevation on summit rather well developed, highest at its dorsal extremity, descending below; surface smooth with an occasional fine puncture or minute granule; vestiture sparse, hairlike.

Pronotum 1.2 times as long as wide; widest just behind middle, sides rather strongly arcuate on posterior two-thirds, rather narrowly rounded in front; anterior third rather coarsely asperate, low, transverse crenulations continuing to base, some crenulations in median area associated with obscure punctures. Vestiture fine, long, moderately abundant.

Elytra 1.7 times as long as wide, 1.5 times as long as pronotum; sides almost straight and parallel on basal three-fourths, very broadly rounded behind; striae not impressed, punctures rather small, moderately impressed, spaced by about two diameters of a puncture; interstriae smooth, twice as wide as striae, equal in size and spacing to those of striae. Declivity steep, broadly flattened; striae 1 and 2 feebly impressed; interstriae 1 weakly elevated, 2 weakly impressed, lateral areas about as high as suture; interstitial punctures not granulate. Vestiture of rows of fine, short, recumbent, strial hair, and rows of erect interstitial bristles; each bristle rather slender, about one and one-fourth times as long as distance between rows, slightly shorter on declivital interstriae 1 and 2.

FEMALE.—Similar to male except frons rather coarsely punctate-granulate, granules mostly arranged in rugae, vertex devoid of median elevation; declivity more nearly convex, impressions and elevations obscure.

TYPE LOCALITY.—Nineteen km E Carapan, Michoacan, Mexico.

TYPE MATERIAL.—The male holotype, female allotype, and 50 paratypes were taken at the type locality on 18-VI-65, 2300 m elevation, No. 75, in cucurbit vine, by S. L. Wood. One paratype is from 5 km W El Salto, Durango, Mexico, 7-VI-65, No. 32, cucurbit vine, S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Dendrocranulus confinis, n. sp.

This species is distinguished from the very closely related *cucurbitae* (LeConte) by the subreticulate pronotal surface between crenulations on the disc and by the slightly shallower, more extensive frontal excavation of the male.

MALE.—Length 2.0 mm (paratypes 1.5-2.0 mm), 2.7 times as long as wide; color very dark reddish brown, pronotum black in some specimens.

Frons as in *cucurbitae* but very slightly less strongly excavated, impression extending higher in lateral areas, median projection on vertex equal in size. Pronotum as in *cucurbitae* except discal punctures slightly larger, surface subreticulate, evidently less irregular. Elytra as in *cucurbitae* except discal punctures very slightly larger.

FEMALE.—Similar to male except frons broadly convex, a slight transverse impression

just above epistoma; surface subreticulate, punctures rather small, shallow, vestiture sparse; declivity more evenly convex, interstriae 2 not as strongly impressed.

TYPE LOCALITY.—Volean de Chiriqui, near Cerro Punta, Chiriqui, Panama.

TYPE MATERIAL.—The male holotype, female allotype, and 38 paratypes were taken at the type locality on 11-I-64, 1800 m, No. 378, from a eueurbit vine, by S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Ips borealis lanieri, subsp. n.

This subspecies is distinguished from *borealis borealis* Swaine by the almost evenly convex female frons, which is sparsely granulate and finely punctured below the upper level of the eyes, and by the transverse row of epistomal granules. It is much more similar to *b. thomasi* Hopping, but it is distinguished by the shorter, finer, less abundant vestiture of the female frons, which is also less strongly inflated, and the granules average much smaller in size.

FEMALE.—Length 3.5 mm (paratypes 3.0-3.8 mm), 2.6 times as long as wide; color very dark brown to almost black.

As in *b. borealis* except for sculpture and ornamentation of female frons as cited in the above diagnosis; entire frons with small, distinct punctures, on lower half intermixed with several small granules.

MALE.—Similar to female except frontal punctures and granules much larger, more numerous.

TYPE LOCALITY.—One mile south of Brownsville, Lawrence County, South Dakota.

TYPE MATERIAL.—The female holotype, male allotype, and 61 paratypes were taken at the type locality on 18-VI-68, No. 47, *Picea glauca*, by S. L. Wood. Additional paratypes were taken as follows: 21 from 2 miles SW Lead, Lawrence Co., South Dakota, 18-VI-68, No. 48, *Picea glauca*, S. L. Wood; 7 from SE $\frac{1}{4}$ S6, T4N, R3E, Black Hills, South Dakota, 17-VIII-67, *Picea glauca*, J. M. Schmidt; 5 from 6 miles SW Buffalo, Johnson Co., Wyoming, 20-VI-68, No. 58, *Picea engelmanni*, S. L. Wood; 6 from about 20 miles NW Pagosa Spring, Hinsdale Co., Colorado, 28-VI-68, *Picea engelmanni*, W. G. Harwood.

The holotype, allotype, and paratypes are in my collection.

Gnathophthorus artus, n. sp.

This species is distinguished from the five previously named species by the smaller size, by the simple declivity, and by the very broadly impressed female frons with much more abundant and longer frontal vestiture.

FEMALE.—Length 1.05 mm (paratypes 0.9-1.05 mm), 4.3 times as long as wide; color of pronotum and declivity rather dark yellowish brown, basal area of elytra pale yellowish brown.

Frons rather shallowly, subcircularly concave from eye to eye, from epistoma to vertex; margins of upper half bearing a dense row of very long hair, lower area appearing spongy and bearing a few moderately long setae; surface largely concealed by vestiture. Antennae small; club distinctly longer than scape, anterior face glabrous, clearly marked by two almost straight, partly septate sutures.

Pronotum 1.84 times as long as wide; subquadrate, sides straight and parallel more than three-fourths of their length, anterior margin feebly arcuate, weakly serrate; anterior tenth weakly declivous, anterior third finely asperate; posterior areas smooth, shining, minutely, shallowly, rather closely punctured. Glabrous.

Elytra 2.4 times as long as wide, 1.4 times as long as pronotum; sides straight and parallel on basal three-fourths, moderately rounded behind; striae not impressed, punctures minute; interstriae four to five times as wide as striae, punctures similar in size and spacing to those of striae. Declivity moderately steep, narrow; sutural interstriae distinctly elevated, convex; punctures of striae 2 and 3 fine, distinct, rather widely spaced on 3; interstriae 2 broad, flat, smooth, shining, with only four or five minute punctures, 3 not elevated or serrate. Vestiture confined to declivity, sparse; consisting of rather fine interstitial bristles on interstriae 3 and on lateral areas, smaller, similar setae on interstriae 1.

MALE.—Similar to female except frons mostly convex, a short, transverse carina at upper level of eyes and immediately below this a small, shallow concave area on median fourth, surface shining, rather closely, coarsely punctured, vestiture of sparse, short hair; ten serrations on anterior margin of pronotum slightly larger; elytral declivity, shallowly, broadly bisulate, interstriae 3 very feebly elevated.

TYPE LOCALITY.—About 260 km N Xavantina, Mato Grosso, Brasil (12°49' S 41°46' W).

TYPE MATERIAL.—The female holotype, male allotype, and 12 paratypes were taken at the

type locality on X-1968, No. F41, by R. A. Beaver. One paratype bears the same data except 23-IX-68, No. 166.

The holotype, allotype, and five paratypes are in the British Museum (Natural History), two paratypes are in the Museu de Zoologia, Universidade de São Paulo, and six paratypes are in my collection.

Dryocoetoides Hopkins

Dryocoetoides Hopkins, 1915, U.S. Dept. Agric. Rept. 99:52 (Type-species: *Dryocoetoides guatemalensis* Hopkins = *Xyleborus capucinus* Eichhoff)

This neotropical genus was placed in synonymy by Schedl (1952, Ent. Blätt. 47-48:161) and, presumably because of the lack of material or interest, it has not been seriously reconsidered since then. The type-species clearly is a representative of the *Xyleborini*. Contrary to the action of Schedl of placing virtually all representatives of this tribe in one enormous genus, *Xyleborus*, I prefer to elevate certain clearly marked groups to generic rank in order to make them more meaningful and to make *Xyleborus* less unwieldy.

Dryocoetoides has the prothoracic tibia inflated and tuberculate on its posterior face; the antennal club is rather strongly flattened, with the basal area slightly thickened and moderately corneous, two clearly marked, almost straight sutures are on the basal half of the anterior face and both continue to and are clearly marked on the distal half of the posterior face; in most species the eyes are rather large and coarsely faceted; the scutellum is flat and moderately large; the pronotum is rather stout, about as long as wide, and armed by several serrations on the anterior margin; and the elytral disc and declivity usually have contrasting sculpture.

In addition to *Xyleborus capucinus* Eichhoff, the following species are transferred into *Dryocoetoides*: *Xyleborus monachus* Blandford, *Bostrichus flavus* Fabricius, *Bostrichus cristatus* Fabricius (= *Xyleborus solitarius* Hagedorn, *X. urichi* Eggers, *X. crenatus* Eggers), and *Xyleborus pseudosolitarius* Eggers. Seven previously undescribed species are added below.

Dryocoetoides monachus (Blandford), n. comb.

Xyleborus monachus Blandford. 1898, Biol. Centr. Amer., Coleopt. 4(6):204 (Syntypes, males; Cerro Zunil, Guatemala; British Mus. Nat. Hist.).

This species was named from two male syntypes and has not been reported in the literature since then.

Four females were collected at Paulin, Esquintla, Guatemala, 19-V-64, 300 m, No. 584, from *Inga* branches; 21 females from Rancho Grande, Pittier National Park, Aragua, Venezuela, 9-IV-70, 1100 m, No. 408, tree seedling; one female from 24 km E Barbosa, Antioquia, Colombia, 18-VII-70, 1200 m, No. 696, from a Rubiaceae sapling; all were taken by me. The Guatemalan specimens and several males of the very closely related *capucinus* (Eichhoff) were compared to both of Blandford's male syntypes. In general form and sculpture the types (2.7-2.9 mm) were exactly as the male *capucinus* (2.3-2.5 mm) except for the body size and details of the elytral structure. The elytral structure and larger size conformed to that of the Guatemalan females. Since there are no other known species in Guatemala with which *monachus* could be confused, I am confident the association is correct even though males were not taken in my series.

Females of this species differ from those of *capucinus* by the larger size (2.8-3.2 mm, compared to 2.2-2.6 mm for *capucinus*), by the longer elytral disc (50 percent of elytral length, compared to 40 percent), by the more shining elytral declivity with some reticulation in the posterolateral areas, and by the more nearly uniseriate interstitial granules on the elytral declivity.

Dryocoetoides verrucosus, n. sp.

This species is distinguished from *flavus* (Fabricius) by the more slender form, by the smaller striae punctures, by the rugose-reticulate, dull, dark, elytral declivity, and by the very different declivital sculpture.

FEMALE.—Length 2.5 mm (paratype 2.4 mm), 3.2 times as long as wide; color reddish brown, elytra much darker.

Frons and pronotum as in *flavus* except pronotum 1.2 times as long as wide.

Elytra 1.9 times as long as wide, 1.6 times as long as pronotum; sides almost straight and parallel on basal two-thirds, tapered then narrowly rounded behind; striae not impressed, punctures very small, very shallow, spaced within a row by two diameters of a puncture; interstriae smooth, shining, about six times as wide as striae, punctures almost as large as striae, uniseriate except slightly confused on 2. Declivity occupying posterior third of elytral length, convex; surface minutely rugose-reticulate; striae feebly impressed, punctures slightly larger than on disc, feebly impressed; interstriae uniseriately, rather coarsely tuberculate, except

at base and lower half of sutural interstriae; sutural interstriae from just above middle to just before apex very strongly, irregularly elevated, elevation as high as wide; interstriae 2 and 3 slightly sinuate to accommodate sutural elevation. Vestiture confined to declivity, consisting of minute strial hair and confused, semi-recumbent interstitial setae, each slightly shorter than width of an interstriae.

TYPE LOCALITY.—Thirty km E Palmar, Bolivar, Venezuela.

TYPE MATERIAL.—The female holotype and one female paratype were taken at the type locality on 12-VI-70, 200 m, No. 579, from a tree known locally as Rosada (Moraceae), by S. L. Wood. One female paratype is from 3 km NE Creele, Barinas, Venezuela, 18-XII-69, 150 m, No. 203, *Inga*, S. L. Wood.

The holotype and paratypes are in my collection.

Dryocoetoides pileatus, n. sp.

This species is distinguished from the closely allied *capueinus* (Eichhoff) by the much larger size, by the much shorter elytral disc, by the more gradual elytral declivity, and by the absence of strial punctures on the declivity.

FEMALE.—Length 3.2 mm (paratypes 3.2-3.3 mm), 2.1 times as long as wide; color almost black.

Frons and pronotum as in *capueinus* except surface of disc less strongly reticulate, punctures deeper.

Elytra 1.1 times as long as wide, 1.3 times as long as pronotum; disc occupying 30 percent of elytral length, transition from disc to declivity rather abrupt; striae not evident, surface smooth, shining, punctures variable, small to very small, close, confused. Declivity gradual, convex; surface minutely rugulose, dull; striae and strial punctures entirely obsolete, numerous small, rounded, confused, scitiferous granules; subapical posterolateral margin acutely, subrenulately elevated from suture to position of interstriae 8. Vestiture confined to declivity, consisting of moderately abundant, short hair.

TYPE LOCALITY.—Forty km SE Socopo, Barinas, Venezuela.

TYPE MATERIAL.—The female holotype and one female paratype were taken at the type locality on 25-I-70, 150 m elevation, No. 263, in *Inga* limb, by S. L. Wood; four female paratypes are from 10 km SE Miri, Barinas, Venezuela, 8-II-70, 150 m elevation, No. 295, in *Inga* limbs, by S. L. Wood; one female paratype is

from 17 km SE Miri, Barinas, Venezuela, 17-XII-69, 150 m elevation, No. 197, from a palm bole 15 cm in diameter, by S. L. Wood.

The holotype and paratypes are in my collection.

Dryocoetoides velutinus, n. sp.

This species is placed in a species group with *pseudosolitarius*, although the relationship is not close. It is distinguished by the larger size, by the stouter body form, and by the steeper elytral declivity that has different sculpture.

FEMALE.—Length 2.8 mm (paratypes 2.7-2.9 mm), 2.4 times as long as wide; color reddish brown.

Frons and pronotum as in *pseudosolitarius*; pronotum 1.1 times as long as wide.

Elytra 1.4 times as long as wide, 1.3 times as long as pronotum; disc occupying basal two-thirds of elytra; striae not impressed except 1 slightly near declivity, punctures very small, shallow, spaced within row by three diameters of a puncture; interstriae smooth, shining, about six times as wide as striae, punctures minute, half as large as those of striae, confused; declivital sculpture commencing on posterior third of disc. Declivity steep, broadly convex; surface minutely rugulose; strial punctures small but larger and deeper than on disc; interstriae with abundant, rather coarse, pointed, confused tubercles; lower half of sutural interstriae moderately protuberant; subapical posterolateral margin subacutely subrenulately from suture to interstriae 8. Vestiture of fine, abundant, moderately long hair on disc and declivity.

MALE.—Length 2.8 mm; essentially as in female, but with all characters less perfectly formed except pronotum 1.3 times as long as wide, excavated as in male *perebeae* (Ferrari) except median tubercle on anterior margin very broad.

TYPE LOCALITY.—Thirty km E Palmar, Bolivar, Venezuela.

TYPE MATERIAL.—The female holotype, male allotype, and 21 female paratypes were taken at the type locality on 12-VI-70, 200 m, No. 538, from the bole 30 cm in diameter of a tree locally named Pandanga, by S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Dryocoetoides rusticus, n. sp.

This species is distinguished from *velutinus* Wood by the larger size, by the confused punctures

tures on the discal interstriae, by the more gradual elytral declivity, with much finer interstitial tubercles, and by the much coarser vestiture.

FEMALE.—Length 3.5 mm (estimated, elytra spread), about 2.4 times as long as wide; color reddish brown.

Frons as in *velutinus* but much narrower due to enlarged eyes. Pronotum as in *velutinus* except punctures on disc closer.

Elytra about 1.4 times as long as wide; elytral disc as in *velutinus* except all punctures deeper, interstitial punctures more numerous, confused, minute, irregular surface lines present. Declivity much as in *velutinus*, surface rugulose, more evenly, more gradually convex; stria punctures larger than in *velutinus*, interstitial tubercles more numerous, much smaller, weakly protuberant toward apex of suture; subapical ventrolateral margin acutely elevated from suture toward but becoming obsolete on interstriae 8, not connected to but continuing toward base of declivity as a row of suberemulate tubercles. Vestiture confined to declivity and sides; consisting of very stout, short bristles on central and lower parts of declivity, some setae on lateral and upper parts of declivity at least twice as long and tapered.

TYPE LOCALITY.—Thirty km E Palmar, Bolivar, Venezuela.

TYPE MATERIAL.—The unique female holotype was taken at the type locality on 12-VI-70, 100 m elevation, No. 582, from an unidentified tree limb, by S. L. Wood.

The holotype is in my collection.

Dryocoetoides severus, n. sp.

Among known forms this species is allied to *rusticus* Wood, but it is distinguished by the large size, by the subquadrate pronotum, and by the very different sculpture of the elytral declivity.

FEMALE.—Length 5.0 mm, 2.6 times as long as wide; color reddish brown; head and prothorax detached and mounted separately on the same paper point as body.

Frons as in *rusticus* but narrower, 1.8 times as wide as width of eye. Pronotum 1.0 times as long as wide; subquadrate; sculpture essentially as in *rusticus*.

Elytra 1.7 times as long as wide, 1.6 times as long as pronotum; sides straight and parallel on basal three-fourths, obtusely subangulate behind; disc occupying basal three-fourths; basal half of disc as in *rusticus*; posterior half of disc

with surface smooth, shining, punctures replaced by rounded granules. Declivity steep, broadly convex; a large, low, conspicuous, rounded prominence at basal margin on interstriae 2; declivital surface smooth, almost shining; sutural interstriae slightly elevated on lower half, impressed toward base; area of striae 1 impressed to middle, area lateral to striae 1 on upper half gradually elevated toward prominence at base on interstriae 2; interstriae 1 with small confused tubercles to apex, others with a few tubercles on basal half only; stria punctures much larger and slightly deeper than on disc; subapical ventrolateral margin acutely, suberemulately elevated from apex to apex of interstriae 8. Vestiture confined to posterior half of elytra; consisting of fine long hair except much shorter on lower half of declivity.

TYPE LOCALITY.—Thirty km E Palmar, Bolivar, Venezuela.

TYPE MATERIAL.—The unique female holotype was taken at the type locality on 12-VI-70, 200 m, No. 548, from *Eschweilera subglanulosa*, by S. L. Wood.

The holotype is in my collection.

Dryocoetoides insculptis, n. sp.

This species is distinguished from the rather remotely related *velutinus* Wood by the larger size, by the strongly impressed declivital striae, by the much less abundant elytral vestiture, and by other characters.

FEMALE.—Length 4.2 mm (paratypes 4.0-4.2 mm), 2.6 times as long as wide; color reddish brown.

Frons essentially as *velutinus* except not as wide due to enlarged eyes.

Pronotum 1.2 times as long as wide; about as in *velutinus* except sides almost straight and parallel on basal two-thirds, broadly rounded in front; anterior margin armed by 14 low serrations; disc shining, lateral areas reticulate, punctures very small, deep, moderately abundant.

Elytra 1.6 times as long as wide, 1.5 times as long as pronotum; disc occupying basal three-fourths; sides straight and parallel on basal three-fourths, rather narrowly rounded behind; striae feebly impressed on basal half, punctures small, rather deep; interstriae on basal half of disc smooth, shining, about three times as wide as striae, punctures very small, confused; declivital sculpture commencing just behind middle of disc. Declivity confined to posterior fourth of elytra, steep, convex; strongly reticulate, dull; striae very deeply impressed, punc-

tures slightly larger than on disc, shallow; interstriae rather strongly convex, uniseriately rather coarsely serrate, tubercles much smaller on lower half of declivity; sutural interstriae moderately protuberant on lower half of declivity. Vestiture confined to reticulate area; consisting of fine, short, strial hair and an occasional similar interstitial hair, and rows of coarse, erect bristles arising from posterior margins of serrations, each bristle about as long as distance between rows.

TYPE LOCALITY.—Eight km S Colonia (near Buenaventura), Valle de Cauca, Colombia.

TYPE MATERIAL.—The female holotype and eight female paratypes were taken at the type locality on 9-VII-70, 30 m elevation, No. 605, in limbs of *Humistrum excelsum*, by S. L. Wood.

The holotype and paratypes are in my collection.

Dryocoetoides indolatus, n. sp.

This species is distinguished from the allied *insculptus* Wood by the slightly smaller size, by the more nearly subquadrate pronotum, by the unimpressed declivital striae, by the finer interstitial tubercles, and by the vestiture.

FEMALE.—Length 3.7 mm, 2.6 times as long as wide; color reddish brown.

Frons as in *insculptus* but narrower. Pronotum subquadrate, serrations on anterior margin poorly developed; sculpture essentially as in *insculptus*.

Elytra 1.5 times as long as wide, 1.4 times as long as pronotum; disc occupying basal half of elytral length; striae not impressed, punctures very small, spaced within a row by one or two diameters of a puncture; interstriae smooth, shining, with shallow, irregular lines, punctures about equal in size to those of striae, confused. Declivity very gradual on its basal half, steep and convex on its posterior half; entire surface closely, finely rugose, dull; striae not impressed, punctures twice as large as on disc, very shallow; interstitial punctures replaced by fine, confused tubercles, slightly larger on basal half of convex area; sutural interstriae weakly protuberant toward apex; subapical posterolateral margin acutely eostate near suture, beoming subcrenulate toward interstriae 8. Vestiture confined to sides and declivity, consisting of fine, long, moderately abundant, confused, interstitial hair; minute strial hair also present on declivity.

TYPE LOCALITY.—Thirty km E Palmar, Bolívar, Venezuela.

TYPE MATERIAL.—The unique female holotype was taken at the type locality on 12-VI-70, 200 m, No. 578, from *Parinari excelsa*, by S. L. Wood.

The holotype is in my collection.

Sampsonius expulsus, n. sp.

This species apparently is more closely allied to *detractus* Wood than to other described species, but it is readily distinguished by the longitudinally concave elytral declivity and by the absence of declivital spines.

FEMALE.—Length 5.1 mm, 3.4 times as long as wide; color reddish brown.

Frons, pronotum and elytral disc as in *detractus*. Elytral declivity slightly longer than disc, its surface reticulate; base of declivity rather abruptly impressed, basal and lateral margins continuously, finely serrate from interstriae 2 to near sutural apex; face of declivity longitudinally concave, broadly flattened to serrate margins, suture rather strongly elevated particularly on lower half; interstriae 3 weakly elevated on lower half. Vestiture of fine, moderately long, rather abundant hair; only slightly longer on declivity.

TYPE LOCALITY.—Eight km S Colonia (near Buenaventura), Valle de Cauca, Colombia.

TYPE MATERIAL.—The female holotype was taken at the type locality on 9-VII-70, at 30 m elevation, No. 619, from a *Pouteria* branch, by S. L. Wood.

The holotype is in my collection.

Sampsonius detractus, n. sp.

The large size and the presence of one pair of long slender spines near the apex of declivital interstriae 3 distinguish this species from other representatives of the genus.

FEMALE.—Length 5.6 mm (paratype 5.8 mm), 3.6 times as long as wide; color reddish brown.

Frons narrow, broadly convex; surface reticulate, with small, low, rather abundant, shining granules; vestiture of sparse, fine, long hair. Eye large, emarginate, very coarsely faceted, 1.9 times as long as wide. Antennal club subcircular, rather strongly flattened, sutures 1 and 2 rather strongly procurved, 2 reaching slightly beyond middle; one strongly procurved suture near apex on posterior surface.

Pronotum 1.4 times as long as wide; sides feebly arcuate and subparallel on posterior two-thirds, narrowly produced on anterior third to

two very coarse, close serrations arming anterior margin, two pairs of small serrations lateral to major ones; summit indefinite, about one-third length from anterior margin; anterior third moderately asperate; posterior areas smooth, shining, minutely, rather sparsely punctured; lateral margins abrupt. Vestiture of sparse, fine hair, slightly coarser and longer on asperate area.

Elytra 2.1 times as long as wide, 1.5 times as long as pronotum; sides almost straight and parallel on basal three-fourths, slightly narrowed, then truncate on median two-thirds; discal striae not impressed, punctures very small, distinct; interstriae smooth, shining, about four times as wide as striae, punctures almost uniseriate, minute. Declivity occupying posterior 46 percent of elytral length, gradual basal margin abruptly impressed and irregularly, finely serrate from interstriae I to posterolateral apical angle; surface reticulate; sutural interstriae not elevated or armed; interstriae 3 posterior to middle broadly elevated and slightly higher than suture, descending to moderate impression just mesad of serrate lateral margin; armed just before apex of interstriae 3 by a pair of very large, subcylindrical spines, each four times as high as wide, equal in length to discal distance from suture to striae 4. Vestiture of fine, moderately long hair on disc and sides, very much longer and slightly more abundant on declivity.

TYPE LOCALITY.—Madden Forest, Canal Zone, Panama.

TYPE MATERIAL.—The female holotype and one female paratype were taken at the type locality on 2-I-64, 70 m elevation, No. 367, from a tree limb, by S. L. Wood.

The holotype and paratype are in my collection.

Sampsonius usurpatus, n. sp.

This species is distinguished from the closely allied *dampfi* Schedl by the larger size, by the longer elytral declivity, by the declivital suture being lower than the lateral convexities, and by the much smaller, contiguous spines near the sutural apex on the elytral declivity.

FEMALE.—Length 4.1 mm (paratypes: females 4.0-4.4 mm; males 2.8-3.3 mm), 3.8 times as long as wide; color reddish brown.

Frons as in *detractus* Wood except slightly narrower. Pronotum as in *detractus*.

Elytra 2.2 times as long as wide; outline as in *detractus* except tapered posteriorly, subtrun-

cate on less than median half; disc and general contour of declivity as in *detractus* except basal margin gradual, denticles smaller, more scattered; apex of interstriae 3 entirely unarmed; sutural interstriae armed by contiguous, subapical, pointed processes about as high as their longitudinal base, height about equal to width of discal interstriae, positioned as in *dampfi* but much smaller. Vestiture as in *detractus*.

MALE.—Dwarfed, head concealed by prolongation of pronotum; pronotum longer than elytra, 1.7 times as long as wide, its anterior three-fifths broadly, rather deeply concave, anterior margin narrowly biemarginate giving appearance of a median and two lateral dentations; elytra similar to female but characters poorly formed, more convex, devoid of subapical spine.

TYPE LOCALITY.—Turrialba, Cartago, Costa Rica.

TYPE MATERIAL.—The female holotype, male allotype, and 23 paratypes were collected at the type locality on 9-III-64, at 700 m elevation, No. 460B, from a cut tree seedling, by S. L. Wood. Other paratypes were taken in Costa Rica as follows: two from San Ignacio de Acosta, 5-VII-63, 1500 m, No. 38, tree seedling, S. L. Wood; three from Finca Gromaco on Rio Coto Brus, Puntarenas, 14-VII-63, 500 m, No. 76, tree seedling, S. L. Wood; one from Rincon de Osa, Puntarenas, 11-VIII-66, 30 m, No. 68, tree branch, S. L. Wood. One paratype is from El Hato del Volcan, Chiriqui, Panama, 11-I-64, 2800 m, No. 374, tree branch, S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Xyleborus (Theoborus) pristis, n. sp.

The antennal club of this species clearly is as in *theobromae* Hopkins, but the relationship is not close. It differs from *theobromae* by the more slender form, by the less strongly serrate anterior margin of the pronotum, by the more broadly convex elytral declivity, and by the different sculpture of the elytral declivity.

FEMALE.—Length 1.8 mm (female paratypes 1.7-2.0 mm), 2.6 times as long as wide; color very dark brown.

Frons broadly convex, a weak, narrow, transverse impression just above epistoma; surface strongly reticulate, punctures sparse, obscure, coarse; vestiture of sparse, fine, inconspicuous, long hair.

Pronotum 1.04 times as long as wide; essentially as in *theobromae* except surface more

strongly reticulate, including in anterior area between asperities, and anterior margin weakly serrate. Vestiture of fine, rather short hair on sides and asperate area, disc almost glabrous.

Elytra 1.3 times as long as wide; sides almost straight and parallel on basal three-fourths, rather narrowly rounded behind, serrate near weakly, narrowly emarginate suture; striae not impressed, punctures minute, shallow, distinct, spaced within a row by three to four diameters of a puncture; interstriae smooth, shining, about eight times as wide as striae, punctures uniseriate, almost indistinguishable from those of striae. Declivity confined to posterior fourth, steep, broadly convex; striae 1 weakly, others feebly impressed, punctures slightly larger, deeper and much closer than on disc; interstriae with punctures closer and uniseriately granulate, granules often obsolete near apex; suture narrowly emarginate, margin with a row of two to four coarse cusps near suture, this row continued along margin as four to eight somewhat smaller granules, margin rather narrowly rounded to interstriae 8. Vestiture confined to sides and declivity; on declivity consisting of rows of fine hair; strial hair short; interstitial hair two to two and one-half times as long as distance between rows.

MALE.—Length 1.5-1.8 mm; essentially as in female, but with characters more poorly formed, and pronotum 1.4 times as long as wide and essentially as in male *theobromae*.

TYPE LOCALITY.—Tapanti, Cartago, Costa Rica.

TYPE MATERIAL.—The female holotype and three female paratypes were taken at the type locality on 2-VII-63, 1300 m, No. 9, from *Miconia*, by S. L. Wood; three paratypes are from the same locality, 17-IX-63, No. 184, from *Miconia caudata* 10 cm in diameter. Four female paratypes were taken at Volcan, Puntarenas, Costa Rica, 11-XII-63, 1000 m, No. 305 in "luarumo" and No. 308 in a tree limb, by S. L. Wood; six additional paratypes bear this same data except they are No. 308, from a tree limb. The male allotype and 44 paratypes were taken 6 km S San Vito, Puntarenas, Costa Rica, 13-21-III-67, from a dead, standing tree.

The holotype, allotype, and paratypes are in my collection.

Xyleborus (Theoborus) micarius, n. sp.

This species is closely related to *pristis* Wood, but it is distinguished by the slightly larger, more closely spaced strial punctures, by

the more gradual, more broadly arched elytral declivity, by the smaller cusps near the suture on the ventrolateral margin of the declivity, and by the very stout, short, declivital setae.

FEMALE.—Length 1.8 mm (female paratypes 1.8-2.0 mm), 2.7 times as long as wide; color very dark brown.

Frons and pronotum as in *pristis* except pronotum outline somewhat more subquadrate and 1.1 times as long as wide.

Elytra 1.5 times as long as wide; outline essentially as in *pristis*, disc as in *pristis* except strial punctures slightly larger, spaced within a row by two to three times diameter of a puncture; interstriae about five to six times as wide as striae, punctures uniseriate, distinctly smaller than those of striae. Declivity occupying 50 percent of strial length, more gradual and more broadly convex than in *pristis*; sculpture as in *pristis* except posterolateral margin subacute, its summit rather weakly crenulate from weak sutural emargination to interstriae 7. Vestiture of rows of strial and interstitial setae, finer and shorter on disc; declivital strial hair very fine and short, interstitial setae coarse, blunt, each about one to one and one-half times as long as distance between rows.

TYPE LOCALITY.—Guapiles, Limon, Costa Rica.

TYPE MATERIAL.—The female holotype and seven female paratypes were taken at the type locality on 22-VII-66, 100 m elevation, No. 120, from a branch of *Cordia* sp. 5 cm in diameter, by S. L. Wood; three female paratypes bear the same data except No. 117 from a palm log. One female paratype was taken at Tapanti, Cartago, Costa Rica, 17-IX-63, 1300 m elevation, No. 182, from a tree branch, by S. L. Wood.

The holotype and paratypes are in my collection.

Xyleborus bicornutus, n. sp.

This species is very closely related to *ebenus* Wood, but it is distinguished by the larger average size, by the more strongly impressed upper half of the declivity, by the different arrangement of minor elytral denticles, and by the larger, longer major declivital spine.

FEMALE.—Length 3.8 mm (paratypes 3.6-4.0 mm), 2.0 times as long as wide; color dark brown to black.

Frons and pronotum as in *ebenus*. Elytra as in *ebenus* except upper third of declivity more strongly impressed; denticles on interstriae 3 at base of declivity larger, 2-6 in number (2 in

ebenus), extending posterior to level of spine of interstriae 2; major spine slightly larger, its basal area less extensive; punctures on declivital face more sharply defined, slightly larger, entire surface smooth, shining (some impressed points at base and extreme lateral areas in *ebenus*).

MALE.—Similar to male *ebenus* except lateral margin of declivity armed by four spines of almost equal size on left side, six spines (abnormal?) on right side.

TYPE LOCALITY.—Seventeen km SE Miri, Barinas, Venezuela.

TYPE MATERIAL.—The female holotype and three female paratypes were taken at the type locality on 17-XII-69, 150 m elevation, No. 195, in *Protium* sp., by S. L. Wood; the male allotype, one male and 23 female paratypes are from 30 km N Cañon Zancudo, Zulia, Venezuela, 4-IV-70, 10 m, No. 515, from a tree sapling, by S. L. Wood. Other paratypes were taken in Venezuela as follows: 7 from 40 km E Canton, Barinas, 8-III-70, 70 m, tree seedlings; 13 from 40 km SE and 7 km NW of Socopo, Barinas, 25-I-70, 13-II-70, from *Inga*, *Hirtella triandra*, *Rhceidia madruno*, *Nectandra* sp., and *Protium*; 3 from 20 km SW El Vigia, Merida, 21-XI-69, 12-VI-70, 10-XII-69, from various hosts; and 1 from Rancho Grande, Aragua, 9-IV-70, 1100 m, tree sapling. Three paratypes are from Campo Capote, 27 km NE Montoya, Santander, Colombia, 2-VII-70, 150 m, tree sapling. One paratype is from 30 km E Palmar, Bolivar, 12-VI-70, 200 m, *Brownia* sp. All were taken by me.

The holotype, allotype, and paratypes are in my collection.

Xyleborus crintulus, n. sp.

Although not closely related, this species is distinguished from the allied *micarius* Wood by the larger size, by the more closely, more deeply punctured pronotal disc, by the confused discal interstitial punctures, and by the steeper elytral declivity that has different sculpture.

FEMALE.—Length 2.2 mm (paratypes 1.9-2.3 mm), 2.3 times as long as wide; color rather dark reddish brown.

Frons as in *micarius* except with moderately numerous, small, rounded granules. Pronotum as in *micarius* except serrations on anterior margin larger and punctures on disc more numerous and deeper.

Elytra 1.3 times as long as wide, 1.2 times as long as pronotum; striae not impressed, punc-

tures small, rather shallow, spaced within a row by one or two times diameter of a puncture; interstriae four to five times as wide as striae, shining, with irregular lines, punctures fine, moderately deep, confused on basal two-thirds, uniseriate toward declivity. Declivity steep, broadly convex, occupying 42 percent of elytral length; striae punctures almost twice as large as on disc; interstriae uniseriately tuberculate, tubercles rather widely spaced, pointed, moderately fine except rather coarse on lower half of I; suture slightly produced just before apex; subapical posterolateral margin acutely, subcrenulate elevated from suture to interstriae 8. Vestiture hairlike, rather abundant, of variable length, mostly rather short.

TYPE LOCALITY.—Forty km SE Socopo, Barinas, Venezuela.

TYPE MATERIAL.—The female holotype and 17 female paratypes were collected at the type locality on 25-I-70, 150 m elevation, No. 280, from a dead branch of *Hirtella triandra* 3-5 cm in diameter, by S. L. Wood. One paratype was taken at Barro Colorado Island, Canal Zone, Panama, 27-XII-63, 70 m, No. 345, from a tree branch, by S. L. Wood; and two paratypes are labeled Fort Clayton, Canal Zone, Panama, 22-XII-63, 30 m, No. 317, tree branch, S. L. Wood.

The holotype and paratypes are in my collection.

Xyleborus pandulus, n. sp.

This rather common species has been incorrectly identified by Schedl and others as *varians* (Fabricius). It differs from *varians* by the smaller average size, by the steeper elytral declivity, by the flatter lower half of the declivity with its ventrolateral margin subacutely elevated and its face irregular and closely, coarsely punctured.

FEMALE.—Length 2.7 mm (paratypes 2.7-3.0 mm), 2.0 times as long as wide; color dark brown, almost black.

Frons and pronotum as in *perebae* (Ferrari) except each minute puncture on pronotal disc with a minute, smooth, shining spot on its posterior margin.

Elytral 1.0 times as long as wide, 1.06 times as long as pronotum; disc limited to basal half; disc as in *perebae* except striae punctures slightly smaller. Declivity abruptly impressed at base, steep, rather broadly, deeply excavated on upper half; lower half more broadly flattened and with its abrupt lateral margin weakly elevated; basal margin abrupt, armed by about 4-8 small, pointed denticles scattered from inter-

striae 1-3; margin at interstriae 3 bearing large, stout, pointed conical spine one-fourth declivital length from basal margin, a large setiferous pore just below its apex; interstriae 4 with four to six small, pointed denticles on and just before declivital margin, 5 with similar denticles extending along margin to or near sutural apex; declivital face closely, deeply, rather coarsely punctured, surface subshining, somewhat irregular. Vestiture limited to stout, scalelike bristles on margin and sides of declivity.

TYPE LOCALITY.—Fort Clayton, Canal Zone, Panama.

TYPE MATERIAL.—The female holotype and nine female paratypes were taken at the type locality on 22-XII-63, 30 m elevation, No. 320, from a broken tree limb, by S. L. Wood. Other female paratypes were taken as follows: 3 at Madden Forest, Canal Zone, Panama, 2-I-64, 70 m, Nos. 364, 367, tree limb, S. L. Wood; 1 at Limon Bay, Canal Zone, 30-XII-63, 5 m, No. 354, tree branch, S. L. Wood; 2 at Dominical, Puntarenas, Costa Rica, 9-XII-63, 3 m, No. 301, tree branch, S. L. Wood; 3 at Boston, Limon, Costa Rica, IX-64, *Theobroma cacao*, J. L. Saunders; and 1 at Finca La Lola, Limon, Costa Rica, VIII-63, *Theobroma cacao*, J. L. Saunders.

The holotype, allotype, and paratypes are in my collection.

Xyleborus varulus, n. sp.

This species is almost identical to *pandulus* Wood, but it may be distinguished by the densely placed minute, impressed points on the elytral declivity on the surfaces between the usual punctures, by the larger average size, by the slightly smaller declivital denticles (the major spine is usually more slender), and by the shorter scales on the margins and sides of the elytral declivity.

FEMALE.—Length 3.2 mm, 2.1 times as long as wide; exactly as in *pandulus* Wood except as noted in the above diagnosis.

TYPE LOCALITY.—Thirteen km SW El Vigia, Merida, Venezuela.

TYPE MATERIAL.—The female holotype and five female paratypes were taken at the type locality on 22-X-69, 100 m elevation, No. 76, from *Inga* branches, by S. L. Wood. Other female paratypes were taken as follows: 4 at 20 km SW El Vigia, 10-XII-69, 50 m, various hosts, S. L. Wood; and 1 at 8 km S Colonia (near Buenaventura), Valle de Cauca, Colombia, 9-VII-70, 30 m, No. 636, *Protium nervosum*, S. L.

Wood; 2 at 27 km NE Montoya (Campo Capote), Santander, Colombia, 2-VII-70, 150 m, No. 583, tree sapling, S. L. Wood.

It is entirely possible that this form represents only a subspecies of *pandulus*; insufficient material is available to make an evaluation at this time.

The holotype, allotype, and paratypes are in my collection.

Xyleborus sharpi lenis, subsp. n.

This subspecies is distinguished from *s. sharpi* Blandford by the absence of the abundant, minute, impressed points on the elytral declivity, and by the more northern distribution.

FEMALE.—Length 3.5 mm, 2.0 times as long as wide; color dark brown. Essentially as in *s. sharpi* except declivital surface almost smooth, punctures very fine, impressed points essentially absent. Entire declivity in *s. sharpi* densely covered by minute impressed points.

TYPE LOCALITY.—Twenty-nine km or 18 miles E Coatzacoaleos, Veracruz, Mexico.

TYPE MATERIAL.—The female holotype was taken at the type locality on 26-VI-67, 30 m, No. 104, from a tree limb, by S. L. Wood.

The holotype is in my collection.

Xyleborus palatus, n. sp.

This species is remotely allied to *squamulatus* Eichhoff, but is distinguished by the slightly stouter body form, by the much steeper, flat elytral declivity, and by the arrangement of declivital tubercles.

FEMALE.—Length 1.9 mm (paratypes 1.8-2.1 mm), 2.3 times as long as wide; color very dark brown to black.

Frons broadly concave, a slight, transverse impression above epistoma; surface strongly reticulate, punctures small, shallow, sparse.

Pronotum 1.1 times as long as wide; sides feebly arcuate, almost parallel on basal two-thirds, rather broadly rounded in front; anterior margin armed by six to ten serrations, median one or two pairs distinctly larger; summit at middle; anterior area rather coarsely asperate; posterior areas mostly reticulate with some shining areas, punctures rather small, shallow, moderately close. Vestiture of moderately abundant, fine, short hair.

Elytra 1.4 times as long as wide, 1.3 times as long as pronotum; sides almost straight and parallel on slightly more than basal two-thirds,

rather narrowly rounded behind; disc occupying basal 60 percent of elytral length; striae not impressed, punctures rather small, moderately deep, spaced within a row by one to two diameters of a puncture; interstriae almost smooth, shining, about three to four times as wide as striae, punctures very fine, slightly confused on basal two-thirds of disc, uniseriate toward declivity. Declivity rather steep, flat on median half from rounded base to near apex; surface shagreened, striae as on disc, apices of 2 and 3 converge toward suture; interstriae 1-3 flat; all interstriae with rows of small, pointed granules, those near base on all interstriae larger, those on 1 and 2 on face of declivity and on lower half of 5, 7, and 8 minute, others slightly larger; posterolateral margin rounded, marked by a row of small tubercles from apex to interstriae 9. Vestiture of minute strial hair on and near declivity, and interstitial bristles each as long as distance between rows on and near declivity, confused on anterior areas of disc.

TYPE LOCALITY.—Twenty-four km (15 mi) W Armeria, Colima, Mexico.

TYPE MATERIAL.—The female holotype and one female paratype were taken at the type locality on 30-VI-65, 30 m, No. 147, in flight, by S. L. Wood; 13 female paratypes bear identical data to the type except Nos. 153, 154, from an unidentified broken tree branch. Other female paratypes were taken in Mexico as follows: one from 53 km (33 mi) S Colima, Colima, 27-VI-65, 700 m, Nos. 125, 127, in flight; one from 6 km (4 mi) S Cihuatlan, 30-VI-65, 70 m, No. 157, from a liana; one from Volcan Colima, Jalisco, 23-VI-65, 2500 m, No. 124, from a shrub limb; four from Laguna Santa Maria, 6-VII-65, 1000 m, No. 193, from a liana; and one from 8 km (5 mi) E San Blas, Nayarit, 12-VII-65, 70 m, No. 232, from a leguminose tree; all were taken by me.

The holotype and paratypes are in my collection.

Xyleborus exutus, n. sp.

This species is distinguished from the allied *tolimannus* Eggers by the complete absence of denticles on the elytral declivity.

FEMALE.—Length 1.9 mm, 3.0 times as long as wide; color reddish brown, pronotum more yellowish brown.

Frons about as in *catulus* Blandford but surface finely granulate to well above eyes. Pronotum 1.2 times as long as wide; basically as in *catulus* except anterior margin rather narrowly rounded and more coarsely serrate.

Elytra 1.9 times as long as wide, 1.6 times as long as pronotum; sides almost straight and parallel on basal half, acutely converging to one-fifth greatest elytral width at narrowly, shallowly emarginate apex; striae not impressed, punctures small, shallow, distinct, spaced within a row by twice diameter of a puncture; interstriae smooth, shining, three to four times as wide as striae, punctures fine, uniseriate, rather widely spaced. Declivity gradual, narrowly convex; striae feebly impressed, punctures slightly larger than on disc; all interstriae equally sculptured, punctures distinct, regularly, rather closely spaced, anterior margin of each rather broadly, weakly granulate; interstriae 1 weakly elevated near acuminate apex; posterolateral margin weakly elevated and rather narrowly rounded near apex, becoming more broadly rounded anteriorly, entirely devoid of granules and denticles. Vestiture entirely abraded except for a few hairlike setae on sides.

TYPE LOCALITY.—Turrialba, Cartago, Costa Rica.

TYPE MATERIAL.—The unique female holotype was taken at the type locality on 9-III-64, 700 m elevation, No. 468, from a new fence post, by S. L. Wood.

The holotype is in my collection.

Xyleborus rusticus, n. sp.

This species is distinguished from *rubricollis* Eichhoff by the larger size, by the proportionately smaller punctures on the declivital striae, and by the uniformly convex elytral striae.

FEMALE.—Length 3.3 mm (paratype 3.5 mm), 2.3 times as long as wide; color dark brown.

Frons broadly, irregularly convex; surface reticulate, shining, punctures rather coarse, close, moderately deep above, obscure below; vestiture sparse, inconspicuous.

Pronotum 0.98 times as long as wide; sub-circular, all margins about equally arcuate, widest slightly behind middle; summit distinctly behind middle, entire surface closely, rather coarsely asperate to base, slightly finer on posterior third; surface between asperities reticulate, dull. Vestiture of fine, rather long, moderately abundant hair.

Elytra 1.5 times as long as wide, 1.6 times as long as pronotum; sides straight on basal two-thirds, slightly wider at base of declivity, broadly rounded behind; disc occupying basal two-thirds; striae 1 feebly, others not impressed, punctures rather small, moderately

deep, spaced within row by one to two diameters of a puncture; interstriae about four times as wide as striae, almost smooth, shining, punctures small, moderately confused, their anterior margins finely granulate. Declivity steep, evenly, broadly convex; striae punctures slightly wider than on disc; interstriae three times as wide as striae, granules on all interstriae distinctly larger, pointed. Vestiture of short striae hair and fine, long, abundant hair; interstitial setae in almost uniseriate rows on declivital interstriae 1 and 2, confused elsewhere.

TYPE LOCALITY.—Ten km NE Teziutlan, Puebla, Mexico.

TYPE MATERIAL.—The female holotype was taken at the type locality on 2-VII-67, 1600 m, No. 150, from an unidentified log by S. L. Wood. One female paratype is from the same locality and collector, taken 27-VI-53, No. 49.

The holotype and paratype are in my collection.

Xyleborus ocellatus, n. sp.

This species is distinguished from *rusticus* Wood by the coarser striae punctures, by the more deeply impressed declivital striae, by the striae punctures on the declivity, each with a granule occupying its central half thereby giving the superficial appearance of an eye, and by the larger interstitial granules on the declivity.

FEMALE.—Length 3.5 mm (paratypes 3.3-3.5 mm), 2.3 times as long as wide, color black.

Frons and pronotum as in *rusticus* except asperities on basal half of pronotum distinctly larger.

Elytra 1.4 times as long as wide, 1.5 times as long as pronotum; outline as in *rusticus*; striae 1 feebly, others not impressed, punctures moderately coarse, rather shallow; interstriae three times as wide as striae, almost smooth, punctures rather fine, finely granulate on their anterior margins, confused on 2 and 3. Declivity convex, steep; striae 1 distinctly, 2 feebly impressed, punctures slightly larger than on disc, each puncture with its central half occupied by a rounded granule; interstriae feebly convex, each armed by a uniseriate row of moderately coarse, pointed tubercles, 7 subacutely elevated and tuberculate. Vestiture as in *rusticus*.

TYPE LOCALITY.—Piedras Blancas, 10 km E Medellin, Antioquia, Colombia.

TYPE MATERIAL.—The female holotype and two female paratypes were taken at the type

locality on 15-VII-70, 2500 m, No. 675, from an unidentified log, by S. L. Wood. Two other female paratypes bear identical data except one is from No. 684 in *Clusia*, and one is No. 677 taken in flight.

The holotype and paratypes are in my collection.

Xyleborus opimus, n. sp.

This species is distinguished from *lecontei* (Hopkins) by the slightly smaller size, by the more strongly rounded anterior and lateral margins of the pronotum, by the finer, less numerous asperities on the pronotal disc, by the convex elytral declivity, and by the different arrangement of declivital tubercles.

FEMALE.—Length 2.4 mm, 2.2 times as long as wide; color reddish brown.

Frons as in *lecontei*. Pronotum 1.0 times as long as wide, as in *lecontei* except anterior and lateral margins more strongly arcuate, summit slightly higher, and asperities behind summit slightly smaller and evidently less numerous.

Elytra 1.36 times as long as wide; outline and disc as in *lecontei* except striae punctures not larger near disc, interstitial punctures near declivity granulate. Declivity rather broadly, evenly convex, steep; striae punctures as large as on disc, deep, smaller than in *lecontei*; interstriae 1 bearing a row of granules on basal half, those near base rather coarse, 2 with several pointed tubercles on basal half, one or two at or slightly below middle distinctly larger, 3 with three to five smaller tubercles; all tubercles smaller than major tubercles of *lecontei*. Vestiture as in *lecontei*.

TYPE LOCALITY.—Sebring, Florida.

TYPE MATERIAL.—The female holotype was taken at the type locality on 20-VI-51, at light, by S. L. Wood.

The holotype is in my collection.

Xyleborus lacunatus, n. sp.

This species is distinguished from *commixtus* Blandford by details in sculpture of the elytral declivity as indicated in the description.

FEMALE.—Length 4.9 mm, 2.5 times as long as wide; color dark brown.

Frons, pronotum, and elytral disc as in *commixtus*. Elytral declivity essentially as in *commixtus* except rather strongly, transversely impressed on lower third; suture distinctly concave on lower two-thirds; striae punctures larger; interstriae about twice as wide as striae; postero-

lateral margin much more strongly, acutely elevated than in *commixtus*, rather strongly concave from its crest to suture on lower third of declivity. Vestiture as in *commixtus*.

TYPE LOCALITY.—Turrialba, Cartago, Costa Rica.

TYPE MATERIAL.—The female holotype was taken at the type locality on 18-IV-63, from *Theobroma cacao*, by J. L. Saunders. One female paratype is from Peralta, Cartago, Costa Rica, 10-III-64, flight, S. L. Wood.

The holotype and paratype are in my collection.

Xyleborus meridensis, n. sp.

This species is distinguished from *caribicus* Eggers by the slightly larger size, by the larger, less deeply impressed punctures on the striae, by the more gradual declivity with the lower median half almost flat, and by the rounded posterolateral margin of the declivity.

FEMALE.—Length 4.1 mm (paratypes 3.7-4.3 mm), 2.7 times as long as wide; color dark brown.

Frons and pronotum as in *caribicus* except posterior areas of pronotum more distinctly reticulate.

Elytra 1.7 times as long as wide, 1.7 times as long as pronotum; sides almost straight and parallel on slightly less than basal two-thirds, slightly tapered then rather narrowly rounded behind; striae not impressed, punctures moderately coarse, shallow; interstriae twice as wide as striae, smooth, punctures fine, uniseriate. Declivity moderately steep, rather narrow, feebly impressed on median area particularly on central half; suture on lower two-thirds straight; striae not impressed, punctures on middle half larger than on disc, interstriae one and one-half times as wide as striae; interstriae smooth, shining, each armed by about five small, pointed tubercles; posterolateral margin rather narrowly rounded (not carinate), armed by a series of rather widely spaced, small, pointed granules.

MALE.—Length 3.4 mm; head and elytra essentially as in female. Pronotum 1.2 times as long as wide, 0.86 times as long as elytra; quadrate, anterior third broadly, concavely excavated, anterolateral margins abruptly angulate, acutely elevated; anterior margin acutely elevated, slightly produced into an obtuse, median point; subglabrous.

TYPE LOCALITY.—La Carbonera experimental forest, about 50 km (airline) NE Merida, Merida, Venezuela.

TYPE MATERIAL.—The female holotype, male allotype, and four paratypes were taken at the type locality on 23-IV-70, 2500 m, Nos. 450, 451, from an unidentified log by S. L. Wood. Other paratypes were taken at the same locality as follows: 5 on 16-IX-69, No. 21 in *Prunus sphaerocarpa*; 1 on 16-IX-69, No. 20 on *Ficus*; 1 on 14-X-69, No. 66; 2 on 27-X-69, No. 92; 6 on 9-XII-69, No. 171; 8 on 28-IV-70, Nos. 450, 451, and 457, from unidentified logs; all by S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Xyleborus actinis, n. sp.

This species is distinguished from *meridensis* Wood by the much smaller size, by the more strongly convex declivity, and by the presence of only one tubercle on declivital interstriae 2.

FEMALE.—Length 3.1-3.3 mm, 2.9 times as long as wide; color dark brown.

Frons and pronotum as in *meridensis* except pronotum 1.14 times as long as wide.

Elytra 1.8 times as long as wide, 1.6 times as long as pronotum; outline and disc as in *meridensis* except interstitial punctures more widely spaced. Declivity moderately steep, convex; longitudinal axis of suture feebly convex on lower half; striae not impressed, punctures little if any larger than on disc; interstriae smooth, shining, 1 and 3 each armed by about three to six pointed granules of variable size, 2 armed by one moderately coarse denticle one-third declivital length from apex, a few small granules in lateral areas; posterolateral margin as in *meridensis*, narrowly rounded, its crest armed by several small, isolated granules. Vestiture confined to declivity, sparse, one short bristle arising from posterior basal margin of each granule, each about half as long as width of an interstriae.

TYPE LOCALITY.—Cerro Punta near Volcan de Chiriqui (Baru), Chiriqui, Panama.

TYPE MATERIAL.—The female holotype and three female paratypes were taken at the type locality on 11-I-64, 1800 m, No. 386, from a stump 15 cm in diameter, by S. L. Wood.

The holotype and paratypes are in my collection.

Xyleborus dissimulatus, n. sp.

This species is distinguished from *meridensis* Wood by the much smaller size, by the smaller striae punctures, by the much smaller granules on declivital interstriae 2, and by the more subangulate, subserrate posterolateral margin of

the declivity. It is distinguished, with difficulty, from *posticus* Eichhoff by the shining, more gradual declivity, and by the shorter, sparse declivital bristles.

FEMALE.—Length 2.2 mm (paratypes 2.2-2.3 mm), 2.6 times as long as wide; color brown.

Frons, pronotum, and elytral disc as in *posticus*.

Elytra 1.6 times as long as wide, 1.6 times as long as pronotum; disc occupying basal 60 percent of elytral length. Declivity moderately steep, rather broadly convex; striae punctures much larger than on disc, very shallow; interstriae smooth, shining, as wide as striae, each with a sparse row of minute granules, 1 and 3 each with about two distinctly larger granules; posterolateral margin subacute, more continuously subserrate than in *posticus*. Vestiture largely confined to declivity, of very short, stout and fine, interstitial bristles, each bristle about one-third as long as distance between rows.

TYPE LOCALITY.—Tapanti, Cartago, Costa Rica.

TYPE MATERIAL.—The female holotype and three female paratypes were taken at the type locality on 17-IX-63, No. 184, from *Miconia caudata*, by S. L. Wood. One female paratype bears identical data except No. 178 from a liana. One paratype is from the same locality and collector taken 2-VII-63, No. 9, *Miconia* sp.

The holotype and paratypes are in my collection.

Xyleborus concentus, n. sp.

This species is distinguished from *parallelocollis* Eggers by the more narrowly convex declivity on the transverse axis, by the serrate posterolateral margin of the declivity, and by the shorter interstitial bristles on the declivity.

FEMALE.—Length 2.5 mm (paratypes 2.5-2.7 mm), 2.7 times as long as wide; color dark brown.

Frons and pronotum as in *caribicus* Eggers except pronotum 1.15 times as long as wide.

Elytra 1.7 times as long as wide, 1.6 times as long as pronotum; sides almost straight and parallel on slightly less than basal two-thirds, tapered, then narrowly rounded behind; striae not impressed, punctures rather small, distinctly impressed; interstriae twice as wide as striae, punctures very fine, uniseriate. Declivity gradual, transversely convex, suture very feebly convex on lower half; surface rather dull in most specimens; striae not impressed, punctures larger than on disc; interstriae flat, slightly wider than

striae, granules small, of uniform size, spaced by distances less than width of an interstriae; posterolateral margin abrupt, subacute, finely serrate. Vestiture largely confined to declivity, consisting of short, stout, interstitial bristles, each bristle equal in length to one-third width of an interstriae; a few similar, much longer bristles on disc.

TYPE LOCALITY.—Tapanti, Cartago, Costa Rica.

TYPE MATERIAL.—The female holotype and two female paratypes were taken at the type locality on 26-XI-63, 1300 m, No. 265, from *Phoebe mexicana*, by S. L. Wood. Other female paratypes were taken as follows: 1 at Rincon de Osa, Puntarenas, Costa Rica, 11-VIII-66, 30 m, No. 90, liana; 1 at Volcan, Puntarenas, Costa Rica, 11-XII-63, 1000 m, No. 308, tree limb; 1 at Guapiles, Limon, Costa Rica, 22-VII-66, 100 m, No. 101, tree limb; and 6 at 30 km E Palmar, Bolivar, Venezuela, 12-VI-70, 200 m, No. 556, *Alexa imperatricis*; all by S. L. Wood.

The holotype and paratypes are in my collection.

Xyleborus tribulatus, n. sp.

This species is distinguished from *semipunctatus* Eggers except as noted in the following description.

FEMALE.—Length 3.8 mm, 2.4 times as long as wide; color very dark brown.

Frons and pronotum as in *semipunctatus* except punctures on posterior half of pronotum distinctly larger, closer.

Elytra as in *semipunctatus* except discal striae 2 distinctly sinuate; interstriae 2 and 3 on disc distinctly confused; striae punctures on disc and declivity distinctly larger, interstriae on disc three times as wide as striae (four times as wide in *semipunctatus*). Declivity as in *semipunctatus* except as noted.

TYPE LOCALITY.—Rio Damitas in the Dota Mountains, San José, Costa Rica.

TYPE MATERIAL.—The unique female holotype was taken at the type locality on 22-VIII-63, 250 m, No. 126, from a liana 10 cm in diameter, by S. L. Wood.

The holotype is in my collection.

Xyleborus vismiae, n. sp.

This species is distinguished from *costaricensis* Blandford by the shorter, steeper declivity which is strongly, transversely impressed on the lower half, by the smooth, shining declivital surface, and by the larger declivital granules. The

costaricensis group of species is characterized by the slightly protuberant, smooth, peculiarly reticulate frons that is devoid of punctures, by the tapered posterior half of the elytra, and by the long, rather narrow declivity.

FEMALE.—Length 3.5 mm (paratypes 3.3-3.7 mm), 2.6 times as long as wide; color dark brown.

Frons shallowly, transversely impressed between eyes, weakly inflated below; surface smooth with very fine reticulation below, more coarsely reticulate toward vertex, punctures rather small, sparse, mostly confined to lateral areas, none on lower third; vestiture very sparse, hairlike, inconspicuous.

Pronotum 1.13 times as long as wide; sides almost straight and parallel on basal half, rather narrowly rounded in front; summit at middle; anterior half rather finely asperate; posterior areas very finely subreticulate; punctures minute, distinct, rather sparse.

Elytra 1.8 times as long as wide, 1.6 times as long as pronotum; sides almost straight and parallel on basal half, then rather strongly tapered, rather narrowly rounded behind; striae not impressed, punctures small, distinct, spaced within a row by one to two diameters; interstriae smooth, moderately shining punctures very minute, distinct, uniseriate. Declivity occupying slightly more than posterior third, strongly, transversely impressed on lower half; transversely flat; longitudinally concave; striae curved toward suture near apex, punctures almost twice as large as on disc; interstriae shining, armed by rows of small granules, alternate granules slightly larger; posterolateral margin narrowly rounded, its crest with a few feeble granules.

TYPE LOCALITY.—Rio Damitas in the Dota Mountains, San José, Costa Rica.

TYPE MATERIAL.—The female holotype and three female paratypes were taken at the type locality on 22-VIII-63, 250 m, No. 126, from *Vismia guayanensis*, by S. L. Wood. Eight female paratypes are from Rancho Grande, Pittier National Park, Aragua, Venezuela, 9-IV-70, 1100 m, No. 433, from a species of Guttiferae near but probably not *Vismia*, by S. L. Wood, except one of these is No. 441 from an unidentified tree limb.

The holotype and paratypes are in my collection.

Xyleborus demissus, n. sp.

This species is distinguished from *deplanatus* Eggers by the more slender body form, by the shorter declivity, by the two sizes of interstitial

tubercles on the declivity, and by the less strongly serrate posterolateral margin of the declivity.

FEMALE.—Length 2.0 mm, 2.9 times as long as wide; color dark brown.

Frons and pronotum as in *deplanatus* except pronotum 1.21 times as long as wide.

Elytra 1.7 times as long as wide, 1.5 times as long as pronotum; sides straight and parallel on basal half, then slightly tapered, narrowly rounded behind, weakly emarginate at suture; disc occupying slightly more than basal half; striae not impressed, punctures small, shallow, distinct; interstriae smooth, shining, three times as wide as striae, punctures uniseriate, slightly smaller than those of striae, their anterior margins feebly granulate at base, becoming more distinctly granulate posteriorly. Declivity rather gradual, moderately convex on both axes; striae not impressed, punctures slightly larger than on disc, lateral margins of punctures on 2 and 3 weakly granulate; interstriae shining, about twice as wide as striae, each armed by a row of granules, granules mostly small except on 2 and 3 distinctly larger granules alternate with small ones. Vestiture of rows of fine, short, strial hair, and interstitial rows of short, almost scalelike bristles, each bristle one-third to one-half as long as distance between rows, slightly closer within a row, each three to five times as long as wide.

TYPE LOCALITY.—Rincón de Osa, Puntarenas, Costa Rica.

TYPE MATERIAL.—The unique female holotype was taken at the type locality on 11-VIII-66, 30 m, No. 70, from a log 20 cm in diameter, by S. L. Wood.

The holotype is in my collection.

Xyleborus meritus, n. sp.

This species is distinguished from *vismiae* by the slightly larger size, by the more gradual, more nearly flattened elytral declivity, and by the much finer interstitial granules on the declivity.

FEMALE.—Length 3.0 mm (paratypes 2.8-3.4 mm), 2.8 times as long as wide; color very dark brown.

Frons, pronotum (1.15 times as long as wide), and elytral disc as in *vismiae* Wood.

Elytra 1.8 times as long as wide, 1.6 times as long as pronotum; outline as in *vismiae*. Declivity occupying slightly less than posterior half of elytral length, its lower half very shallowly concave; striae not impressed, curving toward suture near apex, punctures almost twice as

large as on disc; interstriae smooth, shining, with widely spaced fine granules, those on lower half of 2 and 3 smaller, sometimes almost obsolete. Vestiture sparse, of fine hair, length on declivity equal to about half width of an interstriae.

TYPE LOCALITY.—Tapanti, Cartago, Costa Rica.

TYPE MATERIAL.—The female holotype and one female paratype were taken at the type locality on 17-IX-63, 1300 m, No. 178, liana, S. L. Wood. Thirteen female paratypes were taken at the same locality (2) 2-VII-63, No. 7, liana, (1) 3-VII-63, No. 17, *Conostegia oerstediana*, (2) 17-IX-63, No. 182, *Miconia caudata*, (1) 24-X-63, No. 184, *Miconia caudata*, (6) 26-XI-63, No. 265, *Phoebe mexicana*. Ten female paratypes are from 14 km SE Cartago, Cartago, Costa Rica, 1800 m, (1) 3-VII-63, No. 17, *Conostegia oerstediana*, (8) 24-IX-63, No. 204, *Miconia globuliflora*, and (1) 24-IX-63, No. 200, *Myrica pubescens*; all by S. L. Wood.

The holotype and paratypes are in my collection.

Xyleborus prolatus, n. sp.

This species is distinguished from *costaricensis* Blandford by the larger size, by the longer, more strongly impressed declivity, and by the near absence of granules on declivital interstriae 1 and 2.

FEMALE.—Length 4.2 mm (paratypes 4.0-4.4 mm), 2.8 times as long as wide; color dark brown.

Frons and pronotum as in *costaricensis*.

Elytra 1.7 times as long as wide, 1.7 times as long as pronotum; outline about as in *costaricensis* except more strongly tapered on posterior half, more narrowly rounded behind; disc confined to basal third, as in *costaricensis*. Declivity very gradual, shallowly, broadly bisulcate; surface dull; striae punctures twice as large as on disc; interstriae almost twice as wide as striae, smooth, 1 distinctly elevated toward suture, 2 broadly, subconcavely impressed, 3 distinctly, gradually elevated toward broad summit at striae 4, 3 and 4 each with a row of widely spaced, moderately large granules, 1 and 2 sometimes with one or two smaller granules near apex (one paratype with five granules on 2 on left side). Vestiture as in *costaricensis* except almost entirely absent on declivital interstriae 1 and 2.

TYPE LOCALITY.—Tapanti, Cartago, Costa Rica.

TYPE MATERIAL.—The female holotype and eight female paratypes were taken at the type

locality on 24-X-63, 1300 m, No. 265, from a recently cut limb of *Phoebe mexicana* 10 cm in diameter, by S. L. Wood.

The holotype and paratypes are in my collection.

Xyleborus dissidens, n. sp.

This species is placed near *sparsipilosus* Eggers because of the slender pronotum and steep elytral declivity; however, it probably is more closely related to species placed in the subgenus *Euwallacea*. In addition to the slender pronotum with its procurved anterior margin, this species has the elytral declivity steep, convex, and interstriae 1-3 equally armed by pointed granules.

FEMALE.—Length 3.1 mm (paratypes 3.0-3.2 mm), 3.0 times as long as wide; color black.

Frons as in *costaricensis* Blandford but with lower area less strongly inflated.

Pronotum 1.22 times as long as wide; as in *sparsipilosus* except posterior areas subreticulate.

Elytra 1.8 times as long as wide, 1.5 times as long as pronotum; sides straight and parallel on slightly more than basal two-thirds, rather broadly rounded behind; disc occupying slightly more than basal two-thirds; striae not impressed, punctures rather small, distinct, spaced within a row by diameter of a puncture; interstriae smooth, shining, twice as wide as striae, punctures uniseriate, minute, distinct, almost obsolete. Declivity steep, rather broadly convex; striae about as on disc; interstriae 1-3 each equally armed by six to ten pointed granules of slightly irregular size; posterolateral margin obtuse, abrupt. Vestiture confined to declivity, of rows of rather coarse, interstitial setae, each seta about one and one-half times as long as distance between rows, more widely spaced within a row.

TYPE LOCALITY.—Nine km NE Tezuitlan, Puebla, Mexico.

TYPE MATERIAL.—The female holotype and three female paratypes were taken at the type locality on 2-VII-67, 1500 m, No. 141, from *Alnus* cordwood, by S. L. Wood. Two female paratypes bear identical data except one is No. 147, from an unidentified log, and one is No. 141, taken in flight.

The holotype and paratypes are in my collection.

Xyleborinus dirus, n. sp.

Superficially this species might be confused with *Xyleborus ferox* Blandford, but the conical

scutellum and emarginate elytral base show the true relationships to be very different.

FEMALE.—Length 3.5 mm (paratypes: females 3.4-3.6 mm, males 2.5-2.7 mm), 2.7 times as long as wide; mature color black.

Frons convex, epistoma slightly elevated; surface reticulate, punctures rather large, impressed, indefinite; vestiture inconspicuous.

Pronotum 1.06 times as long as wide, widest a third of its length from base; sides rather weakly arcuate on basal two-thirds, converging very slightly, then rather strongly rounded in front, median area rather narrowly produced but unarmed (in many paratypes anterior margin rather broadly rounded); summit very slightly in front of middle; posterior area reticulate, indistinctly so near base, punctures small, distinct, rather close; vestiture rather long and abundant on sides and in asperate area.

Elytra 1.6 times as long as wide, 1.5 times as long as pronotum; sides almost straight and parallel on basal half, then arcuately converging to apex of ventrolateral spine, rather broadly U-shaped between spines; striae 1 weakly, others not impressed, punctures moderately large, deep, somewhat confused on 1; interstriae mostly twice as wide as striae, punctures similar to those of striae but deeper, uniseriate except partly confused on 1 and 2. Declivity moderately steep, broadly, shallowly excavated, lateral margins armed by three pairs of major spines; spine 1 at upper margin in line with striae 2, spine 2 on lateral margin two-thirds declivital length from upper margin, spine 3 at posterolateral margin; spine 1 slightly more than half as long as 3, 2 slightly smaller than 3, 2 equal in length to width of antennal club; one minor tooth in front of spine 1, two others between 1 and 2; declivital face with confused punctures similar to those on disc. Vestiture consisting of rather long, slender hair arising from interstitial punctures on disc and sides, setae minute on excavated area.

MALE.—Length 2.5-2.7 mm; similar to female except smaller, eye reduced, pronotum not strongly arched, with asperities somewhat reduced; elytral declivity much longer, more gradual, with spine 1 greatly reduced, minor teeth mostly absent.

TYPE LOCALITY.—Rincon de Osa, Puntarenas, Costa Rica.

TYPE MATERIAL.—The female holotype, male allotype, and 34 paratypes were collected at the type locality on II-VIII-66, at about 30 m elevation, from cut limbs 10-20 cm in diameter in the primary forest. Nineteen additional para-

types were taken at Rio Damitas in the Dota Mountains, San José, Costa Rica, 22-VIII-63, 250 m, from a stump 25 cm in diameter in the primary forest; all specimens were collected by myself. The tunnels were of a branching type that included several enlarged cavities.

The holotype, allotype, and paratypes are in my collection.

Xyleborinus tribulosus, n. sp.

This species is distinguished from *dirus* Wood by the smaller size, by the more slender body form, by the smaller, uniseriate striae and interstitial punctures on disc and declivity, and by the different elytral declivity.

FEMALE.—Length 2.5 mm (paratype 2.4 mm), 2.8 times as long as wide; color very dark brown.

Frons and pronotum essentially as in *dirus* except pronotum 1.1 times as long as wide; pronotal disc glabrous.

Elytra 1.6 times as long as wide (spines excluded), 1.4 times as long as pronotum; outline essentially as in *dirus*; striae not impressed, punctures small, uniseriate, close; interstriae smooth, shining, slightly more than twice as wide as striae, punctures half as large as those of striae, uniseriate. Declivity occupying two-thirds of elytral length; broadly flattened to feebly impressed, its margin armed by about 24 rather coarse, pointed denticles on interstriae 1-6 from base to near sutural apex; interstriae 3 armed at middle and near apex by two pairs of very large spines, each spine one and one-half times as long as its basal width, about equal in length to discal distance from suture to striae 3; face of declivity with striae punctures in rows, slightly larger than on disc; interstitial punctures largely obsolete. Vestiture of rows of rather coarse interstitial setae, on disc each seta about as long as distance between rows, distinctly closer within a row, on declivity distinctly longer and less regularly placed.

TYPE LOCALITY.—Madden Forest, Canal Zone, Panama.

TYPE MATERIAL.—The female holotype and one female paratype were taken at the type locality on 2-I-64, 70 m, No. 367, from a tree limb by S. L. Wood.

The holotype and paratype are in my collection.

Xyleborinus protinus, n. sp.

This odd species is not closely related to any American species known to me.

FEMALE.—Length 1.7 mm (paratypes 1.6-1.7 mm), 2.7 times as long as wide; color rather light brown, prothorax distinctly lighter.

Frons very weakly convex from upper level of eyes to epistomal margin; surface reticulate, rather coarsely, obscurely punctured; vestiture inconspicuous.

Pronotum 1.25 times as long as wide; widest one-third pronotum length from base, sides weakly arcuate, basal and anterior angles more strongly rounded, rather narrowly rounded in front; asperities fine, largely isolated; summit indefinite, in front of middle; surface reticulate in front of summit, mostly smooth and brightly shining behind, punctures small, deep, not close; vestiture largely confined to sides and asperate area.

Elytra 1.6 times as long as wide, 1.3 times as long as pronotum; sides essentially straight and parallel on basal three-fourths, then rather abruptly rounded, shallowly emarginate on median third behind; scutellum conical; striae not impressed, punctures small, deep; interstriae twice as wide as striae, punctures small, indefinite; elytra arched from base to apex. Declivity beginning on basal third of elytra, gradual; lateral margins on lower half gradually elevated and continuing almost to apex, elevation rather high, not at all acute, evidently entirely unarmed; lower half transversely concave; striae 1 and 2 with punctures larger than on disc, strongly impressed; interstriae 2 wider than 1; interstitial punctures obscure. Vestiture consisting of stout, hairlike setae, more abundant on declivity, particularly on inner slope of lateral elevation.

TYPE LOCALITY.—Finca La Lola, Limon, Costa Rica.

TYPE MATERIAL.—The female holotype and four female paratypes were collected at the type locality on 7-II-63, from *Theobroma cacao*, by J. L. Saunders.

The holotype and paratypes are in my collection.

Xyleborinus celatus, n. sp.

This species differs from *reconditus* Schedl by the much finer punctures on the pronotal disc and by the reduction of the denticles on declivital interstriae 2.

FEMALE.—Length 1.7 mm (paratypes 1.6-1.8 mm), 2.5 times as long as wide; color dark brown, almost black.

Frons and pronotum as in *reconditus* except posterior areas of pronotum with punctures much finer, less numerous.

Elytra 1.4 times as long as wide, 1.3 times as long as pronotum; sides almost straight and parallel on basal three-fourths, then rather abruptly rounded, straight on median half behind; disc confined to basal third of elytral length; striae not impressed, punctures minute; interstriae almost smooth, subshining, at least six times as wide as striae, punctures slightly smaller than those of striae. Declivity gradual, longitudinally flat and transversely very weakly convex on its basal half, slightly steeper and broadly, shallowly sulcate on its lower half; base commencing much more abruptly than in *reconditus*; lower half of declivity with contours as in *reconditus* but striae punctures smaller and interstriae 3 armed by only two denticles, one just behind middle of declivity and one on its apical fourth; interstriae on basal half armed by rows of fine granules. Vestiture confined to declivity, consisting of minute striae hair and interstitial rows of stout bristles; each bristle as long as distance between rows.

TYPE LOCALITY.—Eight km S Colonia (near Buenaventura), Valle de Cauca, Colombia.

TYPE MATERIAL.—The female holotype and five female paratypes were taken at the type locality on 9-VII-70, 30 m, No. 646, from *Inga* sp., by S. L. Wood. Nine female paratypes bear identical data except they are No. 628 from *Icica altissima* or No. 631 from *Protium nervosum*.

The holotype and paratypes are in my collection.

Araptus insinuatus, n. sp.

This species is distinguished from the very closely related *foveifrons* Schedl by the strongly impressed declivital interstriae 2, by the longer elytral vestiture, and by the more finely, more closely punctured pronotal disc.

MALE.—Length 1.6-2.1 mm, 2.4 times as long as wide; color reddish brown.

Frons and pronotum as in *foveifrons* except punctures on pronotal disc distinctly smaller, closer. Elytra as in *foveifrons* except discal punctures averaging slightly longer, finer than in *foveifrons*.

FEMALE.—Similar to male except frons (concealed) apparently as in female *foveifrons*.

TYPE LOCALITY.—Guatemala.

TYPE MATERIAL.—The male holotype, female allotype, and two male paratypes were intercepted from Guatemalan seeds at San Pedro, California, 7-III-63. One male paratype is from

La Ceiba, Atlantida, Honduras, 17-VI-49, at light, by E. C. Becker.

The holotype, allotype, and paratypes are in my collection.

Araptus interjectus, n. sp.

This species is distinguished from *foveifrons* Schedl by the larger size, by the more elongate form, by the near absence of interstitial punctures, and by the different frons in both sexes.

MALE.—Length 2.4 mm (paratypes 2.4-2.7 mm), 2.9 times as long as wide; color rather dark reddish brown.

Frons strongly, transversely impressed from eye to eye from middle to well above upper level of eyes, its margins obtuse, its lower lateral angles armed by a pair of rather coarse tubercles and with a large, pointed, median tubercle at same level; lower third of area below upper level of eyes subaciculate; all surfaces shining; vestiture sparse except along epistomal margin. Antennal club as in *foveifrons*.

Pronotum 1.15 times as long as wide; widest behind middle, sides moderately arcuate on more than posterior half, weakly constricted on anterior third, rather broadly rounded in front; anterior margin armed by about eight irregular serrations; indefinite summit one-third of pronotum length from anterior margin; asperities fine, confused; posterior areas obscurely reticulate in some areas, numerous minute, impressed points present, punctures rather small, deep, moderately close. Glabrous except for a few setae on asperate area and lateral margins.

Elytra 1.7 times as long as wide, 1.7 times as long as pronotum; sides straight and parallel on basal two-thirds, broadly rounded behind; striae not impressed except I near declivity, punctures moderately coarse, spaced by diameter of a puncture; interstriae twice as wide as striae, shining, with rather numerous minute points and moderately abundant, subtransverse impressed lines, punctures obsolete except for an occasional puncture on some specimens. Declivity steep, broadly convex; sutural interstriae distinctly, rather abruptly elevated, 2 slightly wider than 1 or 3 and impunctate, 1 and 3 each with a few small punctures. Vestiture largely abraded, a few short interstitial bristles on declivity.

FEMALE.—Similar to male except frons broadly flattened, weakly impressed near median line, median line with a conspicuous, blunt carina from epistoma to well above eyes; frontal vestiture of moderately abundant, fine,

uniformly distributed long hair, distinctly longer at margins.

TYPE LOCALITY.—Volcan de Agua, Guatemala.

TYPE MATERIAL.—The male holotype, female allotype, and 12 paratypes were taken at the type locality on 19-V-64, 1000 m, Nos. 609 and 612, from pith tunnels in a cut vine, by S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Araptus accinctus, n. sp.

This species is distinguished from *foveifrons* Schedl by the more slender body form, by the sparse discal interstitial punctures, and by the very different frons in both sexes.

MALE.—Length 2.2 mm (paratypes 2.1-2.5 mm), 2.8 times as long as wide; color dark reddish brown.

Frons excavated as in *foveifrons* but with lateral cusps longer, extending ventrad to upper level of eyes, a sharply elevated median carina extending from deepest point of excavation ending on epistomal margin in a small tooth, lateral margins of lower half of excavation armed by one or more pairs of small tubercles. Antennal club as in *foveifrons*.

Pronotum and elytra as in *interjectus* Wood except odd-numbered discal interstriae punctured, even-numbered interstriae very sparsely punctured, and declivity as in *foveifrons* except more narrowly convex, punctures smaller.

FEMALE.—Similar to male except frons shallowly concave from eye to eye from epistoma to vertex, surface shining, finely punctured, subaciculate, a distinctly elevated median carina extending from center of excavation to denticulate epistomal margin; margins of frontal excavation ornamented by a rather dense fringe of fine, long hair.

TYPE LOCALITY.—Three km (2 miles) SE Acatlan, Puebla, Mexico.

TYPE MATERIAL.—The male holotype, female allotype, and five paratypes were taken at the type locality on 15-V-67, 1500 m, No. 38, from pith tunnels in a cut vine, by S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Araptus delicatus, n. sp.

This species is distinguished from *genialis* Wood by the smaller size, by the more slender form, and by the very different sculpture of the frons.

MALE.—Length 1.9 mm (paratypes 1.7-2.5 mm), 2.8 times as long as wide; color dark brown except basal half of elytra light brown.

Frons deeply impressed on triangular area from epistoma to vertex, upper angle of triangle on vertex an inverted U-shaped area having its margins acutely costate, floor of impressed area obscurely aciculate and with a low, long, acute carina; vestiture fine, short, moderately abundant, with a conspicuous epistomal brush. Antennal club as in *foveifrons*.

Pronotum 1.2 times as long as wide; sides on basal half almost straight and parallel, broadly rounded in front; anterior margin armed by about 12 low serrations; indefinite summit one-third pronotum length from anterior margin; asperities small, confused; posterior areas shining with numerous impressed points, punctures moderately coarse, deep, close. Vestiture of moderately abundant, fine, very short hair.

Elytra 1.6 times as long as wide, 1.4 times as long as pronotum; sides straight and parallel on basal two-thirds, rather broadly rounded behind; striae not impressed except 1 weakly, punctures rather small, deep, spaced by diameter of a puncture; interstriae two to three times as wide as striae, shining, marked by irregular lines, punctures almost as large as those of striae, irregularly placed. Declivity steep, broadly convex, strial and interstitial punctures smaller than on disc; sutural interstriae feebly elevated, area from striae 1 to 3 flat on middle half. Vestiture of rows of short strial and slightly longer interstitial hair, longest interstitial setae slightly shorter than distance between rows.

FEMALE.—Similar to male except frons more extensively, subcircularly impressed, U-shaped carina as in male, vestiture on margins abundant and very long.

TYPE LOCALITY.—Eight km S La Huerta, Jalisco, Mexico.

TYPE MATERIAL.—The male holotype, female allotype, and 62 paratypes were taken at the type locality on 1-VII-65, 500 m, No. 161, from axial pith tunnels in stems of a vine, by S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Araptus genialis, n. sp.

This species is distinguished from *delicatus* Wood by the larger size, by the stouter body form, and by the sculpture of the frons.

MALE.—Length 3.0 mm (paratypes 2.8-3.4 mm), 2.7 times as long as wide; color dark reddish brown.

Frons deeply, triangularly impressed on median three-fourths from epistoma to vertex, upper angle more strongly impressed, its margins armed by one median and two lateral acutely elevated cusps; floor of impression punctate to obscurely aciculate, with a broad, strongly elevated carina from emarginate epistoma to deepest part of concavity, both upper and lower ends terminate abruptly. Antennal club as in *foveifrons*.

Pronotum 1.16 times as long as wide; as in *delicatus* except discal punctures smaller, not as deep.

Elytra 1.7 times as long as wide, 1.4 times as long as pronotum; as in *delicatus* except discal interstriae three to four times as wide as striae and declivital interstriae 3 feebly elevated.

FEMALE.—Similar to male except frontal impression more extensive, its margins ornamented by a dense fringe of long, yellow hair.

TYPE LOCALITY.—Volcan de Agua, Guatemala.

TYPE MATERIAL.—The male holotype, female allotype, and 18 paratypes were taken at the type locality on 19-V-64, 1000 m, No. 609 (two are 608), from axial pith tunnels in a cut vine, by S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Araptus dentifrons, n. sp.

This species is distinguished from *confinis* (Blandford) by the impressed male frons, with the carina much stronger, and with a series of small tubercles arming the lateral and dorsal margins of the impressed area, by the different female frons, and by the coarser elytral punctures.

MALE.—Length 1.8 mm (paratypes 1.6-1.9 mm), 3.0 times as long as wide; color very dark reddish brown.

Frons subconvexly impressed to upper level of eyes with median area on lower half very strongly produced into a short, dentate, median carina, upper and lateral margins of impressed area armed by a row of about nine tubercles; surface shining, subaciculate near epistoma; vestiture sparse, inconspicuous except on epistoma.

Pronotum as in *confinis* except posterior areas with numerous impressed points (obscure-

ly reticulate in some specimens), punctures coarse, deep. Elytra as in *confinis* except discal surface smooth, shining, with impressed points, stria punctures larger, interstriae less than twice as wide as striae, declivital punctures strongly reduced in size, almost obsolete.

FEMALE.—Similar to male except frons flattened, very shallowly concave on median third, with an obscure median impressed line below, a weak carina above, marginal areas subgranulate, not tuberculate, vestiture rather uniformly distributed but more abundant and longer on margins.

TYPE LOCALITY.—Three km (2 miles) SE Acatlan, Puebla, Mexico.

TYPE MATERIAL.—The male holotype, female allotype, and 21 paratypes were taken on 15-VI-67, 1500 m, No. 38, from axial pith tunnels of a cut vine, by S. L. Wood; nine paratypes are from Volcan Colima, Jalisco, Mexico, 23-VI-65, No. 104, S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Araptus facetus, n. sp.

This species is distinguished from *exquisitus* Blackman by the smaller size, by the shorter or obsolete elytral vestiture, and by the ornamentation of the female frons.

FEMALE.—Length 1.3 mm (paratypes 1.2-1.4 mm), 2.5 times as long as wide; color reddish brown.

Frons shallowly concave from eye to eye from epistoma to vertex, its surface smooth, impunctate on lower fourth, finely, closely punctured above, vestiture confined to area above eyes, consisting of a dense brush of long yellow hair.

Pronotum and elytra as in *exquisitus* except elytra glabrous.

MALE.—Similar to female except frons as in male *exquisitus*.

TYPE LOCALITY.—Rio Tempisque, Guanacaste, Costa Rica.

TYPE MATERIAL.—The female holotype, male allotype, and two paratypes were taken at the type locality on 25-III-64, 15 m, No. 501, from *Ficus* twigs, by S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Araptus cuspidis, n. sp.

This species and *eruditus* (Schedl) have a conspicuous median process at the posterior

margin of abdominal sternum 5 that distinguishes them from all other species in the genus. This species is distinguished from *eruditus* by the convex, unarmed elytral declivity and by the different female frons.

FEMALE.—Length 1.3 mm (paratypes 1.2-1.4 mm), 2.6 times as long as wide; color yellowish brown.

Frons shining, convex, slightly flattened on median half below upper level of eyes, this area punctured on its lateral and upper margins, smooth and shining in central area, punctured area with moderately abundant, short, inconspicuous hair.

Pronotum 1.0 times as long as wide; widest on basal third, sides moderately arcuate, converging toward rather narrowly rounded anterior margin; anterior margin armed by about 12 low serrations; summit definite, very slightly in front of middle; asperities moderately coarse, confused; posterior areas strongly reticulate, punctures small, obscure. Glabrous.

Elytra 1.5 times as long as wide, 1.6 times as long as pronotum; sides straight and parallel on basal two-thirds, rather narrowly rounded behind; striae not impressed, punctures small, distinct; interstriae three times as wide as striae, almost smooth, impressed points rather obscure, impunctate. Declivity steep, convex; sutural interstriae feebly elevated, 2 indistinctly impressed; stria and interstitial punctures minute, almost obsolete. Vestiture largely confined to declivity, of interstitial rows of slender bristles, each slightly longer than distance between rows, similarly spaced within a row. Sternum 5 with a conspicuous median elevation on posterior margin.

MALE.—Similar to female except frons convex, shining, surface obscurely, rather coarsely punctured. Antennal club rather small, subcircular, sutures rather strongly procurved, 1 extending one-third, 2 two-thirds club length from base, 1 finely septate.

TYPE LOCALITY.—Eight km (5 miles) E San Blas, Nayarit, Mexico.

TYPE MATERIAL.—The female holotype, male allotype, and 14 paratypes were taken at the type locality on 12-VII-65, 70 m, No. 233, from a broken tree branch, by S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Araptus placatus, n. sp.

This species is distinguished from *obsoletus* (Blandford) by the larger size, by the more

strongly impressed, more finely punctured male frons, by the short, sparse female frontal vestiture, by the clytral vestiture, and by other characters.

MALE.—Length 1.7 mm (paratypes 1.5-1.8 mm), 2.8 times as long as wide; color dark brown.

Frons broadly impressed from epistoma to upper level of eyes, upper limits attaining a distinct summit on median half; surface shining, rather finely, deeply, closely punctured; an obscure, median carina sometimes present; vestiture fine, sparse, inconspicuous. Antennal club as in *obsoletus*.

Pronotum 1.13 times as long as wide; widest just behind middle, sides weakly arcuate, rather broadly rounded in front; anterior margin armed by about 10-12 low serrations; indefinite summit one-third pronotum length from anterior margin; asperities small, confused; posterior areas smooth to obscurely reticulate, punctures rather fine, moderately close. Glabrous.

Elytra 1.7 times as long as wide, 1.6 times as long as pronotum; sides straight and parallel on more than basal two-thirds, rather broadly rounded behind; striae not impressed except 1 near declivity, punctures small, spaced within row by twice diameter of a puncture; interstriae almost smooth, subshining, about four times as wide as striae, impunctate. Declivity steep, rather broadly convex; striae 1 distinctly impressed, interstriae 1 distinctly elevated, 2 weakly impressed, interstitial punctures minute. Vestiture confined to declivity, of rows of stout, blunt interstitial bristles, each slightly shorter than distance between rows, similarly spaced within a row.

FEMALE.—Similar to male except planoconvex, a median callus on lower half, area at upper level of eyes not elevated; surface shining, rather finely, closely punctured, vestiture very fine, moderately abundant, rather short.

TYPE LOCALITY.—Five km (3 miles) W Jalpitan, Veracruz, Mexico.

TYPE MATERIAL.—The male holotype, female allotype, and 27 paratypes were taken at the type locality on 25-VI-67, 50 m, Nos. 117, 100, from the hollow central axis of a cut vine, by S. L. Wood; two paratypes are from 37 km or 23 miles N Matias Romero, Veracruz, 29-VI-67, No. 126, S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Araptus decorus, n. sp.

This unique species is distinguished by the shallow declivital impression, confused clytral punctures, slender form, and fine sculpture, and by the very different female frons.

MALE.—Length 1.9 mm (paratypes 1.8-1.9 mm), 2.8 times as long as wide; color yellowish brown.

Frons convex, except weakly flattened on central half below upper level of eyes, a small callus near upper margin of flattened area, a pair of calluses in ventrolateral parts of this area; surface shining, rather finely punctured except impunctate in median area on lower half; vestiture fine, sparse, inconspicuous. Antennal club oval, sutures moderately procurved, suture 1 weakly septate.

Pronotum 1.25 times as long as wide; about as in *placatus* Wood except median serrations on anterior margin distinctly larger, and posterior area reticulate, dull, moderately fine, deep, rather widely separated. Glabrous.

Elytra 1.6 times as long as wide, 1.3 times as long as pronotum; outline as in *placatus*; surface shining, with minute points, punctures confused, rather small, moderately close. Declivity moderately steep, shallowly impressed, almost flat on median half; striae punctures in rows; interstriae 1 weakly elevated, 2 distinctly impressed; interstitial punctures fine. Vestiture confined to declivity, consisting of rows of sparse, stout bristles except absent on 2, bristles spaced in all directions by distances slightly greater than length of a bristle.

FEMALE.—Similar to male except frons flattened almost from eye to eye from epistoma to vertex, with an elevated, transverse, obtuse summit just below upper level of eyes, area from summit to epistoma on median third smooth, shining, impunctate, remaining area punctured and ornamented by rather abundant, long, yellow hair.

TYPE LOCALITY.—Rincon de Osa, Puntarenas, Costa Rica.

TYPE MATERIAL.—The male holotype, female allotype, and seven paratypes were taken at the type locality on 11-VIII-66, 30 m, No. 64, from the phloem of a recently cut log 20 cm in diameter, by S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Araptus blanditus, n. sp.

This species is distinguished from *deyrollei* (Blandford) and *schwarzi* (Blackman) by the

smaller size, by the impunctate interstriae, and by the more deeply concave, more finely punctured female frons, with longer, more abundant frontal vestiture.

FEMALE.—Length 1.8 mm, 2.6 times as long as wide; color very dark reddish brown.

Frons moderately concave on central two-thirds from distinctly elevated epistoma to slightly above eyes; surface smooth, shining, very finely, closely, uniformly granulate-punctate; vestiture of uniformly distributed, rather abundant, fine, long hair, marginal setae distinctly longer. Antennal club oval, external sutures obsolete, internal septum of anterior half of suture 1 conspicuous.

Pronotum 1.1 times as long as wide; widest on basal third, sides on basal half moderately arcuate, distinctly constricted on anterior half, rather broadly rounded in front; anterior margin armed by about 12 low serrations; broad summit near middle; asperities rather small, confused; posterior areas smooth, shining, impressed points very small, moderately abundant, punctures rather coarse, deep, moderately close. Glabrous.

Elytra 1.55 times as long as wide, 1.65 times as long as pronotum; sides almost straight and parallel on basal two-thirds, rather narrowly rounded behind; striae 1 moderately, others not impressed, punctures moderately large, deep, very close, rows slightly irregular; interstriae smooth, shining, points obscure to absent, impunctate. Declivity moderately steep convex, shallowly sulcate; sutural striae narrowly impressed, interstriae 2 moderately impressed, ascending laterally, 3 higher than suture; striae punctures slightly smaller than on disc; interstitial punctures small, obsolete on 2. Vestiture largely confined to declivity, of interstitial rows, except on 2, of moderately stout bristles, each as long as distance between rows, similarly spaced within a row.

TYPE LOCALITY.—Fortín de las Flores, Veracruz, Mexico.

TYPE MATERIAL.—The female holotype was taken at the type locality on 22-V-65, at light, by D. Rabago.

The holotype is in my collection.

Araptus medialis, n. sp.

This species is distinguished by the impressed elytral declivity, by the confused punctures on the elytral disc, and by the very different female frons.

FEMALE.—Length 1.5 mm (paratypes 1.4-1.6

mm), 2.7 times as long as wide; color yellowish brown.

Frons flattened almost from eye to eye from epistoma to vertex, area below eyes dull, densely, finely punctured, central area above eyes smooth, shining, impunctate, entire lower area and marginal areas above bearing abundant, long, yellow hair, longest on upper margin. Antennal club small, oval, suture 1 weakly procurved, septate throughout, 2 very obscure.

Pronotum 1.1 times as long as wide; widest on posterior half, sides feebly arcuate on posterior half, then distinctly constricted, rather narrowly rounded in front; anterior margin armed by 10 coarse serrations, summit rather broad, at middle; asperities rather coarse, confused; posterior areas shining, almost smooth to subreticulate, impressed points rather obscure, punctures fine, not sharply impressed, rather sparse. Glabrous.

Elytra 1.5 times as long as wide, 1.4 times as long as pronotum; sides almost straight and parallel on slightly less than basal two-thirds, rather broadly rounded behind; striae not impressed; punctures rather small, confused on more than basal half of disc, in rows posteriorly; surface shining, with numerous impressed points. Declivity rather steep, strongly sulcate; striae punctures in rows, small, rather obscure; interstriae 1 weakly elevated, 2 impressed, rather abruptly, moderately elevated laterally, lateral margins rounded, distinctly higher than suture, interstriae 1 and 3 each bearing a row of small granules. Vestiture confined to declivity, consisting of rows of rather long, slender bristles except absent on interstriae 2.

MALE.—Similar to female except 2.5 times as long as wide; frons convex, shining, a small median callus at upper level of eyes, punctures small, shallow, rather close, vestiture fine, sparse, inconspicuous; declivital bristles stout, blunt, shorter, each distinctly longer than distance between rows, similarly spaced within a row.

TYPE LOCALITY.—San Isidro del General, San José, Costa Rica.

TYPE MATERIAL.—The female holotype, male allotype, and 21 paratypes were taken at the type locality on 5-XII-63, 1000 m, No. 288, from a tree branch by S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Araptus conditus, n. sp.

This species is distinguished from *medialis* Wood by the larger size, by the absence of the

lateral half of the septum of suture 1 of the antennal club, by the coarser punctures on the pronotum and elytra, and by the very different frons in both sexes.

FEMALE.—Length 2.0 mm (paratypes 1.9-2.2 mm), 2.4 times as long as wide; color yellowish brown.

Frons shallowly, evenly concave from eye to eye from epistoma to vertex, densely, finely, uniformly punctured, covered by abundant erect, short, yellow hair of uniform length except slightly longer at margins. Antennal club moderately large, subcircular, suture 1 strongly subangulate, its median half septate, suture 2 almost obsolete.

Pronotum 1.12 times as long as wide; sides feebly arcuate and almost parallel on basal half, slightly constricted anteriorly, rather narrowly rounded in front; anterior margin acute, subserrate; summit indefinite, at middle; asperities fine, confused, covering anterior two-thirds; posterior areas shining, obscurely reticulate, punctures moderately coarse, close, deep. Glabrous.

Elytra 1.4 times as long as wide, 1.26 times as long as pronotum; outline and disc as in *medialis* except striae 1 impressed, punctures rather coarse, deep. Declivity steep, bisulcate; interstriae 1 moderately elevated, 2 rather strongly impressed, narrowly above, broadly below, lateral areas rather strongly elevated, rounded, higher than suture, 1 and 3 each with a sparse row of granules; punctures in rows, rather small, shallow. Vestiture largely confined to declivity, of interstitial rows (absent on 2) of short, coarse bristles, each almost as long as distance between rows, similarly spaced within a row.

MALE.—Similar to female except frons broadly, transversely impressed from epistoma to upper level of eyes, a rounded median summit at its upper limits; surface smooth, finely, very closely, uniformly punctured; vestiture of rather abundant, fine, short, semirecumbent hair.

TYPE LOCALITY.—Puerto Viejo, Heredia, Costa Rica.

TYPE MATERIAL.—The female holotype, male allotype, and 14 paratypes were taken at the type locality on 12-III-64, 70 m, No. 478 (except one is No. 481), from radiate tunnels in the cambium of a cut woody vine, by S. L. Wood. One paratype is labeled Turrialba, Costa Rica, 1970, R. I. Gara.

The holotype, allotype, and paratypes are in my collection.

Araptus frugalis, n. sp.

This species is distinguished from *conditus* Wood by the minute pronotal and elytral punctures, by the much more abundant elytral vestiture, by the glabrous female frons, and by the antennal club.

FEMALE.—Length 2.1 mm (paratypes 1.9-2.2 mm), 2.7 times as long as wide; color yellowish brown.

Frons essentially as in male *conditus* except more brightly polished, less closely punctured, subglabrous, with a definite median tubercle at upper level of eyes. Antennal club elongate-oval, anterior half of suture 1 represented by a longitudinal septum extending one-third of club length from base, 2 indicated externally, profoundly procurved, extending three-fourths of club length from base.

Pronotum 1.2 times as long as wide; about as in *conditus* except summit distinctly anterior to middle, anterior margin armed by 18 rather coarse serrations, posterior areas with punctures much smaller. Vestiture of moderately abundant fine, short hair.

Elytra 1.5 times as long as wide, 1.3 times as long as pronotum; outline as in *conditus*; striae not impressed, punctures very fine, mostly in rows; interstriae four or more times as wide as striae, shining, with impressed points and very fine, irregular lines, punctures as small or smaller than those of striae, in rows. Declivity steep; sulcate; essentially as in *conditus* except punctures on striae 1 and 2 obsolete, others minute. Vestiture of rows of minute striae hair, and longer, rather fine, interstitial bristles on disc and declivity, bristles about as long as distance between rows, similarly spaced within a row, absent on declivital interstriae 2.

MALE.—Similar to female except frons convex, rather coarsely, closely punctured, median area weakly elevated and impunctate; elytral bristles slightly longer, stouter.

TYPE LOCALITY.—Rincon de Osa, Puntarenas, Costa Rica.

TYPE MATERIAL.—The female holotype, male allotype, and 36 paratypes were taken at the type locality on 11-VIII-66, 30 m, No. 80, from a cut vine 2 cm in diameter, by S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Araptus laudatus, n. sp.

This species is distinguished from *frugalis* Wood by the narrow, convex frons in both sexes, with a distinct impression just above

the epistoma in the female, by the more narrowly, deeply sulcate clytral declivity, and by the subtriangular antennal club.

FEMALE.—Length 2.0 mm (paratypes 1.7-2.1 mm), 2.8 times as long as wide; color reddish brown.

Frons convex except lower third rather strongly, transversely impressed; epistoma with median area distinctly elevated; surface dull, reticulate, rather coarsely, somewhat obscurely punctured; glabrous. Antennal club subtriangular, apex somewhat pointed; mesal half of suture 1 septate, sutures not indicated externally.

Pronotum 1.2 times as long as wide; sides almost straight and parallel on basal half, rather narrowly rounded in front; anterior margin armed by 10-12 low serrations; summit rather indefinite, one-third pronotum length from anterior margin; asperities rather fine, confused; posterior areas smooth, shining, with numerous impressed points, punctures rather small, moderately close. Glabrous.

Elytra 1.8 times as long as wide, 1.6 times as long as pronotum; sides almost straight and parallel, then slightly tapered, bisinuate truncate on median half behind; striae not impressed; all punctures rather small, confused; surface smooth, shining, with minute impressed points. Declivity narrow, steep, broadly, rather deeply sulcate; interstriae 1 distinctly elevated, 2 impressed, lateral areas abruptly, strongly elevated, rounded, armed on inner margin by a series of two to six small denticles, 1 usually with one or more small granules on basal half; punctures on striae 1 and 2 obscure to obsolete. Vestiture largely confined to declivity, consisting of a few, short, interstitial bristles.

MALE.—Similar to female except frons more evenly convex, transverse impression almost obsolete, punctures coarser, deeper; serrations on anterior margin of pronotum larger; declivital sulcus deeper, more abrupt, sutural interstriae more regularly granulate.

TYPE LOCALITY.—San Isidro del General, San José, Costa Rica.

TYPE MATERIAL.—The female holotype, male allotype, and 48 paratypes were taken at the type locality on 13-XII-63, 1000 m, No. 313, from a broken tree branch, by S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Araptus vesculus, n. sp.

This species is distinguished from *exigialis* Wood by the smoother elytral surface and by

the very different frons, particularly in the female.

FEMALE.—Length 1.2 mm (paratypes 1.1-1.3 mm), 2.5 times as long as wide; color very dark reddish brown.

Frons almost flat, median line above eyes weakly elevated, epistomal margin rather weakly elevated medially; surface reticulate, punctures rather coarse, close, sparsely punctured toward center; vestiture of rather sparse, very long hair. Antennal club subcircular, suture 1 moderately procurved, weakly septate, 2 obscure.

Pronotum 1.1 times as long as wide; as in *eruditus* (Schedl) except posterior areas shining, weakly reticulate, punctures fine, shallow, rather widely spaced. Almost glabrous.

Elytra 1.5 times as long as wide, 1.4 times as long as pronotum; outline as in *eruditus*; striae not impressed, punctures fine, deep; interstriae almost smooth, shining, twice as wide as striae, impressed points almost obsolete, impunctate. Declivity steep, sulcate; essentially as in *eruditus*. Vestiture as in *eruditus* except less abundant.

MALE.—Similar to female except frons more distinctly, more evenly convex, punctures coarser, more evenly distributed, almost glabrous.

TYPE LOCALITY.—Gnapiles, Limon, Costa Rica.

TYPE MATERIAL.—The female holotype, male allotype, and two paratypes were taken at the type locality on 22-VII-66, 100 m, No. 121, from a cut vine, by S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Araptus exigialis, n. sp.

This species is distinguished from *vesculus* Wood by the more abundant, more conspicuously impressed lines on the clytral disc, by the more slender form, and by the different frons in both sexes.

FEMALE.—Length 1.3 mm (paratypes 1.3-1.4 mm), 2.7 times as long as wide; color reddish brown.

Frons shallowly, broadly concave from epistoma to above upper level of eyes; surface shining, minutely, densely, uniformly punctured; vestiture of fine, very short, abundant hair, very slightly longer on margins. Antennal club as *vesculus*.

Pronotum 1.2 times as long as wide; as in *vesculus* except posterior areas very finely,

rather strongly reticulate, punctures very fine, shallow, rather sparse. Glabrous.

Elytra 1.7 times as long as wide, 1.4 times as long as pronotum; as in *vesculus* except discal surface with points and fine, irregular lines.

MALE.—Similar to female except frons strongly convex, weakly impressed along upper margin of epistoma; surface reticulate, punctures rather coarse, close, shallow, vestiture fine, short, sparse, inconspicuous.

TYPE LOCALITY.—Fort Clayton, Canal Zone, Panama.

TYPE MATERIAL.—The female holotype, male allotype, and 10 paratypes were taken at the type locality on 22-XII-63, 30 m, No. 318, from a cut woody vine, by S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Araptus refertus, n. sp.

This species is distinguished from the preceding members of this genus by the much coarser strial punctures, with impunctate discal interstriae, by the rather strongly bisulcate elytral declivity, and by the frons in both sexes.

FEMALE.—Length 2.0 mm (paratypes 1.9-2.3 mm), 2.8 times as long as wide; color light brown (mature color probably dark brown).

Frons broadly, weakly convex; surface shining, smooth and impunctate on triangular area on lower, median half, finely, closely, rather deeply punctured on lateral and upper areas; vestiture of rather abundant, moderately long, fine hair. Antennal club oval, suture 1 moderately procurved, septate, not reaching middle of club, suture 2 virtually obsolete, near apical margin.

Pronotum 1.13 times as long as wide; as in *vesculus* Wood except posterior area smooth shining, with numerous impressed points, punctures moderately coarse, deep, close. Glabrous.

Elytra 1.7 times as long as wide, 1.5 times as long as pronotum; sides straight and parallel on basal two-thirds, rather broadly rounded behind; striae not impressed, punctures coarse, deep, close; interstriae as wide as striae, smooth, shining, with moderately numerous impressed points, impunctate. Declivity steep, broadly, rather strongly bisulcate; strial punctures impressed, slightly smaller than on disc; interstriae 1 moderately, gradually elevated, 2 rather strongly impressed, flat, narrow at base, rather broadly expanded on middle half, 3 rather abruptly, moderately elevated, 1 and 3 each armed on basal half by about three very small,

pointed, semirecumbent denticles, a few punctures on lower half. Vestiture sparse, hairlike, mostly on or near declivity.

MALE.—Similar to female except frons strongly, evenly convex; surface shining, rather coarsely, deeply, closely punctured, subglabrous except on and near epistoma; elytral declivity more strongly impressed, denticles slightly larger.

TYPE LOCALITY.—Volcan Zunil, Quezaltenango, Guatemala.

TYPE MATERIAL.—The female holotype, male allotype, and 16 paratypes were taken at the type locality on 27-V-64, 1000 m, No. 625, from a composite shrub, by S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Araptus trepidus, n. sp.

This species is distinguished from the closely allied *poricollis* (Blandford) by the absence of declivital denticles, and by the almost continuous transverse epistomal elevation in the male.

FEMALE.—Length 1.8 mm (paratypes 1.6-1.8 mm), 2.7 times as long as wide; color dark reddish brown.

Frons broadly flattened from epistoma to vertex, median third of lower half smooth, shining, distinctly elevated, remaining area densely, finely, deeply punctured; vestiture on punctured area abundant, fine, rather long, uniformly distributed.

Pronotum 1.15 times as long as wide; as in *refertus* Wood except median line of posterior area impunctate.

Elytra 1.6 times as long as wide, 1.5 times as long as pronotum; outline and disc as in *refertus* except impressed points obscure to obsolete. Declivity steep, bisulcate; interstriae 1 abruptly, distinctly elevated, 2 rather strongly impressed, flat, wider than 1 or 3, 3 abruptly, moderately elevated, 1 and 3 finely punctured, not granulate; strial punctures small, rather obscure. Vestiture of rows of very minute strial hair, and longer, slender interstitial bristles on disc and declivity, each slightly longer than distance between rows, similarly spaced within a row.

MALE.—Similar to female except frons strongly convex on upper half, strongly, transversely impressed just below middle, lower margins of impressed area elevated laterally, elevations continue to a weak median subcarinate elevation dividing impression; upper area of

frons coarsely, deeply punctured, vestiture sparse except for epistomal brush.

TYPE LOCALITY.—Volcan de Agua, Esquintla, Guatemala.

TYPE MATERIAL.—The female holotype, male allotype, and 56 paratypes were taken at the type locality on 19-V-64, 1000 m, Nos. 608 (type), 609, 612, from *Menisperma* sp., by S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Araptus frontalis, n. sp.

This species is distinguished from *trepidus* Wood by the larger size, by the punctured declivital interstriae 2, and by the different frons in both sexes.

FEMALE.—Length 2.7 mm (paratypes 2.4-2.7 mm), 2.8 times as long as wide; color dark reddish brown.

Frons broadly flattened from epistoma to vertex, weakly concave on small median area above eyes, weakly convex on small, median, impunctate area on lower half; surface shining, finely, closely, deeply punctured; vestiture of moderately abundant, fine, long hair. Antenna as in *trepidus*.

Pronotum 1.1 times as long as wide; essentially as in *trepidus*.

Elytral outline and disc as in *trepidus* except interstriae near declivity with punctures. Declivity about as in *trepidus* and *refertus* except interstriae 2 with a row of punctures as coarse as those of striae; lateral margins without granules. Vestiture confined to declivity, of fine, sparse hair.

MALE.—Similar to female except frons deeply, transversely concave on upper half of area below upper level of eyes on median three-fourths, lateral and lower margins of concavity strongly, acutely carinate except carina interrupted at median line, vestiture inconspicuous except on epistoma; anterior margin of pronotum rather coarsely serrate; declivity more strongly impressed.

TYPE LOCALITY.—Volcan Zumil, Quezaltenango, Guatemala.

TYPE MATERIAL.—The female holotype, male allotype, and five paratypes were taken at the type locality on 27-V-64, 1000 m, Nos. 625, 626, from a composite shrub, by S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Araptus nigrellus, n. sp.

This and the following three form a distinctive transitional group between species previously placed in *Neodryocoetes* Eggers and *Spheroceros* Schedl. They have the antennal club large, with finely marked, strongly procurved sutures, the costal apex of the elytra ascends slightly, the declivity is convex, and the elytral vestiture tends to be confined to the declivity, closely spaced and more or less scale-like. This species is distinguished from others in the group by the more slender body, by the slender interstitial bristles, and by the subglabrous female frons.

FEMALE.—Length 1.9 mm (paratypes 1.7-2.0 mm), 2.7 times as long as wide; color black.

Frons convex, a weak, transverse impression above epistoma; surface strongly reticulate-subgranulate above eyes, almost smooth and with a few small punctures below. Antennal club rather large, oval, sutures strongly arcuate, 1 septate.

Pronotum 1.1 times as long as wide; widest on basal third, sides moderately arcuate, converging toward narrowly rounded serrate anterior margin; summit at middle; asperities moderately coarse, confused; posterior areas shining, partly subreticulate, with low, longitudinal subasperate crenulations continuing almost to base, punctures obscure, associated with crenulations. Glabrous.

Elytra 1.7 times as long as wide, 1.7 times as long as pronotum; sides straight and parallel on slightly less than basal two-thirds; tapered, then rather broadly rounded; striae not impressed except 1 weakly, punctures small, deep, spaced within row by diameter of a puncture; interstriae four times as wide as striae, almost smooth, with obscure, minute points, impunctate. Declivity moderately steep, convex; striae obscurely impressed, punctures smaller and less distinct than on disc; interstriae each with a row of very fine granules. Vestiture confined to declivity, of rows of narrowly spatulate interstitial bristles, each bristle as long as distance between rows, more closely spaced within a row.

MALE.—Similar to female in all respects.

TYPE LOCALITY.—Ten km SE Cartago, Cartago, Costa Rica.

TYPE MATERIAL.—The female holotype, male allotype, and 67 paratypes were taken at the type locality on 24-IX-63, No. 205 (type), and 3-VII-63, Nos. 13 and 15, 1800 m, from *Myrica pubescens*, by S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Araptus vinnulus, n. sp.

This species is distinguished from *nigrellus* Wood by the smaller size, by the stouter form, by the more widely spaced, stouter interstitial bristles, by the almost obsolete striae punctures, and by the frons.

FEMALE.—Length 1.3 mm (paratypes 1.2-1.5 mm), 2.4 times as long as wide; color very dark brown, almost black.

Frons broadly convex, lower third with broad, smooth, shining, median line; surface densely, coarsely, deeply punctured; upper two-thirds on median two-thirds with moderately abundant, fine, long hair. Antenna essentially as in *nigrellus*.

Pronotum 1.03 times as long as wide; as in *nigrellus* except less strongly tapered anteriorly, moderately rounded in front, posterior areas dull. Glabrous.

Elytra 1.44 times as long as wide, 1.44 times as long as pronotum; sides straight and parallel on basal half, tapered then rather narrowly rounded behind; striae not impressed, punctures minute, shallow, many almost obsolete; interstriae shining, with many very minute impressed points and shallow, irregular lines, impunctate. Declivity rather steep, convex; as on disc except interstriae each with a row of small, rounded granules. Vestiture confined to declivity, of rather stout, spatulate bristles, each slightly shorter than distance between rows, similarly spaced within a row.

MALE.—Similar to female except frons rather strongly convex, surface strongly reticulate, subglabrous.

TYPE LOCALITY.—San Ignacio de Acosta, San José, Costa Rica.

TYPE MATERIAL.—The female holotype, male allotype, and 18 paratypes were taken at the type locality on 5-VII-63, 1500 m, No. 31, from small branches of *Roupala complicata*, by S. L. Wood.

Araptus furvus, n. sp.

This species is distinguished from *vinnulus* Wood by the larger size, by the more closely spaced interstitial setae, by the presence of striae hair, and by the longer more abundant setae on the female frons.

FEMALE.—Length 2.1 mm (paratypes 1.7-2.2

mm), 2.4 times as long as wide; color almost black.

Frons convex, strongly reticulate, punctures rather small, sparse; upper two-thirds with rather dense marginal fringe of long hair, longest setae on vertex extend about two-thirds distance to upper level of eyes. Antenna as in *vinnulus*.

Pronotum 1.03 times as long as wide; as in *vinnulus* except more distinctly constricted on anterior half.

Elytra 1.5 times as long as wide, 1.6 times as long as pronotum; as in *vinnulus* except striae punctures on basal half of disc more distinct; declivital striae punctures obsolete. Vestiture confined to declivity, of rows of minute, fine, striae hair, and rows of longer, spatulate, interstitial bristles, each bristle slightly shorter than distance between rows, more closely spaced within a row, each bristle very slender on its basal half, flattened on its apical half.

MALE.—Similar to female except frons broadly convex, glabrous.

TYPE LOCALITY.—Cerro Punta (labeled Volcan Chiriqui), Chiriqui, Panama.

TYPE MATERIAL.—The female holotype, male allotype, and 45 paratypes were taken at the type locality on 11-I-64, 1800 m, No. 422, from broken *Roupala* sp. limbs, by S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Araptus furvescens, n. sp.

This species is distinguished from *furvus* Wood by the smaller average size, by the feebly impressed declivital striae, with minute striae punctures indicated, and by the longer female frontal pubescence, with pubescent area extending higher on the vertex.

FEMALE.—Length 1.9 mm (paratypes 1.5-1.9 mm); as in *furvus* Wood except female frontal pubescent area extending higher on vertex, distance from upper level of eyes to upper limits of pubescent area 1.5 times distance from epistoma to upper level of eyes, longest setae on vertex almost reach epistomal margin, pubescent area extending ventrad in lateral areas almost to epistoma; declivital striae weakly impressed, punctures very small but usually visible; declivital interstitial bristles more nearly scaldlike, each flattened on two-thirds or more of its length.

MALE.—Similar to female except frons more broadly convex, glabrous.

TYPE LOCALITY.—Volcan Pacaya, Esquintla, Guatemala.

TYPE MATERIAL.—The female holotype, male allotype, and 40 paratypes were taken at the type locality on 1-VI-64, 1300 m, Nos. 652, 657, 658, and cut *Roupala* limbs, by S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Araptus lepidus, n. sp.

This species is distinguished from the above three species in this group by the presence of discal interstitial punctures and by the stouter body form. It is distinguished from *aztecus* Wood by the narrowly rounded, serrate anterior margin of the female pronotum and by the very different female frons.

FEMALE.—Length 1.8 mm (paratypes 1.7-2.0 mm), 2.26 times as long as wide; color dark brown.

Frons convex, median area strongly impressed from slightly above upper level of eyes to just above epistoma, lower lateral margins of impressed area moderately elevated; surface shining, smooth, punctures rather fine, deep, sparse; glabrous except near epistoma. Antennal club very large, about as in *nigrellus* Wood, only median half of suture 1 septate.

Pronotum 1.05 times as long as wide; essentially as in *vinulus* Wood except crenulations or ridges on posterior half almost obsolete, posterior areas smooth, shining, punctures very small, shallow, rather sparse. Glabrous.

Elytra 1.3 times as long as wide, 1.2 times as long as pronotum; sides almost straight and parallel on basal half, rather broadly rounded behind; striae not impressed, punctures small, shallow, rows irregular on anterior two-thirds; interstriae smooth, shining, about four times as wide as striae, punctures uniseriate, similar to those of striae. Declivity steep, convex, sculpture essentially as on disc except punctures slightly smaller, deeper. Vestiture largely confined to posterior half, consisting of interstitial rows of slender scalelike bristles, each slightly shorter than distance between rows, similarly spaced within a row.

TYPE LOCALITY.—Volcan, Puntarenas, Costa Rica.

TYPE MATERIAL.—The female holotype and three female paratypes were taken at the type locality on 11-XII-63, 1000 m, No. 304, from a broken branch, by S. L. Wood.

The holotype and paratypes are in my collection.

Araptus mendicus, n. sp.

This species is distinguished from *medialis* Wood by the smooth, polished male frons, with much finer, less abundant punctures, by the finely reticulate, much more distinctly punctured female frons, with the pubescence slightly less abundant, finer, and shorter, and by the larger size.

FEMALE.—Length 1.8 mm (paratypes 1.7-1.9 mm), 2.8 times as long as wide; color rather dark reddish brown.

Frons broadly, evenly convex, reticulate and finely, distinctly, closely punctured on lower two-thirds, almost smooth and shining in small area above eyes; vestiture fine, moderately long, rather abundant, distinctly longer on margins, particularly above, shining area above eyes subglabrous. Antennal club about as in *medialis* except slightly wider.

Pronotum and elytra as in *medialis*.

MALE.—Similar to male *medialis* except frons glabrous, smooth, polished, shagreened, punctures much smaller, less abundant.

TYPE LOCALITY.—Cartago, Cartago, Costa Rica.

TYPE MATERIAL.—The female holotype, male allotype, and 22 paratypes were taken at the type locality XII-1965, from Avocado (*Persea americana*) branches, by N. L. H. Krauss.

The holotype, allotype, and paratypes are in my collection.

Araptus nanulus, n. sp.

This species evidently is not closely allied to any known species. It is distinguished by the small size, by the simple, unadorned frons in both sexes, by the greatly reduced, almost obsolete striae punctures, by the regular, almost scalelike interstitial bristles, and by other characters.

FEMALE.—Length 1.2 mm (paratypes 1.1-1.3 mm), 2.6 times as long as wide; color dark reddish brown.

Frons convex, feebly impressed just above epistoma in lateral areas; surface shining, rather coarsely, sparsely punctured and with more numerous minute points; vestiture fine, sparse, inconspicuous. Antennal club oval, as long as scape, sutures almost straight, suture 1 finely septate.

Pronotum 1.06 times as long as wide; widest near base, sides weakly arcuate on basal half,

feebly constricted on anterior half, rather narrowly rounded in front; anterior margin serrate, about 12 indistinct serrations; summit indistinct; crenulations on anterior slope rather coarse, continued as low, irregular transverse costae to well behind summit; posterior areas shining, with numerous impressed points, appearing almost subgranulate in lateral areas. Vestiture erect, moderately abundant, somewhat similar to elytral setae.

Elytra 1.6 times as long as wide, 1.5 times as long as pronotum; striae not impressed, minute punctures almost obsolete; interstriae shining, setiferous punctures confused with numerous impressed points of almost equal size. Declivity rather narrowly convex; interstriae 1 shallowly impressed; surface sculpture as on disc. Vestiture of interstitial rows of suberect apically flattened bristles; each bristle about as long as distance between rows, somewhat more closely spaced within a row.

MALE.—Similar to female in all respects.

TYPE LOCALITY.—Tampico, Tamaulipas, Mexico.

TYPE MATERIAL.—The female holotype, male allotype, and 12 paratypes were taken at the type locality on 14-VIII-72, from *Disholcopsis* galls on *Quercus virginiana*, by G. F. Frankie.

The holotype, allotype, and paratypes are in my collection.

Pseudopityophthorus festivus, n. sp.

This species is distinguished from *pulvereus* Blackman by the planoconcave male frons, by the more strongly impressed elytral declivity, by the more coarsely punctured elytral surface, and by the very different elytral vestiture.

MALE.—Length 1.8 mm (paratypes 1.6-1.8 mm), 2.8 times as long as wide; color dark brown.

Frons broadly planoconcave from epistoma to vertex; surface smooth, shining in central area, marginal areas finely punctured and bearing a dense tuft of long, yellow hair. Antenna as in *pulvereus*.

Pronotum 1.2 times as long as wide; as in *pulvereus*.

Elytra 1.6 times as long as wide, 1.3 times as long as pronotum; outline as in *pulvereus*; surface smooth, shining, punctures moderately coarse, shallow, confused, very close, width of interspaces about equal to diameter of punctures. Declivity steep flattened; moderately elevated at suture, a moderately strong sulcus in area of interstriae 2, lateral convexities rounded;

punctures minute. Ground vestiture of fine, short, stout, reclining setae; erect scales in interstitial rows except obsolete on lower half of 2 on declivity, each scale about as long as distance between rows, similarly spaced within a row, each about four to eight times as long as wide.

FEMALE.—Similar to male except frons planoconvex, pubescence sparse, fine, much shorter.

TYPE LOCALITY.—Eleven km or 7 miles NE Copala, Sinaloa, Mexico.

TYPE MATERIAL.—The male holotype, female allotype, and two paratypes were taken at the type locality on 22-VII-53, from a *Quercus* branch, by S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Gnathotrichus obscurus, n. sp.

This and *primus* (Bright) are the only species in the genus having confused punctures on the elytral disc. It is distinguished from *primus* by the minutely reticulate elytral surface, by the smaller size, by the steeper declivity, and by other features.

FEMALE.—Length 2.5 mm, 3.0 times as long as wide; color reddish brown.

Frons broad, broadly convex; surface shining, finely, convergently aciculate on lower two-thirds, rather finely, sparsely punctured above, a strongly developed rather low median carina from middle to upper level of eyes (concealed by pronotum above eyes). Vestiture of fine, rather sparse hair.

Pronotum 1.24 times as long as wide; as in *dentatus* Wood except posterior areas reticulate, finely, closely, rather deeply punctured.

Elytra 1.7 times as long as wide; sides straight and parallel on basal two-thirds, narrowly rounded behind; striae obsolete; surface minutely reticulate, punctures minute, obscure, confused, a few granules on interstriae 3 near declivity. Declivity steep, broadly convex; very feebly sulcate on upper half, striae punctures not evident, interstriae marked by rows of very small granules, slightly larger on 3; costal margin at apex rather strongly elevated. Vestiture of fine hair, on disc of short, moderately abundant hair and interstitial rows of very long fine hair; all hair on declivity long, moderately abundant.

TYPE LOCALITY.—Nine km NE Tezuitlan, Puebla, Mexico.

TYPE MATERIAL.—The female holotype was taken at the type locality on 2-VII-67, 1600 m.

No. 152, from a *Quercus* log 15 cm in diameter, by S. L. Wood.

The holotype is in my collection.

Gnathotrichus omissus, n. sp.

This species is distinguished from *sulcatus* (LeConte) by the minute to obsolete stria punctures on the disc, by the confused punctures on the elytral declivity, by the feebly impressed elytral declivity, by the much less strongly aciculate female frons, and by the hosts.

FEMALE.—Length 3.5 mm (paratypes 3.3-3.6 mm), 3.2 times as long as wide; color dark brown, usually with pale areas on anterior pronotum and basal and declivital areas of elytra.

Frons convex, median line obscurely elevated, surface smooth, shining, sparsely, finely punctured, median third below upper level of eyes finely aciculate; vestiture fine, sparse, inconspicuous.

Pronotum 1.3 times as long as wide; essentially as in *materiarius* (Fitch) except serrations on anterior margin coarse.

Elytra 1.8 times as long as wide, 1.5 times as long as pronotum; outline as in *materiarius*; striae not impressed, punctures small, in slightly irregular rows; interstriae smooth, shining, impressed lines and points moderately abundant. Declivity rather steep, convex; weakly, rather narrowly sulcate; stria punctures obsolete or nearly so, evidently confused; lateral convexities distinctly higher than suture, summit armed by two or three small granules. Vestiture confined to declivity, consisting of sparse hair.

MALE.—Similar to female except frontal aciculation much stronger and distributed almost from eye to eye to well above eyes; antenna without long hair; anterolateral angles of pronotum bearing a small tuft of hair.

TYPE LOCALITY.—Volcan Irazu, Cartago, Costa Rica.

TYPE MATERIAL.—The female holotype, male allotype, and 38 paratypes were taken at the type locality on 26-IX-63, 2300 m elevation, No. 207, from a broken limb of *Oreopanax nubigenus*, by S. L. Wood. One other specimen, not included in the type series is from Volcan Pacaya, Guatemala.

The holotype, allotype, and paratypes are in my collection.

Gnathotrupes dilutus, n. sp.

This species is distinguished from *crecentis* Wood by the broadly convex unarmed elytral

declivity, with longer declivital pubescence, by the larger frontal punctures, and by the smaller size.

MALE.—Length 1.7 mm (paratypes 1.6-1.7 mm), 3.2 times as long as wide; color dark brown.

Frons broadly convex, shining, weakly reticulate; punctures sparse, moderately coarse, shallow; epistomal area distinctly impressed except on median line; vestiture sparse, hairlike, inconspicuous. Antennal club subcircular, three strongly areolate sutures marked by grooves and rows of setae, segment 1 very small.

Pronotum 1.2 times as long as wide; sides feebly areolate, subparallel on more than basal half, broadly rounded in front; anterior margin armed by 14 serrations; indefinite summit well in front of middle; anterior slope rather abrupt, rather coarsely asperate; posterior areas subreticulate (mostly wavy lines), punctures very minute, sparse. Glabrous.

Elytra 1.9 times as long as wide, 1.6 times as long as pronotum; sides almost straight and parallel on more than basal three-fourths, very broadly rounded behind, striae not impressed; surface shining, almost smooth, punctures minute, almost obsolete, confused. Declivity confined to less than posterior fourth, very steep, broadly convex; punctures larger and deeper than on disc, confused. Vestiture confined to declivity, of rather abundant, fine, short, and rather long hair.

TYPE LOCALITY.—Tapanti, Cartago, Costa Rica.

TYPE MATERIAL.—The male holotype and two male paratypes were taken at the type locality on 17-IX-63, 1300 m, No. 184, from *Miconia caudata*, by S. L. Wood.

The holotype and paratypes are in my collection.

Gnathotrupes crecentis, n. sp.

This species is distinguished from *dilutus* Wood by the steep, almost flat elytral declivity which is armed by two pairs of moderately large tubercles on interstriae 3, by the very short declivital vestiture, by the much finer frontal punctures, and by the smaller size.

FEMALE.—Length 2.0 mm (paratypes 1.9-2.0 mm), 3.0 times as long as wide; color dark brown.

Frons as in *dilutus* except punctures very fine; sparse setae very long. Pronotum as in *dilutus*.

Elytral outline as in *dilutus*; stria punctures very small, in definite rows, declivity steeper and

much flatter than in *dilutus*, punctures larger, confused, interstriae 3 with two pointed denticles one-third and two-thirds declivital length from base. Vestiture mostly very short, a few longer hairs.

MALE.—Similar to female except lower half of frons more distinctly, transversely impressed, setae short; striae punctures minute, confused; declivital denticles slightly larger, punctures much smaller, vestiture shorter.

TYPE LOCALITY.—Volcan, Puntarenas, Costa Rica.

TYPE MATERIAL.—The female holotype, male allotype, and eight paratypes were taken at the type locality on 11-XII-63, 1000 m, No. 308, from a recently cut tree limb, by S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Tricolus simplicis, n. sp.

In this species the frons is rather coarsely aciculate except for a small, median, raised, central granular area, and declivital spines 2 and 3 are essentially absent.

FEMALE.—Length 1.8 mm, 2.8 times as long as wide; color light brown.

Frons convex, shining, coarsely, convergently aciculate except on small, median, subcircular, raised granular area at center; vestiture inconspicuous. Antennal club broadly obovate; sutures 1 and 2 distinctly procurved, obtusely subangulate, finely septate except at middle, without long setae on posterior face.

Pronotum 1.3 times as long as wide; sides straight and subparallel on basal half, narrowly rounded in front; summit indefinite, anterior to middle; anterior slope finely, closely asperate; anterior margin a rather strongly, acutely elevated continuous costa; posterior areas reticulate, punctures obscure, very shallow, moderately close. Glabrous.

Elytra 1.7 times as long as wide, 1.4 times as long as pronotum; disc smooth, shining, punctures small, shallow, some obsolete, evidently at least slightly confused. Declivity occupying posterior third, excavated as in other members of this genus; face smooth, shining, indistinct punctures small, confused; lateral margins rather strongly, continuously elevated on heart-shaped pattern from suture to moderately near posterior margin, gradually increasing in height posteriorly, ending precipitously on lower, median angle; spine 1 on interstriae 1 at base very small, pointed, 2 feebly indicated, 3 rounded, not projecting. Glabrous.

TYPE LOCALITY.—Palin, Esquintla, Guatemala.

TYPE MATERIAL.—The unique female holotype was taken at the type locality on 19-V-64, at 300 m, No. 685, in a *Ficus* twig, by S. L. Wood.

The holotype is in my collection.

Tricolus inornatus, n. sp.

This species is distinguished from *simplicis* Wood by the much more slender body, by the narrower declivital excavation, and by the absence of declivital spine 1.

FEMALE.—Length 1.8 mm, 3.2 times as long as wide; color very dark brown.

Frons evidently as in *simplicis*, upper half concealed. Antennal club subcircular, sutures almost straight; posterior face with two or three long hairs.

Pronotum 1.4 times as long as wide; essentially as in *simplicis* except punctures on posterior areas deeper, distinct, a slight irregularity at base anterior to scutellum. Glabrous.

Elytra 2.0 times as long as wide; disc as in *simplicis*. Declivity similar to *simplicis* except excavated area much narrower, spine 1 represented only by a small callus, 2 represented by a distinct callus, 3 more broadly rounded, not projecting. Glabrous.

TYPE LOCALITY.—Fifteen km SE Cartago, Cartago, Costa Rica.

TYPE MATERIAL.—The unique female holotype was taken at the type locality on 24-IX-63, at 2800 m, No. 248, from a branch of *Siparuna nicaraguaensis*, by S. L. Wood.

The holotype is in my collection.

Tricolus inaeffectus, n. sp.

This species is distinguished from *inornatus* Wood by the larger, stouter body, by the impressed lower, lateral areas of the frons, by the pronotum, and by slightly wider elytral declivity.

FEMALE.—Length 2.6 mm, 2.9 times as long as wide; color black except elytral disc and antennae yellowish brown.

Frons as in *simplicis* Wood except granular area more strongly elevated, lateral areas impressed just above epistoma; mandibles apparently elongate. Antennal club broadly oval, sutures straight; posterior face ornamented by more than 20 long hairs.

Pronotum 1.2 times as long as wide; outline about as in *simplicis* except sides on slightly more than anterior half distinctly constricted,

anterior costa more nearly serrate; posterior areas reticulate, punctures moderately fine, rather deep. Glabrous.

Elytra 1.8 times as long as wide, 1.6 times as long as pronotum; as in *inornatus* except excavated declivital area distinctly wider, calluses of spines 1 and 2 less conspicuous. Glabrous.

TYPE LOCALITY.—Volcan Poas, Heredia, Costa Rica.

TYPE MATERIAL.—The unique female holotype was taken at the type locality on 19-XI-63, 2600 m, by S. L. Wood.

The holotype is in my collection.

Tricolus cecropii, n. sp.

This species is distinguished by the moderately stout body, by the poorly developed declivital spines, by the strongly produced, acute, strongly serrate anterior margin of the pronotum, by the large, subreniform granular area on the frons, and by the habits.

FEMALE.—Length 2.4 mm (paratypes 2.2-2.5 mm), 2.6 times as long as wide; color dark brown.

Frons somewhat flattened on median three-fourths from epistoma to upper level of eyes, most of flattened area occupied by a raised, granular area of subreniform shape. Antennal club obscurely subtriangular, sutures weakly procurved; very few long setae on posterior face.

Pronotum 1.3 times as long as wide; widest near base, sides weakly converging on basal two-thirds, anterior margin very strongly, subacutely produced and coarsely, closely serrate, 14-16 serrations; summit indefinite, near middle; anterior slope armed by rather large, low asperities; posterior area reticulate, punctures sparse, fine, shallow. Glabrous.

Elytra 1.5 times as long as wide, 1.2 times as long as pronotum; disc smooth, punctures small, shallow, confused. Declivity moderately steep, excavated area narrower and not as deep as in other species; spines 1 and 2 small, pointed tubercles, 1 slightly larger, 3 represented by a low, poorly developed fold; subapical margin subacute, not produced. Subglabrous.

MALE.—Similar to female.

TYPE LOCALITY.—Turrialba, Cartago, Costa Rica.

TYPE MATERIAL.—The female holotype, male allotype, and eight paratypes were taken at the type locality on 5-VII-63, at 700 m, No. 19, from

fallen *Cecropia peltata* leaf petioles, by S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Tricolus intrusus, n. sp.

This species is distinguished from the almost identical *cecropii* Wood by the much more acutely produced anterior margin of the pronotum, by the coarser punctures on the pronotal disc, and by the finer, less numerous punctures in the excavated area of the elytral declivity.

FEMALE.—Length 2.4 mm (paratypes 2.1-2.2 mm), 2.7 times as long as wide; color dark brown.

As in *cecropii*, except anterior margin of pronotum much more acutely produced, tridentate at its apex (a total of nine serrations on entire margin); punctures on discal area of pronotum distinctly larger, evidently more numerous; punctures on elytral disc evidently slightly smaller; punctures in excavated face of declivity much smaller, much less numerous.

TYPE LOCALITY.—El Laurel, 12 km SW Caracas, Venezuela.

TYPE MATERIAL.—The female holotype and two female paratypes were taken at the type locality on 1-V-70, at 1300 m, No. 475, from petioles of fallen *Cecropia* leaves, by S. L. Wood.

The holotype and paratypes are in my collection.

Tricolus ardis, n. sp.

This species is distinguished by the acutely angulate, strongly serrate anterior margin of the pronotum, by the aciculate frons which also has a small, elevated granulate area, and by the elytral declivity.

FEMALE.—Length 2.3 mm (paratypes 2.1-2.5 mm), 3.3 times as long as wide; head, prothorax, and elytral declivity dark brown, basal two-thirds of elytra light brown.

Frons convex, convergently aciculate except for a small, transversely oval granular area at center occupying median third. Antennal club broadly obovate, sutures moderately arcuate; posterior face without long hair.

Pronotum 1.5 times as long as wide; sides almost straight and parallel on basal half, arcuately converging to subacute median point in front; anterior margin coarsely serrate; summit indefinite; anterior slope finely, closely asperate; posterior areas reticulate, punctures fine, shallow, not close, some of those at base connected by transverse lines. Glabrous.

Elytra (including spines) 2.1 times as long as wide; sides straight and parallel to base of declivity, arcuately converging to apex of spine 3, apices of spine 3 separated by a distance equal to width of elytra, posterior emargination broadly, somewhat U-shaped; surface almost smooth, shining, punctures shallow, small, largely confused, their centers apparently reticulate. Declivity moderately steep, excavated in a narrowly heart-shaped area; lateral areas abruptly, rather strongly elevated, spine 1 at base on interstriae 1 rather small, sharply pointed, 2 one-third declivital length from base, twice as long as wide, 3 projecting posteriorly, conspicuously longer than wide (as seen in lateral aspect). Glabrous except for an occasional hairlike seta near declivity.

MALE.—Similar to female except for apical terga of abdomen.

TYPE LOCALITY.—Escasu, San José, Costa Rica.

TYPE MATERIAL.—The female holotype, male allotype, and 22 paratypes were taken at the type locality on 2-X-63, at 1300 m, Nos. 215, 218, from a tree seedling, by S. L. Wood. Two paratypes are from Cerro Punta near Volcan Chiriqui, Chiriqui, Panama, 11-I-64, 1300 m, Nos. 380, 401, tree branches, S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Tricolus parsus, n. sp.

This species is distinguished from *inaffectus* Wood by the more narrowly rounded anterior margin of the pronotum, by the acutely elevated, subapical margin of the declivity, and by the very different declivital spine 3.

MALE(?).—Length 2.3 mm, 2.6 times as long as wide; color almost black.

Frons largely concealed, evidently not aciculate, finely granulate, raised granular area as in *ardis* Wood. Antennal club broadly subquadrate, sutures feebly procurved.

Pronotum 1.3 times as long as wide; about as in *ardis* except anterior margin narrowly rounded, not angulate, serrations with their bases contiguous. Glabrous.

Elytra 1.6 times as long as wide, 1.3 times as long as pronotum; sides straight and parallel on basal two-thirds, gradually narrowed, rather broadly rounded behind, with a conspicuous, rather narrow emargination at suture; surface almost smooth, shining, punctures largely con-

fused, small, moderately deep. Declivity much as in *inaffectus* except slightly wider, margins slightly higher, spine more strongly developed but not pointed, spine 3 more distinctly converging mesad, its crest not as high, its apex rounded, distinctly, weakly projecting; subapical margin acutely elevated, projecting moderately to produce sides of median emargination. Glabrous except for an occasional hairlike seta on sides.

TYPE LOCALITY.—Fifteen km SE Cartago, Cartago, Costa Rica.

TYPE MATERIAL.—The unique holotype, presumably a male, was taken at the type locality on 24-IX-63, at 1800 m, No. 196, from a woody vine 5 mm in diameter, by S. L. Wood.

The holotype is in my collection.

Tricolus rufithorax, n. sp.

This species is distinguished from *parsus* Wood by the larger size, by the well-developed declivital spines, by the subserrate anterior margin of the pronotum and by other characters.

FEMALE.—Length 2.7 mm (male 3.1 mm), 2.4 times as long as wide; color reddish brown except elytra black.

Frons convex, reticulate-granulate above, somewhat punctate laterally, subcircular raised, granular area occupying slightly more than median third to upper level of eyes; glabrous except on epistoma. Antennal club moderately large, almost subtriangular, sutures weakly procurved; posterior face bearing two long hairs.

Pronotum 1.2 times as long as wide; outline as in *parsus* except anterior margin less narrowly rounded, its elevated costa weakly serrate; posterior area strongly reticulate, very low, strongly transverse, asperities continuing from summit to base. Glabrous.

Elytra 1.4 times as long as wide, 1.2 times as long as pronotum; outline about as in *parsus* except sutural emargination smaller and spine 3 projecting very slightly; disc smooth, shining, punctures fine, confused. Declivity with contours much as in *parsus* except spine 1 conical, slightly larger, 2 cylindrical, projecting slightly more than its basal width, 3 low, costate, ending abruptly, not projecting, directed toward sutural apex but ending remote from it, subapical margin acutely elevated but less strongly than in *parsus*. Glabrous except for a few setae on sides.

MALE.—Similar to female except without long hair on posterior face of antennal club; declivital spine 2 abnormal, apparently chewed off on both sides.

TYPE LOCALITY.—Finca Gromaco on Rio Coto Brus, Puntarenas, Costa Rica.

TYPE MATERIAL.—The female holotype and male allotype were taken at the type locality on 14-VII-63, at 500 m, No. 65, from a woody vine (liana) less than 1 cm in diameter, by S. L. Wood.

The holotype and allotype are in my collection.

Tricolus badius, n. sp.

This species is distinguished from *nodifer* Blandford by the smaller size, by the reddish brown color, and by the more widely spaced third spines which are very close to the subapical margin.

FEMALE.—Length 2.8 mm (paratypes 2.3-2.8 mm), 2.6 times as long as wide; color reddish brown.

Frons as in *rufithorax* Wood except raised granular area occupying one-fourth space between eyes. Antennal club subcircular, sutures rather weakly procurved; posterior face with up to a dozen long hairlike setae.

Pronotum 1.2 times as long as wide; as in *rufithorax*.

Elytra 1.5 times as long as wide; outline as in *rufithorax* except spine 3 projecting more strongly; disc smooth, shining, with very fine, irregular lines, punctures fine, shallow, confused. Declivity as in *rufithorax* except spine 2 more slender, twice as long as wide; 3 close to costal margin, separated by about half its basal width, subapical margin reaching its posterior margin, spine 3 projecting, subtriangular, almost as high as its basal width; subcostal margin acutely, not strongly elevated. Subglabrous.

MALE.—Similar to female except antennal club with fewer long setae.

TYPE LOCALITY.—Pandora, Limon, Costa Rica.

TYPE MATERIAL.—The female holotype, male allotype, and 16 paratypes were taken at the type locality on 23-VIII-63, 50 m, Nos. 147, 150, from a tree branch, by S. L. Wood. One paratype is from Peralta, Cartago, Costa Rica, 10-III-64, 500 m, No. 462, woody vine, one paratype is from Cerro Punta near Volcan Chiriqui, Chiriqui, Panama, 11-I-64, 1800 m, No. 376, tree branch; 13 paratypes are from Ft. Clayton, Canal Zone, Panama, 22-XII-63, from various collections; all taken by me.

The holotype, allotype, and paratypes are in my collection.

Tricolus partilis, n. sp.

This species is distinguished from *nodifer* Blandford by the smaller size, by the brown color, by the more slender body form, by the more slender spine 3 on the elytral declivity, and by other characters.

MALE.—Length 1.8 mm (paratypes 1.7-1.8 mm), 2.8 times as long as wide; color brown.

Frons as in *nodifer* except granular area distinctly elevated; antennal club subcircular.

Pronotum 1.3 times as long as wide; as in *nodifer* except transverse crenulations in discal area reduced to a few transverse lines.

Elytra 1.7 times as long as wide, 1.3 times as long as pronotum; essentially as in *nodifer* except spines 1, 2, and 3 more slender, 3 distinctly longer; lower declivity less broadly flattened; subapical margin more strongly elevated.

FEMALE.—Similar to male except posterior face of antennal club with several long hairlike setae.

TYPE LOCALITY.—Volcan, Puntarenas, Costa Rica.

TYPE MATERIAL.—The male holotype, female allotype, and one paratype were taken at the type locality on 11-XII-63, at 1000 m, No. 304, from a tree branch, by S. L. Wood. One paratype is from Finca Gromaco on Rio Coto Brus, Puntarenas, 14-VII-63, 500 m, No. 59, tree branch, S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Tricolus fenoris, n. sp.

This species is distinguished from *partilis* Wood by the larger size, by the more slender body form, and by the longer, more slender declivital spines.

MALE.—Length 2.1 mm, 3.0 times as long as wide; color very dark brown.

Frons, antenna, and pronotum as in *partilis*; pronotum 1.3 times as long as wide.

Elytra 1.7 times as long as wide, 1.3 times as long as pronotum; as in *partilis* except spine 2 three times as long as wide, spine 3 about one and one-half times as long as wide; subapical margin more strongly produced.

TYPE LOCALITY.—Fifteen km SE Cartago, Cartago, Costa Rica.

TYPE MATERIAL.—The unique male holotype was taken at the type locality on 24-IX-63, at 1800 m, No. 196, from a woody vine, by S. L. Wood.

The holotype is in my collection.

Tricolus frontalis, n. sp.

This species is distinguished by the aciculate frons, with the granular area absent, and by the slender declivital spine 3.

FEMALE.—Length 2.4 mm, 3.1 times as long as wide; color dark brown.

Frons convex, aciculate, granulate area absent.

Pronotum 1.3 times as long as wide; as in *fenoris* Wood except anterior margin more broadly rounded.

Elytra 1.9 times as long as wide, 1.5 times as long as pronotum; about as in *fenoris* except declivital spine 3 longer, almost three times as long as wide, spine 3 similar in shape to 2 but larger, about two and one-half times as long as wide; subapical margin rather poorly elevated.

TYPE LOCALITY.—Eight km NE Teziutlan, Puebla, Mexico.

TYPE MATERIAL.—The unique male holotype was taken at the type locality on 27-VI-53, at 1600 m, from a tree branch, by S. L. Wood.

The holotype is in my collection.

Tricolus capitalis, n. sp.

This species is distinguished from *ruficollis* (Fabricius) by the slightly smaller size and by the much less strongly elevated subapical margin of the elytral declivity (thereby eliminating the sutural notch).

FEMALE.—Length 2.1 mm, 2.7 times as long as wide; color rather dark reddish brown.

Frons convex, finely rugose-reticulate; granular area distinctly elevated, subcircular, occupying median third to upper level of eyes; glabrous. Antennal club rather broadly obovate, sutures moderately procurved.

Pronotum 1.3 times as long as wide; sides straight and parallel on basal half, rather narrowly rounded in front; anterior margin armed by about eight coarse teeth (bases of some contiguous); summit indefinite, about one-third pronotum length from anterior margin; anterior slope rather coarsely, closely asperate; posterior areas reticulate, punctures fine, those near base with transverse line or minute shining elevation. Glabrous.

Elytra 1.6 times as long as wide, 1.2 times as long as pronotum; disc smooth, shining, punctures rather fine, shallow, confused. Declivity excavated basically as in other members of the genus; spine 3 stout, subtriangular, projecting

slightly, as in *ruficollis*, separated from subapical margin by width of spine; lower declivity flattened below spine 3 to lateral margin of spine 3; subapical margin almost straight, rather weakly elevated, without sutural emargination, not at all produced as in *ruficollis*.

TYPE LOCALITY.—Thirteen km S El Hato del Volcan, Chiriqui, Panama.

TYPE MATERIAL.—The female holotype and one female paratype were taken at the type locality on 7-I-64, at 1000 m, No. 371, from a tree seedling, by S. L. Wood.

The holotype and paratype are in my collection.

Tricolus naevus, n. sp.

This species is distinguished from *ovicollis* Blandford by the slightly larger size, by the very broad subreniform granular area on the frons, by the narrowly flattened area below declivital spine 3, and by the much stouter declivital spine 3.

FEMALE.—Length 2.9-3.3 mm, 2.7 times as long as wide; color almost black.

Frons broadly convex, with lateral areas just above epistoma conspicuously impressed; sculpture of lower area irregular, smooth and shining laterally, becoming subreticulate above; granular area very broad, occupying median two-thirds of area between eyes at least three times longer than wide, its lower margin almost straight, strongly emarginate on its upper margin. Antennal club subtriangular but narrower than in *ovicollis*.

Pronotum 1.3 times as long as wide; as in *ovicollis* except anterior margin more narrowly rounded and more coarsely serrate.

Elytra 1.6 times as long as wide, 1.2 times as long as pronotum; as in *ovicollis* except declivital area below spine 3 flattened only to median margin of spine 3; spine 3 stout, subtriangular, its length about equal to its basal width. Subglabrous.

TYPE LOCALITY.—Tapanti, Cartago, Costa Rica.

TYPE MATERIAL.—The female holotype and two female paratypes were taken at the type locality on 24-X-64, 1300 m, No. 241, from a *Phoebe mexicana* branch, by S. L. Wood. One female paratype bears identical data except it is No. 244, from a woody vine, and one with identical data is 26-XI-64, No. 271, *Werklia insignata*.

The holotype and paratypes are in my collection.

Tricolus scitulus, n. sp.

This species is distinguished from *ovicollis* Blandford by the smaller size, by the uniform brown color, and by the flatter lower declivity below spine 3.

FEMALE.—Length 1.9-2.3 mm, 2.6 times as long as wide; color dark brown, young adults uniformly brown.

Frons and pronotum as in *ovicollis* except anterior margin of pronotum more narrowly rounded. Antennal club not quite as broad.

Elytra as in *ovicollis* except area below spine 3 flatter.

MALE.—Similar to female except antennal club slightly smaller, with fewer long setae on posterior face.

TYPE LOCALITY.—Tapanti, Cartago, Costa Rica.

TYPE MATERIAL.—The female holotype, male allotype, and nine paratypes were taken at the type locality on 26-XI-63, at 1300 m, Nos. 241, 265, from *Phoebe mexicana* branches, by S. L. Wood. One paratype is from Turrialba, Cartago, Costa Rica, 5-VII-63, 700 m, No. 23, *Crotalaria*, S. L. Wood. One paratype is from Cerro Punta near Volcan Chiriqui, Chiriqui, Panama, 11-I-64, 1800 m, No. 406, tree branch, S. L. Wood. A series from La Carbonera Experimental Forest, 50 km NW Merida, Merida, Venezuela, was not included in the type series.

The holotype, allotype, and paratypes are in my collection.

Tricolus peltatus, n. sp.

This species is distinguished from the similar but remotely related *nodifer* Blandford by the subapical tubercle on declivital spine 3, by the less strongly elevated subapical margin on the declivity, by the longer declivital spine 3, and by other characters.

FEMALE.—Length 3.0 mm (paratypes 2.7-3.1 mm), 3.0 times as long as wide; color very dark brown.

Frons, pronotum, and elytral disc as in *nodifer*, except granular area on frons slightly larger. Pronotum 1.3 times as long as wide.

Elytral declivity with basic contours as in *nodifer*, except spine 1 slightly larger, spine 2 more slender; spine 3 slightly longer than wide, more erect than in *nodifer*, with a conspicuous tubercle on dorsomedian subapical margin; subapical margin less strongly produced and less strongly elevated than in *nodifer*.

MALE.—Similar to female except posterior face of antennal club without long hair.

TYPE LOCALITY.—Cerro Punta near Volcan Chiriqui, Chiriqui, Panama.

TYPE MATERIAL.—The female holotype, male allotype, and two paratypes were taken at the type locality on 11-I-64, 1800 m, No. 376 (holotype), 392 (allotype), 372 and 385 (paratypes), from tree branches and a woody vine (No. 385), S. L. Wood. Three paratypes are from Volcan Poas, Heredia, Costa Rica, 19-XI-63, 2500 m, No. 260, tree seedling, S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Tricolus aciculatus, n. sp.

This species is distinguished from *peltatus* Wood by the smaller size, by the more slender form, by the absence of a raised granular area on the frons, and by the presence of a very small granule in each puncture in the excavated area of the declivity.

FEMALE.—Length 2.7 mm (paratypes 2.2-2.7 mm), 3.1 times as long as wide; color very dark brown.

Frons convex, rather weakly impressed above epistoma in lateral areas; surface shining, conspicuously aciculate on lateral thirds, obscurely on median third, granular area found in other species entirely absent; median area above epistoma with a broad, low, elevated area somewhat similar to allied species. Antennal club large, broadly, asymmetrically oval, sutures almost straight, obscure, indistinctly septate on central third; a very few long setae on posterior face.

Pronotum 1.3 times as long as wide; pronotum as in *nodifer* Blandford except anterior margin finely subserrate.

Elytra 1.7 times as long as wide, 1.4 times as long as pronotum; elytra as in *peltatus* except more slender, discal punctures slightly larger, punctures on declivital face each with a fine granule; declivital spines 2 and 3 more slender than in *peltatus*, 3 distinctly longer, bearing a subapical tubercle as in *peltatus*; subapical margin of declivity as in *peltatus* except from dorsal aspect median fifth abruptly, shallowly emarginate. Subglabrous.

MALE.—Similar to female except posterior face of antennal club without long hair.

TYPE LOCALITY.—Ten km or 6 miles SE Tezuitlan, Puebla, Mexico.

TYPE MATERIAL.—The female holotype, male allotype, and 46 paratypes were taken at the

type locality on 2-VII-67, at 1600 m, Nos. 137 and 145, from small *Miconia* branches, No. 142 from *Rubus*, No. 149 host unknown, by S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Tricolus bicolor, n. sp.

This species is distinguished by the color pattern, by the more dorsal position of the frontal granular area, and by the unique declivity.

FEMALE.—Length 3.4 mm (paratype 3.1 mm), 2.7 times as long as wide; color of dorsal surface yellowish brown except pronotal disc from summit to base and elytral declivity black, ventral surface black except legs light brown.

Frons largely concealed, evidently convex above, shallowly impressed on lateral thirds of lower half, median area distinctly elevated above epistoma; granular area more dorsal in position than normal, largely above upper level of eyes, apparently wider than long. Antennal club slightly asymmetrical, sutures weakly procurved.

Pronotum 1.1 times as long as wide; sides feebly arcuate and subparallel on basal half, rather strongly converging anteriorly to rather narrowly rounded, serrate anterior margin; sculpture about as other *Tricolus*.

Elytra 1.7 times as long as wide, 1.5 times as long as pronotum; sides straight and parallel to level of sutural apex, truncate behind except for projecting spine 3 and small sutural emargination; disc and upper declivity about as in *nodifer* Blandford except declivital excavation more broadly impressed; spine 3 on extreme posterolateral margin, somewhat laterally compressed, appearing quadrate from lateral aspect, distinctly longer than wide, with a conspicuous tubercle on dorsomedian apical angle, its mesal surface somewhat concave or grooved toward its apex; subapical margin acutely, weakly elevated, a shallow sutural emargination.

TYPE LOCALITY.—Lower slopes of Volcan Poas, 24 km NW Heredia, Costa Rica.

TYPE MATERIAL.—The female holotype and one female paratype were taken at the type locality on 14-VII-63, 1500 m, No. 44, from a small branch, by S. L. Wood.

The holotype and paratype are in my collection.

Tricolus amplus, n. sp.

This species is distinguished by the large size, by the black color, by the displaced de-

clivital spine 2, by the subtriangular granular area on the frons, and by other characters.

FEMALE.—Length 3.7 mm (paratypes 3.6-3.9 mm), 2.5 times as long as wide; color black.

Frons convex above, lateral areas above epistoma moderately impressed, lateral areas below upper level of eyes distinctly acieulate; median granular area largely above eyes, wider than long, subtriangular, its apex directed orad; vestiture of short, sparse hair. Antennal club slightly asymmetrical, obscurely subtriangular, sutures weakly procurved.

Pronotum 1.13 times as long as wide; about as in *bicolor* except basal area of disc more coarsely, more extensively asperate.

Elytra 1.4 times as long as wide, 1.3 times as long as pronotum; outline as in *bicolor* except posterior margin bisinuate; disc subshining, almost smooth, punctures very fine, shallow, confused. Declivity much as in allied species except lateral margin less abruptly, less strongly elevated; spine 1 in usual position at base on interstriae 1; spine 2 larger and stouter than usual and in position of interstriae 2, its base beginning at level of apex of spine 1 (much more anterior in position than all other species); spine 3 strongly, laterally compressed, on lateral margin, quadrate, distinctly wider than long, a conspicuous tubercle on its dorsomesal apical angle; subapical margin acute, distinctly, not strongly produced, extending to base of spine 3. Subglabrous.

MALE.—Similar to female, including long hair on posterior face of antennal club.

TYPE LOCALITY.—Ten km or 6 miles NE Teziutlan, Puebla, Mexico.

TYPE MATERIAL.—The female holotype, male allotype, and six paratypes were taken at the type locality on 2-VII-67, at 1600 m, No. 140, from a limb 5-15 cm in diameter, by S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Amphicranus mirandus, n. sp.

This species is distinguished from *hybridus* Blandford by the pronounced sexual dimorphism, by the cleft female epistoma, by the more slender antennal club, by the absence of an elevated line on the lateral margins of the pronotum, and by the very different declivity.

FEMALE.—Length 2.5 mm (paratypes: females 2.5-2.8 mm, males 2.8-3.5 mm), 3.3 (male 3.9) times as long as wide; color yellowish

brown except anterior third of pronotum and elytral declivity darker brown.

Frons convex above, weakly, transversely impressed just below upper level of eyes, epistomal area protuberant and sharply cleft on median line from epistomal margin to transverse impression; surface subrugose-reticulate, a few fine punctures obscurely indicated; glabrous except along epistomal margin and on sides of head near eyes. Antennal funicle 2-segmented; club 1.6 times as long as wide, oval, sutures weakly procurved, posterior face with some long hair.

Pronotum 1.4 times as long as wide; widest at base, sides straight distinctly converging on basal three-fourths, very broadly rounded in front; anterior margin unarmed; summit on anterior fifth; anterior slope very steep, asperities rather sparse; posterior areas finely reticulate, punctures minute, obscure. Glabrous.

Elytra 1.9 times as long as wide, 1.4 times as long as pronotum; sides almost straight and parallel on basal three-fourths, broadly, rather deeply U-shaped behind between lateral processes; declivity confined to posterior two-fifths; disc as in *hybridus*. Declivity basically as in *hybridus*; interstriae 1 at base with a minute tubercle, 2 with a slender spine about three times as long as its basal width; lateral margin following same course as in *hybridus* but only weakly elevated and not serrate; lateral processes about as long as their basal widths, separated by slightly greater distance than depth of emargination between them; mesal margin of terminal processes bearing a strongly elevated, laterally compressed, longitudinal process, its upper margin horizontal, its posterior margin subvertical. Disc glabrous, rather sparse, fine hair on declivity.

MALE.—Similar to female except frons broadly convex, epistomal area normal; anterior margin of pronotum vertical, appearing shallowly, broadly emarginate from above; declivital spines and lateral processes distinctly longer; lateral declivital processes with margins directed mesad (not dorsad) thereby forming a pronounced constriction in area of emargination just anterior to its middle; face of declivity glabrous.

TYPE LOCALITY.—Rincon de Osa, Puntarenas, Costa Rica.

TYPE MATERIAL.—The female holotype, male allotype, and 30 paratypes were taken at the type locality on 11-VIII-66, at 30 m, No. 85, from a tree limb 5-15 cm in diameter, by S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Amphicranus tornatilis, n. sp.

This species is distinguished from *spectabilis* (Wood) by the larger size, by the color, by the coarsely serrate, more narrowly rounded anterior margin of the pronotum, and by the more gradual, more strongly explanate elytral declivity.

FEMALE.—Length 2.7 mm (paratypes 2.5-2.8 mm), 3.5 times as long as wide; color yellowish brown with head, anterior half of pronotum, and posterior half of elytra black.

Frons as in *spectabilis*.

Pronotum 1.6 times as long as wide; as in *spectabilis* except anterior margin more narrowly rounded and armed by nine coarse serrations, median one prominent, and posterior areas less strongly reticulate, more shining.

Elytra 1.9 times as long as wide, 1.3 times as long as pronotum; as in *spectabilis* except disc very smooth, brightly shining, declivity not as steep, posterior margin more strongly explanate, and upper slope of lower major prominence on margin of declivity horizontal (as in *speciosus* Schedl), not ascending. Glabrous.

TYPE LOCALITY.—Six km S San Vito, Puntarenas, Costa Rica.

TYPE MATERIAL.—The female holotype and seven paratypes, apparently all females, were taken at the type locality on 19-21-III-67, from a dead tree, by D. D. Sliwa.

The holotype and paratypes are in my collection.

Amphicranus macellus, n. sp.

This species is distinguished from *balteatus* Blandford by the much smaller size, by the color, by the absence of a granular area on the frons, by details of the declivital sculpture, and by other characters.

MALE.—Length 1.9 mm (paratypes 1.8-1.9 mm), 4.0 times as long as wide; color yellowish brown.

Frons uniformly convex; surface evidently minutely rugose-reticulate. Antennal funicle 3-segmented; club 1.3 times as long as wide, broadly oval, sutures rather weakly procurved.

Pronotum 1.8 times as long as wide; sides straight and almost parallel on basal three-fourths, rather narrowly rounded in front; anterior margin acutely elevated, subserrate except median serration slightly larger and basally separate from marginal costa; indistinct summit

on anterior fourth; anterior slope steep, convex, most conspicuous asperities arranged in a sub-transverse row; surface subreticulate, punctures small, very shallow. Glabrous.

Elytra 2.4 times as long as wide, 1.4 times as long as pronotum; outline as in *balteatus* except apical emargination wider, U-shaped; disc smooth, stria punctures fine, shallow, in rows. Declivity broadly, deeply excavated much as in *balteatus* except steeper and somewhat less strongly explanate; basal margin with spines on interstriae 1 and 2 minute, spine on 3 moderately large, pointed, lateral margin acutely, strongly elevated to small denticle on mesal side at level of sutural apex, margin obliquely descending from denticle to apex of lateral process on a straight line; sutural emargination narrowly U-shaped, 1.5 times as deep as wide; declivital face reticulate, shining, punctures very obscurely indicated. Glabrous.

FEMALE.—Similar to male except declivity less strongly explanate, its lateral margin less strongly elevated; sutural emargination as long as wide.

TYPE LOCALITY.—Rincon de Osa, Puntarenas, Costa Rica.

TYPE MATERIAL.—The male holotype, female allotype, and two male paratypes were taken at the type locality on 11-VIII-66, at 30 m, No. 85, from a tree limb, by S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Amphicranus spinescens, n. sp.

This species is distinguished by the absence of a fine, raised line on the lateral margins of the pronotum, by the very coarse, slender serrations on the anterior margin of the pronotum, and by the different armature on the elytral declivity.

FEMALE.—Length 2.4 mm (paratypes 2.0-2.4 mm), 4.4 times as long as wide; color yellowish brown, anterior half of pronotum and posterior third of elytra a darker brown.

Frons transversely concave, lower third weakly, transversely impressed, surface rugose-reticulate except subgranular on oval area on median half at upper level of eyes; vestiture confined to epistomal margin. Antennal funicle 3-segmented; club oval, 1.4 times as long as wide.

Pronotum 1.8 times as long as wide; sides straight and parallel on basal two-thirds, narrowly, strongly produced in front; anterior margin armed by 10-12 very coarse, basally sepa-

rate serrations, median ones slender; summit on anterior third; anterior slope moderately steep, convex, anterior asperities coarse, smaller toward summit; posterior areas finely reticulate, punctures minute, almost obsolete. Glabrous.

Elytra 2.4 times as long as wide, 1.4 times as long as pronotum; sides straight and parallel to declivity, broadly emarginate behind, posterolateral angles produced into long forceps-like processes; disc smooth, subshining, stria punctures almost obsolete. Declivity steep, excavated; basal margin subacutely elevated, armed by three small, pointed denticles one each at interstriae 1, 2, and 3; lateral margin subacutely elevated, bearing just below middle of declivity a very large, cylindrical, blunt spine 3.5 times as long as its basal width, directed caudad, below this spine lateral margin continues to apex of ventrolateral process; ventrolateral process subcylindrical, curving slightly mesad, its length measured from apex of suture equal to more than half width of elytra; posterior emargination very broad, deep, broadly U-shaped, very slightly deeper than wide.

MALE.—Similar to female except declivital spines slightly longer.

TYPE LOCALITY.—Rincon de Osa, Puntarenas, Costa Rica.

TYPE MATERIAL.—The female holotype, male allotype, and 18 paratypes were taken at the type locality on 11-VIII-66, at 30 m, No. 85, tree limb, by S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Amphicranus spinosus, n. sp.

This species is distinguished from *spinescens* Wood by the larger size, by the finely punctured pronotal disc, and by the more brightly shining elytra.

FEMALE.—Length 2.7 mm (male paratypes 2.8-3.0 mm), 4.0 times as long as wide; color brown.

As in *spinescens* except posterior areas of pronotal disc reticulate, with moderately abundant, fine, distinctly impressed punctures in both discal and lateral areas and elytra much more brightly shining.

MALE.—Similar to female except declivital spines slightly longer.

TYPE LOCALITY.—Rincon de Osa, Puntarenas, Costa Rica.

TYPE MATERIAL.—The female holotype, male allotype, and two male paratypes were taken

at the type locality on 11-VIII-66, at 30 m, No. 85, from a tree limb, by S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Amphicranus mucronatus, n. sp.

This species is distinguished from *fastigiatus* Blandford by the smaller size, by the very different female frons, and by the narrower posterolateral elytral processes of the male on which the spine at the level of the sutural apex is positioned equidistant from the lateral and mesal margins (not on the lateral margin as in *fastigiatus*).

FEMALE.—Length 2.7 mm, 4.0 times as long as wide; color light brown, pronotum and elytral declivity darker.

Frons convex, reticulate below upper level of eyes, shining above, punctures fine, moderately abundant, obscure on reticulate area; median fourth from epistoma more than half distance to upper level of eyes with a sharply elevated, low, oval, granulate area; vestiture inconspicuous. Antennal club transversely oval, slightly wider than long.

Pronotum 1.7 times as long as wide; as in *fastigiatus* except submarginal grooves and callus on anterior slope much more poorly developed.

Elytra as in *fastigiatus* except discal punctures slightly smaller.

MALE.—Length 3.0-3.3 mm; similar to male *fastigiatus* except antennal club slightly more broadly oval; anterior margin of pronotum more strongly, narrowly acuminate, process on its ventral surface almost obsolete; elytral declivity slightly less strongly explanate, lateral margins much less strongly elevated, denticles on basal margin much smaller, denticle at level of sutural apex in center of floor of lateral process (not on inner surface of lateral margin as in *fastigiatus*).

TYPE LOCALITY.—Cerro Punta near Volcan Chiriqui, Panama.

TYPE MATERIAL.—The female holotype, male allotype, and one male paratype were taken at the type locality on 11-I-64, at 1800 m, from a tree branch, by S. L. Wood.

The holotype, allotype, and paratype are in my collection.

Amphicranus acus, n. sp.

This species is distinguished from *fastigiatus* Blandford by the smaller size, by the different

female frons, by the more slender male pronotal process, and by the male elytral declivity.

FEMALE.—Length 2.5 mm (female paratype 2.5 mm), 4.0 times as long as wide; color light reddish brown, anterior parts of pronotum and elytral declivity sometimes darker.

Frons about as in female *fastigiatus* except reticulate to vertex, median area on lower half rather strongly elevated but not sharply defined, its summit narrowly flattened and granular. Antennal club obscurely subtriangular, 1.3 times as wide as long.

Pronotum 1.8 times as long as wide; as in *fastigiatus* except grooves and submarginal ridges on anterior slope more pronounced. Elytra as in *mucronatus* Wood.

MALE.—Length 2.5-2.8 mm; as in male *mucronatus* except granular area on frons narrower, extending to upper level of eyes; lower surface of pronotal mucronate process with a rather strongly developed, conical tubercle directed ventrad; lateral margin of declivity slightly higher, a coarse denticle displaced just mesad of lateral margin at level of sutural apex, posterodorsal angle rounded and entirely devoid of a tubercle, sutural emargination much narrower.

TYPE LOCALITY.—El Laurel Experiment Station, 12 km SW Caracas, Venezuela.

TYPE MATERIAL.—The female holotype, male allotype, and three paratypes were taken at the type locality on 1-V-70, 1800 m, Nos. 457, 458, from a tree bole 13 cm in diameter, No. 513 in flight, by S. L. Wood. One broken male paratype is from Merida, Merida, Venezuela, 11-IX-69, 2000 m, No. 4, *Croton* bole, S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

Paracorthylus mutilus, n. sp.

This species is distinguished from *concisus* Wood by the smaller size, by the shallowly divaricate sutural apex of the elytra, and by the distinctive elytral declivity.

FEMALE.—Length 2.0 mm (paratypes 1.9-2.0 mm), 2.7 times as long as wide; color reddish brown.

Frons as in *velutinus* Wood except surface reticulate above shining epistomal margin. Antennal club 1.4 times as long as wide, apical segment only slightly modified.

Pronotum 1.1 times as long as wide; as in *velutinus* except surface reticulate, punctures very fine, much less closely spaced.

Elytra 1.4 times as long as wide, 1.2 times as long as pronotum; as in *velutinus* except declivity. Declivity subvertical, subtruncate, shallowly concave; lateral margins distinctly elevated, rounded, armed on middle third on median margin by two pointed tubercles, upper one slightly larger; sutural interstriae weakly elevated; posterolateral margin subacute at apex, suture weakly emarginate; surface rugose-reticulate; punctures obscure. Very minute setae moderately abundant on declivity, similar but less abundant on disc.

MALE.—Similar to female except apical segment of antennal club slightly shorter and more broadly rounded; anterior margin armed by eight serrations of moderate size; declivity more evenly concave, its margins weakly, subacutely elevated on more than lower three-fourths, upper margin armed by three pairs of small teeth on interstriae 1-3, lateral pair conspicuously larger, sutural apex more distinctly emarginate, sutural interstriae more distinctly elevated.

TYPE LOCALITY.—Fort Sherman, Canal Zone, Panama.

TYPE MATERIAL.—The female holotype, male allotype, and two female paratypes were taken at the type locality on 10-XI-57, at light.

The holotype, allotype, and paratypes are in my collection.

Paracorthylus concisus, n. sp.

This species is distinguished from *velutinus* Wood by the larger size, by the subconcave elytral declivity, with different armature in the

female, by the sparse pubescence, and by other characters.

FEMALE.—Length 2.6 mm (paratypes 2.3-2.6 mm), 2.6 times as long as wide; color reddish brown.

Frons as in *velutinus* except obscurely reticulate, shining, median carina extending from epistomal margin to median callus on lower third. Antennal club 1.9 times as long as wide, about intermediate in shape between *velutinus* and *mutilus*.

Pronotum 1.1 times as long as wide; as in *mutilus*.

Elytra 1.4 times as long as wide, 1.2 times as long as pronotum; as in *mutilus* except tubercles slightly larger and apex of suture entire.

MALE.—Similar to female except antennal club less elongate, its apex more broadly rounded; anterior margin of pronotum armed by eight serrations; declivity much more broadly, evenly impressed, margins on lower half more distinctly, more narrowly elevated but not angulate, sutural apex entire and bent slightly dorsad, two pair of tubercles on interstriae 3 displaced mesad from lateral margin, lower one at middle, upper one on basal fourth.

TYPE LOCALITY.—Moravia, Cartago, Costa Rica.

TYPE MATERIAL.—The female holotype, male allotype, and 14 paratypes were taken at the type locality on 11-III-64, 500 m, No. 473, from a cut tree 35 cm in diameter, by S. L. Wood.

The holotype, allotype, and paratypes are in my collection.

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**TAXONOMY OF THE GENUS
CHLORIS (GRAMINEAE)**

by

Dennis E. Anderson



BIOLOGICAL SERIES — VOLUME XIX, NUMBER 2
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TAXONOMY OF THE GENUS *CHLORIS* (GRAMINEAE)

by

Dennis E. Anderson¹

ABSTRACT

This study is a worldwide taxonomic treatment utilizing endomorphic characters such as cytology, histology, and embryology, in addition to the traditional exomorphic features. New chromosome numbers and histological information are reported. Relationships between *Chloris* and other genera in the Chlorideae are discussed. A total of 56 species is recognized in the genus; each is described and illustrated. Complete synonymies are included as well as a list

of unidentified or rejected names. Distributions and maps are given for each species, along with lists of specimens examined during studies at various herbaria. Reports of field studies involving introgression among certain species are also included. A new species, *Chloris burmensis*, is described from Burma, and a new combination, *Chloris canterai* Arecb. var. *grandiflora* (Rosengurtt & Izaguirre de Artucio) Anderson, is also proposed.

ACKNOWLEDGMENTS

These studies were begun in the summers of 1963 and 1964 as part of a National Science Foundation program in Research Participation for College Teachers sponsored by the Department of Botany, University of Texas. Additional financial support was provided by this program through grants (NSF GY-3002, NSF GE-6958). The assistance of Dr. Harold Bold, director of the summer program, is also gratefully acknowledged. Initially, Dr. Walter V. Brown pointed out to me many of the biosystematic problems of *Chloris* in Texas, and I am grateful to him for his continued encouragement.

Additional direct assistance was received from the National Science Foundation in 1969 (NSF GB-7235), enabling me to visit a number of major overseas herbaria and to do additional field work. The curators were most helpful and allowed me to borrow many specimens. Their cooperation is much appreciated.

A special debt is owed to Dr. W. D. Clayton of the Royal Botanic Gardens, Kew, England, who provided advice, cooperation and friendship, and thus made my stay at Kew most productive.

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I would also like to thank Mr. Rupert C. Barneby for his aid in the preparation of the Latin description of *Chloris burmensis*.

Michael Lazarides kindly let me examine his manuscript treatment of *Chloris* in Queensland, prior to its publication.

I am grateful to my wife, Nancy, for the endless hours she contributed in filing and organization, in establishing and verifying geographical locations, and, finally, in cartography.

INTRODUCTION

With its delicate, digitate clusters of spikes, *Chloris* must certainly be among the most striking of grass genera. The distribution spans the warmer regions of most of the continents, from the pampas of Argentina to the sandhills

of Nebraska, from the Cape of Good Hope to the sands of the Sahara, from Afghanistan to the island archipelagoes of the South Pacific, and from the subcontinental islands of New Guinea and Borneo through the continent of

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Australia. Thus, it is likely that taxonomists in these areas have seen one or more of the taxa in the genus. Though these attributes would seem to insure popularity among agrostologists, *Chloris* nevertheless has not been subjected to any systematic review for nearly a century. This has been an era characterized by extensive exploration and collection of hitherto unknown areas, as well as the development of revolutionary systematic thought.

My interest in *Chloris* began with studies in hybridizing species in Texas; this interest spread later to similar studies in the Southeast; and ultimately it encompassed more classical investigations in many of the major herbaria of the United States, Great Britain, and Europe. Initially, my interests centered in experimental studies but the continuing frustration of not being able to name species with confidence led

me to conclude that a classical study was needed and that experimental studies could then be made on a sounder foundation.

Well over 15,000 herbarium specimens and many mass collections from hybridizing populations were studied. The numbers of specimens available vary widely. Some taxa are represented only by the holotype. Others are known from such large numbers of specimens that population descriptions may be advanced with confidence. Still others have been collected so thoroughly that the enormous complexity of the population has revealed the necessity for further intensive investigation.

This study, then, attempts to bring the taxonomy of the genus *Chloris* up to date. It is largely morpho-geographical in nature, with occasional incursions into biosystematics as the nature and availability of materials allow.

NOMENCLATURAL HISTORY OF THE GENUS

Swartz first described *Chloris* in 1788, including two new species, *C. ciliata* and *C. petraea*, and transferred into the genus three Linnaean species: *Agrostis cruciata*, *Agrostis radiata*, and *Andropogon polydactylon*.

With the description of the genus *Eustachys* by Desvoux (1810) and the transfer to it of *Chloris petraea* Swartz, the basic nomenclatural pattern at the generic level was established, though many authors now consider *Eustachys* as a subgenus of *Chloris*.

Other genera, based on various species of *Chloris*, have been proposed: *Rabdochloa* Beauvois (1812), including *C. cruciata* and several species from other genera; *Schultesia* Sprengel (1815) containing *C. petraea* only; and *Phacellaria* Willdenow ex Steudel (1840), including *C. submutica*. None of these genera have been accepted by recent authors.

More recently, Camus proposed the subgenera *Monanthochloris*, including within it *C. perrieri* (1949), and *Pterochloris*, which contains *C.*

humbertiana (1950). Subsequently, Camus (1957) elevated the latter subgenus to the generic level.

Generic conspecti of *Chloris* have been written sporadically, but all are of the nature of catalogs rather than revisions or monographs. Of these, the treatment by Steudel (1854) is the most complete. In it he recognized 69 taxa and included a synoptic key as well as an enumeration of species, each with a short description. Later listings by Regel (1862, 1863), based upon the specimens at Leningrad, included a total of only 21 taxa.

Regional revisionary studies restricted to *Chloris* are few, the most notable being those of the North American species by Nash (1898), the treatment by Swallen (1939) in *North American Flora*, and the publications by Everist (1935a,b, 1937, 1938) on the Queensland species. Subsequently, Lazarides (1972) treated *Chloris* in his study of the tribe *Chlorideae* in Australia.

TAXONOMIC RELATIONSHIPS OF CHLORIS

Most recent classifications of the Gramineae are based heavily upon cytological and anatomical characteristics; in contrast, the older systems were constructed primarily on the basis of spikelet morphology. The higher categories recognized in the older classifications (especially subfamilies) may be quite artificial. This is reflected most strikingly in the modern systems

by the redefinition of the subfamily Festucoideae, which has had many of its genera distributed to other subfamilies.

All recent treatments have placed *Chloris* and most of the rest of the genera in the tribe Chlorideae in a separate subfamily, which is usually called the Eragrostoideae or Chloridoideae. The number of tribes included in this

subfamily has varied considerably; for example, Gould (1968a) recognized seven.

Throughout the development of the more modern classifications, the group of genera forming the Chlorideae has remained relatively stable, including such familiar genera as *Bouteloua*, *Buchloë*, *Ctenium*, *Cynodon*, *Enteropogon*, *Eustachys*, *Gymnopogon*, and *Tetrapogon*, among others.

The taxonomic parameters of these genera have been widely accepted; yet intensive study of certain complexes immediately reveals the artificiality of many of the genera. Most investigations of generic relationships have been confined to the study of various species of selected genera; seldom have attempts been made to examine the majority of species from a number of viewpoints, especially for endomorphic characters.

A report of such an attempt for *Chloris* follows. The limited availability of material for many taxa has frustrated certain phases of study, most notably those requiring living materials. Areas and species deserving further investigation will be immediately apparent.

The discussion is divided into three areas: cytological, histological, and morphological evidence. An attempt to synthesize these lines of evidence as a basis of classification of the species in the genus follows.

Cytology

No single, extensive attempt to determine chromosome numbers in *Chloris* has been made, and the counts reported in Table 1 are largely taken from incidental reports of chromosome numbers of a variety of grasses. In some cases I have been able to verify the identification of the plant by examining the voucher specimen; for these, the herbarium containing the voucher is indicated in parentheses after the counter's name. Chromosome numbers followed by my name are reported for the first time. Vouchers for these are deposited in the California State University Herbarium at Humboldt.

From Table 1 it can be seen that chromosome numbers have been listed for fewer than half of the species in *Chloris*, and thus, only limited conclusions can be drawn. Most species have a base number of $x=10$ and only infrequently have other numbers been noted. Relatively few diploids have been identified; most species are at various polyploid levels, with the decaploid number of $2n=100$ being the highest known in the genus. Several species have varying chromosome numbers. *Chloris gayana* is noteworthy in this respect, with $2n=20, 30$, and 40 .

There are few studies of reproductive mechanisms. Again, the best-known species is *Chloris gayana*. Moffett (1944) suggested that the spe-

Table 1. Chromosome numbers in the genus *Chloris*.

Species	$2n^1$	Geographic origin	Counted by
<i>Chloris andropogonoides</i>	40	Texas (without precise locality) Texas: Nueces Co. (TAES!); San Patricio Co. (TAES!); Starr Co. (TAES! TEX! UC!) Texas: Hays Co.	Brown (1950) Gould (1960) Anderson 3,282 (HSC)
<i>C. aristata</i>	100	Mexico: Oaxaca (US!) Mexico: Hidalgo (UC! US!) Mexico: Queretaro Mexico: Chiapas	Tateoka (1962a) (as <i>C. rufescens</i>) Gould (1965) (as <i>C. rufescens</i>) Gould (1966) (as <i>C. rufescens</i>) Gould & Soderstrom (1970) (as <i>C. rufescens</i>)
<i>C. berroi</i>	40	Texas: Brazos Co. (as a weed in a grass nursery)	Gould (1960)
<i>C. bournei</i>	40	India (without precise locality)	Janaki-Ammal in Darlington & Janaki-Ammal (1945)
	50	Without locality	Krishnaswamy (1940)
<i>C. canterai</i>	72	Texas: Milam Co. (TAES! UC! US!)	Gould (1958) (as <i>C. polydactyla</i>)
<i>C. chloridea</i>	40	Mexico: Chiapas	Gould & Soderstrom (1970)
	80	Mexico: San Luis Potosi (US!)	Gould (1965)
<i>C. ciliata</i>	40	Texas: Wharton Co. (TEX!) Texas: Walker Co. Botanical Garden, Lyon (cultivated) Dominican Republic: Santiago Texas: Bee Co. (TAES!) Texas: Cameron Co.	Brown (1950) Gould (1958) Singh & Godward (1960) Gould & Soderstrom (1967) Gould (1968b) Anderson 4,546 (HSC)
<i>C. crinita</i>	40	Texas (without precise locality) Argentina: Cafayate	Brown (1951) Bowden & Senn (1962)

Table 1. (continued)

<i>C. cucullata</i>	40	Without locality Texas: Willacy Co. (TEX!) Mexico: Coahuila Texas: Brooks Co. (TAES!); Kerr Co. (TAES!); Kimble Co. (TAES!); Maverick Co. (TAES!); Terrell Co. (TAES! TEX! UC!); Val Verde Co. (TAES!)	Avdulov (1928) Brown (1950) Gould (1966)
	40	Texas: Hays Co. Texas: Travis Co. (3 locations)	Gould (1968b) Anderson 3,279 Anderson 2,609; 2,612; 2,614; 2,654; 3,274; 3,347; 3,356 (all HSC)
<i>C. gayana</i>	20	England (cultivated) Ethiopia; Kenya (Nzoia); South Africa; Southern Rhodesia (Katambora); Sudan; Uganda Southern Rhodesia Texas (without precise locality) central Africa Kenya: Kitale Kenya (cultivated) Texas: Brazos Co. (as a weed in a grass nursery) (TAES!); Kenedy Co.	Hunter (1934) Moffett (1944) Moffett & Hurcombe (1949) Brown (1950) Brown & Emery (1958) Singh & Godward (1963) Pritchard & Gould (1964)
	30	Kenya (cultivated)	Gould (1968) Pritchard & Gould (1964)
	40	Africa Southern Rhodesia central Africa Congo: Kenya (Alengo); Southern Rhodesia; Tanzania; Uganda Kenya: Kitale Tanzania: Kisarawe Kenya: Sierra Leone (cultivated)	Moffett (1944) Moffett & Hurcombe (1949) Brown & Emery (1958) Hutton (1961) Singh & Godward (1963) Tateoka (1965a) Pritchard & Gould (1964)
		Bolivia: Cochabamba	Bowden & Senn (1962)
		Without locality Without locality Without locality Taiwan Dominican Republic: Santiago Mexico: Yucatán Texas: Cameron Co. Pakistan: Karachi, Nazimabad	Avdulov (1928) (as <i>C. barbata</i>) Krishnaswamy (1940) Janaki-Ammal in Darlington & Janaki-Ammal (1945) (as <i>C. barbata</i>) Chen & Hsu (1962) (as <i>C. barbata</i>) Gould & Soderstrom (1967) (as <i>C. barbata</i>) Gould & Soderstrom (1970) Anderson 4,545 (HSC) Baquar and Saeed (1969) (as <i>C. barbata</i>)
<i>C. pilosa</i>	20	Nigeria (seed from USPI, no. 212-386)	Anderson 3,435 (HSC)
	30	Sudan	Thomas in Darlington & Wylie (1955)
<i>C. pluriflora</i>	80	Texas: San Patricio Co. (TAES!); Willacy Co. (TAES!) (Label on voucher indicates that n=42)	Gould (1968b)
<i>C. pycnothrix</i>	30	South Africa	de Wet (1954)
	36	tropical Africa (without precise locality)	Thomas in Darlington & Wylie (1955)
	40	Transvaal: Irene Kenya: Nairobi	Moffett & Hurcombe (1949) Tateoka (1965a)
<i>C. radiata</i>	40	Botanical Garden, Lyon (cultivated)	Singh & Godward (1960)
<i>C. roxburghiana</i>	20	Kenya	Pritchard & Gould (1964)
<i>C. scariosa</i>	40	Australia: Queensland (K!)	Singh & Godward (1960)
<i>C. submutica</i>	ca 65	Without locality	Krishnaswamy (1940)
	80	Mexico (without precise locality) Mexico: Durango Botanical Garden, Berlin (cultivated) Mexico: Michoacán (UC!) Mexico: Chihuahua Mexico: (seed from USPI, no. 216-386)	Avdulov (1931) Gould (1960) Singh & Godward (1960) Gould (1965) Reeder (1971) Anderson (HSC)

Table 1. (continued)

<i>C. truncata</i>	40	Australia (without precise locality) Without locality Australia (seed from USPI, no. 212-389)	Avdulov (1928) Krishnaswamy (1940) Anderson (HSC)
<i>C. verticillata</i>	n=ca 28 2n=40	Texas, Mason Co. Texas: Gray Co. Texas: Archer Co.; Bosque Co.; Brazos Co.; Eastland Co.; Jack Co.; Wise Co.	Gould (1960) Brown (1950) Gould (1968b)
	ca 40 40	Kansas: Shawnee Co. Nebraska: Dundy Co. Texas: Sterling Co. Texas: Travis Co.	Anderson 2,768; 2,769 (HSC) Anderson 2,774; 2,776 (HSC) Anderson 3,002 (HSC) Anderson 3,338; 3,347; 3,356; 3,361; (HSC) Gould (1968b)
<i>C. virgata</i>	63 20	Texas: Montague Co. South Africa: Cape Provinces, Mafeking (K!) Texas (without precise locality) Botanical Garden, Berlin (cultivated) Mexico: Baja California Sur; Coahuila; Queretaro Australia (without precise locality) Texas: Castro Co. (TAES!) India: Gorakhpur Texas: Brewster Co. Madagascar (seed from USPI, no. 219-956)	Moffett & Hurcombe (1949) Brown (1950, 1951) Singh & Godward (1960) Gould (1966) Pritchard & Gould (1964) Gould (1968b) Gupta (1969) Anderson 2,579 (HSC) Anderson (HSC)
	26 30 40	Without locality Without locality Without locality	Thomas in Darlington & Wylie (1955) Krishnaswamy (1940) Krishnaswamy (1940) (as <i>C. caudata</i>)
<i>Chloris</i> -probable hybrids	n=ca 20 n=ca 20 n=ca 31 n=ca 32 n=ca 33 n=ca 36 n=42 2n=ca 56 2n=ca 63	Texas: Brazos Co. (TAES!) Texas: San Patricio Co. Texas: Willacy Co. (TAES!) Texas: Brazos Co. (TAES!) Texas: Llano Co. (TAES!) Texas: Lampasas Co. (TAES!) Texas: Llano Co. Texas: Mason Co. Texas: Williamson Co.	Gould (1960) (as <i>C. subdolicho-stachya</i>) Gould (1960) (as <i>C. latisquamea</i>) Gould (1960) (as <i>C. latisquamea</i>) Gould (1958) (as <i>C. latisquamea</i>) Gould (1960) (as <i>C. subdolicho-stachya</i>) Gould (1958) (as <i>C. latisquamea</i>) Gould (1958) (as <i>C. latisquamea</i>) Gould (1968b) (as <i>C. latisquamea</i>) Gould (1968b) (as <i>C. latisquamea</i>)

*The *n* number is given where the count originally reported is not logically convertible to the *2n* number.

cies was an apomict. Brown and Emery (1958) reported the occurrence of four-nucleate embryo sacs, a character associated with apomicts. Hutton (1961), working with different material, reported eight-nucleate, apparently normal, embryo sacs that also showed delayed embryo and endosperm formation (an unusual feature). These studies were carried out primarily on tetraploids. Bogdan (1961) reported both diploid and tetraploid forms to be sexual. This same conclusion was borne out by circumstantial evidence in the study by Pritchard and Gould (1964).

My own field observations in the *Chloris andropogonoides*-*C. cucullata*-*C. verticillata* hybrid complex show high seedset in plants with low pollen stainability, circumstantially suggesting apomixis in this group.

Leaf Epidermis

The epidermal studies in *Chloris* which are reported here were initiated by Rogers (1967), who examined 36 species in this and allied genera. These studies were later expanded by myself, and a total of 55 species has now been examined.

Rogers studied many epidermal features of a large number of specimens of the wide-ranging species, *Chloris virgata*, in order to establish a basis for the selection of epidermal characters, to determine the spectrum of variation, and to assess the relationship of geographic origin to character expression. Table 2 gives the origin of these specimens and the epidermal characters surveyed.

Rogers's study indicated that the density of prickles varied randomly with respect to geog-

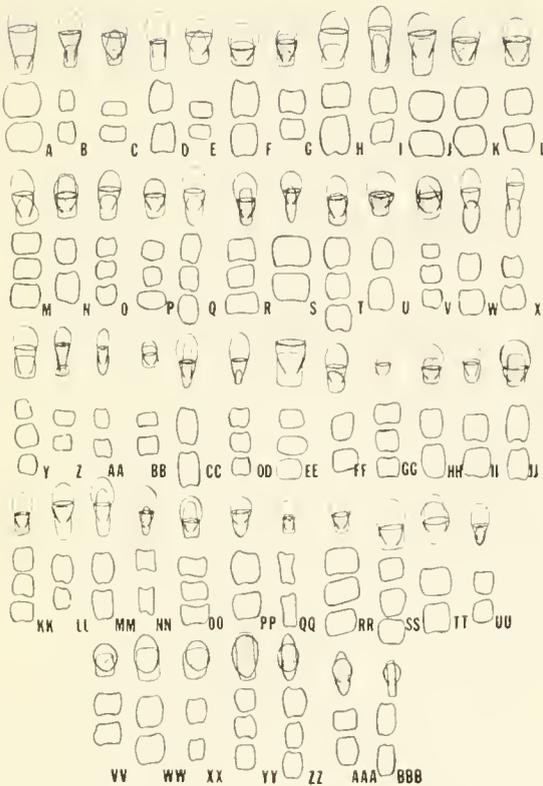


Fig. 1. Microhairs (upper figure of each set) and costal silica cells (lower figure) of *Austrochloris*, *Chloris*, *Enteropogon*, *Eustachys*, and *Tetrapogon*. (A) *Austrochloris dichanthioides* (Everist) Lazarides; (B) *Chloris brandegei* (Vasey) Swallen; (C) *C. divaricata* R. Brown; (D) *C. submutica* Humboldt-Bonpland-Kunth; (E) *Eustachys petraea* Swartz; (F) *Chloris bournei* Rangachariar and Tadulingam; (G) *Eustachys distichophylla* Lagasca; (H) *Chloris scariosa* F. von Mueller; (I) *Eustachys retusa* Lagasca; (J) *Chloris halophila* Parodi; (K) *C. vetricosa* R. Brown; (L) *C. mossambicensis* Schumann; (M) *Tetrapogon macranthus* (Jaubert and Spach) Benthams; (N) *Chloris pectinata* Benthams; (O) *C. robusta* Stapf in Chevalier; (P) *C. paniculata* Scribner in Robinson; (Q) *C. roxburghiana* Schultes; (R) *Tetrapogon spathaceus* (Hochstetter) Hackel ex Durand and Schinz; (S) *Chloris ciliata* Swartz; (T) *C. plicurii* Kunth; (U) *C. sagracana* A. Richard; (V) *C. suringari* Hitchcock in Urban; (W) *Tetrapogon tenellus* (Roxburgh) Chiovenda; (X) *Chloris chloridea* (Presl) Hitchcock; (Y) *C. somaleusis* Rendle; (Z) *Enteropogon dolichostachya* (Lagasca) Lazarides; (AA) *Chloris elementis* Merrill; (BB) *C. radiata* (Linnaeus) Swartz; (CC) *C. texensis* Nash; (DD) *C. mollis* (Nees) Swallen; (EE) *Tetrapogon villosus* Desfontaines; (FF) *Eustachys paspaloides* (Vahl) Lanza and Mattei; (GG) *E. glauca* Chapman; (HH) *Chloris ekmanii* Hitchcock; (II) *C. pumilio* R. Brown; (JJ) *C. cubensis* Hitchcock and Ekman; (KK) *C. dandyana* C. D. Adams; (LL) *Enteropogon acicularis* (Lindley) Lazarides; (MM) *Eustachys neglecta* Nash; (NN) *Chloris truncata* R. Brown; (OO) *C. andropogonoides* Fournier; (PP) *C. berroi* Arechavaleta; (QQ) *C. cruciata*

(Linnaeus) Swartz; (RR) *C. canterai* Arechavaleta; (SS) *C. amethystea* Hochstetter; (TT) *C. lobata* Lazarides; (UU) *Eustachys tenera* (Presl) A. Camus; (VV) *Chloris pycnothrix* Trinius; (WW) *C. aristata* (Cervantes) Swallen; (XX) *C. virgata* Swartz; (YY) *C. pilosa* Schumacher; (ZZ) *C. gayana* Kunth; (AAA) *C. inflata* Link; (BBB) *C. orthoton* Doell in Martius. Arrangement is by overall similarity of microhairs. X 475.

raphy, from absent to moderately abundant. Because of this random variability, prickles were not emphasized as a taxonomic character.

Of the other epidermal characters studied, Rogers concluded that the most stable were shape, size, and type of microhair and the shape of the costal silica cells. Typical microhairs and costal silica cells are illustrated (Fig. 1) for 40 species of *Chloris* and for 14 other species which were formerly placed in *Chloris*, but which are now placed in other genera.

Two types of microhairs, uniceellular and bi-cellular, were observed in the taxa studied. Table 3 lists the species showing these two microhair types. One species complex (consisting of *C. aristata*, *C. gayana*, *C. inflata*, *C. orthoton*, *C. pilosa*, *C. pycnothrix*, and *C. virgata*) possesses uniceellular microhairs. The spikelets and inflorescences of these species are similar to one another, yet they are not unique in the genus, and several strongly resemble particular species with bi-cellular hairs. The remaining species all have bi-cellular microhairs. While several different shapes and sizes of hairs are recognizable, these cannot be correlated with any macroscopic features.

Virtually all of the taxa examined have costal silica cells varying from cuboidal to saddle shaped (Fig. 1; Table 3). Only one species differs from this pattern: *C. cruciata* has costal silica cells which tend to be more elongated and to have more deeply indented end walls than the remaining species.

Anatomy, Embryology, and Seedling Morphology

Anatomical, embryological, and seedling studies on a selected group of 28 taxa in *Chloris* and allied genera were completed by Jensen (1969). The species were selected to be representative of as many different sections of the genus as possible in terms of spikelet morphology. Characteristics studied included leaf anatomy, embryo structure, root-hair position and aspect, shape of the first seedling leaf, and type of starch grains. Individual discussions of these features follow.

Jensen examined several anatomical features of leaf cross sections, including the shape of the

Table 2. Comparison of various epidermal features of *Chloris virgata* collected from different locations. All measurements are in microns. (After Rogers, 1968)

Collection site	Number of prickles per 196 μ^2	Costal silica cells		Stomatal Height	Stomatal apparatus Shape	Intercostal Length	long cells Height	Microhairs Length
		Length	Width					
USA, New Mexico	none to rare	14-17	10-13	21-25	med.-high dome	40-60	11-14	14-16
Mexico, Durango	none	11-15	10-14	14-24	med.-triang. dome	39-65	11-14	12-15
Mexico, Durango	none to 2	13-15	13-15	19-22	med.-triang. dome	40-60	10-12	13-15
Mexico, Yucatan Peninsula	none to 2	9-14	14-16	20-22	med.-triang. dome	40-60	11-13	11-13
Argentina	4-10	11-15	11-14	23-25	med.-triang. dome	40-60	11-13	11-15
Bolivia	2-5	11-12	11-13	19-21	med.-triang. dome	40-60	14-16	11-14
Abyssinia	9-12	10-12	11-14	20-23	med.-triang. dome	60-90	11-13	13-15
Northern Rhodesia	12-20	9-12	10-12	19-21	med. dome	26-40	7-9	12-15
China	none	8-10	8-10	21-25	med. dome	40-50	8-10	11-14
India	none	9-12	11-14	21-23	med.-triang. dome	40-60	9-12	11-14

Table 3. Epidermal characteristics of selected species of *Austrochloris*, *Chloris*, *Enteropogon*, *Eustachys*, and *Tetrapogon*.

Species	Costal silica cell shape	Figure 1 reference
<i>Chloris</i> species with bicellular microhairs		
<i>C. amethystea</i>	cuboidal	SS
<i>C. andropogonoides</i>	saddle	OO
<i>C. berroi</i>	cuboid-saddle	PP
<i>C. bournei</i>	cuboid-saddle	F
<i>C. brandegei</i>	short saddle	B
<i>C. canterai</i>	cuboidal	RR
<i>C. chloridea</i>	saddle	X
<i>C. ciliata</i>	cuboidal	S
<i>C. clementis</i>	cuboid-saddle	AA
<i>C. cruciata</i>	very short saddle to cross shaped	QQ
<i>C. cubensis</i>	short saddle	JJ
<i>C. dandyana</i>	saddle	KK
<i>C. divaricata</i>	narrow saddle	C
<i>C. ekmanii</i>	cuboidal	III
<i>C. halophila</i>	cuboid-saddle	J
<i>C. lobata</i>	cuboidal	TT
<i>C. mollis</i>	saddle	DD
<i>C. mossambicensis</i>	cuboid-saddle	L
<i>C. paniculata</i>	round-cuboid	P
<i>C. pectinata</i>	short saddle	N
<i>C. pricurii</i>	saddle	T
<i>C. pumilio</i>	cuboid-saddle	H
<i>C. radiata</i>	cuboid-saddle	BB
<i>C. robusta</i>	saddle	O
<i>C. roxburghiana</i>	short saddle	Q
<i>C. sagracana</i>	short saddle	U
<i>C. scariosa</i>	cuboid-saddle	H
<i>C. somalensis</i>	cuboid-saddle	Y
<i>C. submutica</i>	short saddle	D
<i>C. suringari</i>	saddle	V
<i>C. tensensis</i>	short saddle	CC
<i>C. truncata</i>	cuboid-saddle	NN
<i>C. ventricosa</i>	cuboid-saddle	K
<i>Chloris</i> species with unicellular microhairs		
<i>C. aristata</i>	cuboid-saddle	WW
<i>C. gayana</i>	cuboid-saddle	ZZ
<i>C. inflata</i>	cuboid-saddle	AAA
<i>C. orthonoton</i>	cuboid-saddle	BBB
<i>C. pilosa</i>	cuboid-saddle	YY
<i>C. pycnothrix</i>	saddle	VV
<i>C. virgata</i>	short saddle	XX
<i>Species formerly in Chloris, now excluded and placed in related genera, all with bicellular microhairs</i>		
<i>Austrochloris dichanthioides</i>	cuboid-saddle	A
<i>Enteropogon acieularis</i>	short saddle	LL
<i>E. dolichostachys</i>	cuboidal	Z
<i>Eustachys distichophylla</i>	cuboid-saddle	G
<i>E. glauca</i>	cuboid-saddle	GG
<i>E. neglecta</i>	short-saddle	MM
<i>E. paspaloides</i>	cuboidal	FF
<i>E. petraea</i>	cuboidal	E
<i>E. retusa</i>	saddle	I
<i>E. tenera</i>	cuboidal	UU
<i>Tetrapogon macranthus</i>	cuboidal	M
<i>T. spathaceus</i>	cuboid-saddle	R
<i>T. tenellus</i>	saddle	W
<i>T. villosus</i>	cuboidal	EE

keel, the disposition of vascular bundles, the texture of the adaxial surface (ribbed or smooth), the extent of the sclerenchyma girder, the distribution of bulliform cells, and the nature of the vascular bundle sheath. While individual species may show stable and recognizable patterns, few correlations between leaf anatomy and spikelet morphology could be made. Likewise, there were no consistent correlations of anatomical features with either microhair or costal silica cell types.

The classical study of Reeder (1957) in comparing anatomical features of embryos of various genera of grasses is well known. Reeder separated the grass genera studied into essentially two groups, panicoid and festucoid, on the basis of four embryo characteristics: (1) whether the lower portion of the scutellum is separate from the rest of the embryo (panicoid) or fused (festucoid); (2) the presence of an epiblast (festucoid) or its absence (panicoid); (3) whether both vascular traces diverge from about the same point (festucoid) or are separated by an elongated area of vascular tissue between points of divergence (panicoid); and (4) whether the margins of the embryonic leaf overlap (panicoid) or just meet (festucoid).

Jensen (1969) studied three of these characteristics for 25 selected species in *Chloris* and certain related segregate genera (Table 4). Typically, all species studied had the scutellum separate from the rest of embryo (panicoid), an epiblast present (festucoid), and vascular traces separated by an elongated area of vascular tissue (panicoid).

The fourth feature, whether or not the margins of the embryonic leaf overlap, was studied on 19 of Jensen's 25 taxa (Table 5). While both festucoid and panicoid types are represented among these species, consistent correlations with other anatomical features or with

Table 5. Comparison of embryonic leaf types in selected species of *Chloris* and related genera.

Species with panicoid embryonic leaves	
<i>Chloris berroi</i>	<i>C. plicurii</i>
<i>C. chloridea</i>	
Species with festucoid embryonic leaves	
<i>Chloris aristata</i>	<i>C. polydactyla</i>
<i>C. bournei</i>	<i>C. pycnothrix</i>
<i>C. canterai</i>	<i>C. radiata</i>
<i>C. cruciata</i>	<i>C. robusta</i>
<i>C. divaricata</i>	<i>C. virgata</i>
<i>C. halophila</i>	<i>Eustachys distichophylla</i>
<i>C. mollis</i>	<i>E. glauca</i>
<i>C. orthonoton</i>	<i>E. neglecta</i>

gross spikelet morphology are absent. Those species with festucoid embryonic leaves, for example, represent diverse forms with respect to microhairs and costal silica cells, as well as spikelet characteristics.

Tateoka (1962b) recognized four starch-grain types—simple, compound, or some variation of each—as being characteristic of various groups of grasses. Jensen reported that compound starch grains were widespread in the species studied, with one notable exception, *Enteropogon acicularis*, which had simple starch grains. This species had been placed in *Chloris* until recently, when it was removed by Lazarides (1972). Jensen found that the following species all have compound starch grains: *Chloris aristata*, *C. berroi*, *C. bournei*, *C. canterai*, *C. chloridea*, *C. cruciata*, *C. dandyana*, *C. divaricata*, *C. gayana*, *C. halophila*, *C. inflata*, *C. mollis*, *C. orthonoton*, *C. plicurii*, *C. pycnothrix*, *C. radiata*, *C. robusta*, *C. submutica*, *C. truncata*, *C. virgata*, *Eustachys distichophylla*, *E. glauca*, *E. neglecta*, and *E. petraea*. I have examined the starch grains of *C. crinita*, *C. pluriflora*, and *C. scariosa*; they are all compound.

Differences in root hair development in grasses were first shown by Sinnott (1939) and Sinnott and Bloch (1939). Later, the taxonomic significance was pointed out by Reeder and von Maltzahn (1953) and Row and Reeder (1957). These authors described one type in which the root hair projects forward at about a 45° angle from the smaller of two epidermal cells. A second kind has the root hair developing near the middle of either sister epidermal cell and projecting outward at an angle of about 90°. A third type has sister cells of the epidermis slightly different in size, with the root hair projecting at an angle of about 60° near one end of the cell, though Row and Reeder suggest that the variability in size of the sister cells is more reliable than the angle of projection. Because

Table 4. Taxa in *Chloris* and related segregate genera having panicoid scutellum type, an epiblast present (festucoid), and a panicoid arrangement of vascular tissue.

<i>Chloris aristata</i>	<i>C. plicurii</i>
<i>C. berroi</i>	<i>C. pycnothrix</i>
<i>C. bournei</i>	<i>C. radiata</i>
<i>C. canterai</i>	<i>C. robusta</i>
<i>C. chloridea</i>	<i>C. submutica</i>
<i>C. cruciata</i>	<i>C. truncata</i>
<i>C. dandyana</i>	<i>C. virgata</i>
<i>C. divaricata</i>	<i>Enteropogon acicularis</i>
<i>C. gayana</i>	<i>Eustachys distichophylla</i>
<i>C. halophila</i>	<i>E. glauca</i>
<i>C. inflata</i>	<i>E. neglecta</i>
<i>C. mollis</i>	<i>E. petraea</i>
<i>C. orthonoton</i>	

of the limited availability of viable seeds, Jensen was able to examine only ten species for this characteristic, all of which had the root hair projecting at an angle of about 60° near one end of the cell. The species examined were: *Chloris canterai*, *C. gayana*, *C. inflata*, *C. pilosa*, *C. pycnothrix*, *C. submutica*, *C. truncata*, *Eustachys caribaea*, *E. distichophylla*, *E. petraea*, and *E. retusa*.

The first seedling leaf in panicoid grasses is relatively wide and curled; that of festucoids is long and narrow (Stebbins, 1956). The species listed above all had panicoid seedling leaves, according to Jensen.

Relationships of *Chloris* and Other Genera

As with many genera in the Gramineae, generic delimitations in the Chlorideae may be difficult to assess; and they, of necessity, may be somewhat arbitrary and artificial. The complex that includes *Chloris* is no exception. While most of the species have long been included within the genus and most of the characteristics recognized, some species have been placed in adjacent genera in the past, a few more recently so. A graphical conspectus of *Chloris* and re-

lated genera is presented in Fig. 2. The number of taxa commonly accepted in each is indicated by the relative size of the circle. Also given are those species in *Chloris* that resemble the satellite genera, as well as those in the satellite genera that have been included in *Chloris*.

There is little information, aside from spikelet morphology, that is useful in generic delimitation within this group. Chromosome counts are mostly of the same basic number; leaf epidermal and anatomical characteristics do not appear unique to particular genera; genetic information is virtually nonexistent. Consequently, speculation on relationships, both intergeneric and interspecific, rests heavily upon information gleaned primarily from the structure of the inflorescence and spikelet and, secondarily, upon data concerning vegetative features. However, the genera in this complex have been long recognized and have remained relatively unchanged. The description of each of these, as commonly accepted today, is given in Table 6, and their relationships to *Chloris* follow.

Eustachys. This genus was first described in 1810 by Desvaux, but it has been treated subsequently as a subgenus of *Chloris* by the

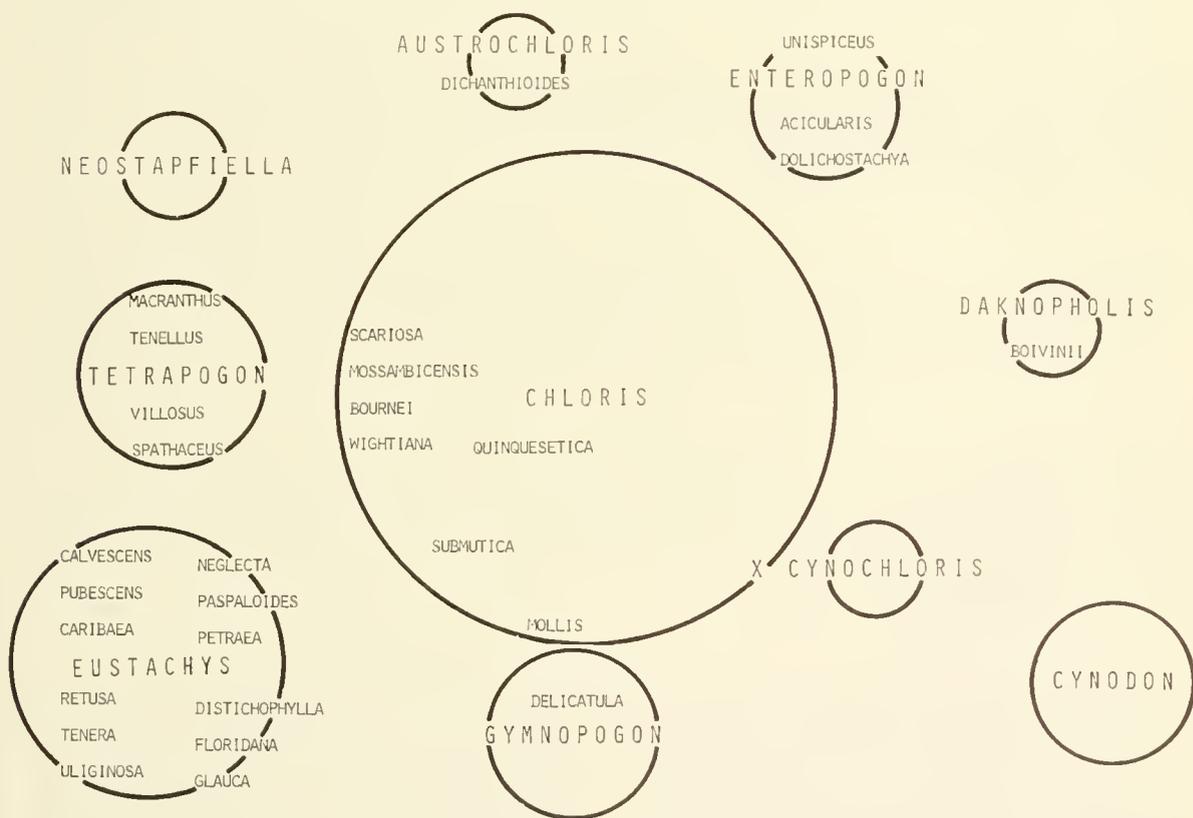


Fig. 2. Relationships of *Chloris* and allied genera.

Table 6. Comparison of various characteristics of *Chloris* and related genera.

Genus	Vegetative characteristics	Inflorescence type	Glumes	Number
<i>Chloris</i>	tufted, rhizomatous or stoloniferous; sheaths usually overlapping at the base, blades narrow to broad, not distichous	usually a single radiate series of 4-10 spikes, occasionally 2-more approximate or only slightly separated series of 10-20 spikes; rarely an indefinite number of terminal spikes or as few as 1-2 spikes	both glumes similar, narrowly ovate to lanceolate; acute to acuminate; awnless or only awn-tipped	usually 1, rarely 2 and then in the same inflorescence as spikelets with 1
<i>Cynodon</i>	rhizomatous to stoloniferous; sheaths usually overlapping at the base, blades generally narrow, acute, distichous	a single radiate series of 4-9 spikes	both glumes narrowly lanceolate to ovate	1
<i>Daknopholis</i>	prostrate, repent to stoloniferous; leaves basal, sheaths overlapping, blades small, subelliptic, obtuse	a single radiate series of 2-4 spikes	first glume ovate; second glume truncate, apex markedly truncate and erose	1
<i>Enteropogon</i>	erect, tufted, sheaths usually not markedly overlapping at the base, blades narrow, flat or convolute	usually a single terminal spike, sometimes several to many in a radiate or subverticillate series	both glumes narrowly lanceolate to ovate	1
<i>Eustachys</i>	tufted, rhizomatous or stoloniferous; sheaths strongly overlapping, largely basal, equitant; blades generally broad, obtuse, occasionally acute	usually a single radiate series of 4-30 spikes, rarely only 1-2	first glume ovate-lanceolate, acute, awn-tipped or awnless; second glume linear-lanceolate, retuse, short awned between the lobes	1
<i>Gymnopogon</i>	tufted, sheaths strongly overlapping, largely basal; blades markedly distichous, stiff, acute to acuminate	a single series of 6-20 spikes, generally borne singly at a node	both glumes narrowly lanceolate, acuminate	usually 1, sometimes 2
<i>Neostapfiella</i>	erect, tufted; sheaths somewhat overlapping; blades narrow	2-3 spikes	both glumes narrowly lanceolate, acuminate	1 or 2
<i>Tetrapogon</i>	tufted to short stoloniferous or rhizomatous; sheaths usually overlapping at the base, blades narrow to broad, not distichous	a single radiate series of 1-4 spikes	both glumes similar, ovate to lanceolate	usually 2 or 3

majority of authors, the most notable exception being Nash (1898). *Eustachys* is obviously closely related to *Chloris*, though distinct in several features. Vegetatively, the strongly flattened, folded, equitant leaf sheaths set *Eustachys* apart from most species in *Chloris*. In addition, the second glume in *Eustachys* is bi-

lobed at the apex, with a short awn arising between the lobes; in *Chloris* the second glume is acute to acuminate and is rarely awned. The fertile and sterile florets of *Eustachys* are commonly pale to dark brown to almost black and are awnless or short-awned. Florets in *Chloris* are usually pale to tawny, seldom darker, and

Spikelet characters						
Fertile floret(s)						
Shape and color	Awn	Pubescence			Sterile floret(s)	
		Keel	Margins	Callus	Number	Size and shape
elliptic to lanceolate to ovate; often acute, sometimes obtuse or acuminate, rarely bifid; usually laterally compressed; tawny to light brown, rarely black or dark brown	usually well developed, rarely absent	glabrous to pilose to long-ciliate	usually ciliate or appressed pubescent	bearded	usually 1—sometimes 2—more rarely several	usually markedly dissimilar from fertile floret; usually well developed, rarely reduced
ovate to lanceolate; prominently laterally compressed; tawny	awnless	short ciliate	short ciliate	short-pubescent	0 to 1, highly reduced	absent, or, if present, reduced and forming only a knob at apex of rachilla joint
lanceolate to elliptic; prominently laterally compressed; tawny	short awned to mucronate	scabrous	scabrous	bearded	obsolete	
dorsally compressed to nearly latetere, but not laterally compressed, linear in side view, elliptic to lanceolate in dorsal view; tawny to greenish	usually well developed	scabrous	scabrous	bearded	1	similar to fertile floret, but much smaller
elliptic, lanceolate or ovate, acute to shortly acuminate; strongly laterally compressed; often dark brown or black, rarely light brown	short or absent	usually glabrous, sometimes pilose	commonly appressed pubescent	bearded	usually 1, sometimes 2	markedly dissimilar from fertile floret; usually well developed, rarely reduced
usually narrowly elliptic; nearly terete to slightly dorsally or laterally compressed; tawny, brown or purplish	usually well developed	glabrous, scabrous, or pilose	sparsely to densely ciliate	bearded	1-2	highly reduced to obsolete
ovate to lanceolate; laterally compressed; tawny	well developed	glabrous to pilose	glabrous to sparsely ciliate	densely long bearded	1	similar to fertile floret but slightly smaller
elliptic to broadly lanceolate; laterally compressed; usually tawny	usually well developed	densely pubescent	densely pubescent	densely bearded	usually 2-4, sometimes 1	similar to fertile floret but smaller; lower well developed, upper smaller

are usually prominently awned. *Chloris submutica* is perhaps most similar to *Eustachys*, primarily because of the lack of prominent awns.

Sanchez (1971) enumerated several anatomical features by which the leaves of *Chloris* and *Eustachys* differ. Sanchez reported that *Eustachys* has, for the most part, relatively thick-

walled, uniformly sized bulliform cells; a prominent epidermal band of these lies adaxial to the midrib. By contrast, *Chloris* has unequally sized, thin-walled bulliform cells and lacks a concentration of these in the midrib region. While none of these characters appear to be exclusive to either genus, the trend shown clearly re-

inforces the exomorphic differences between them.

Tetrapogon. This Old World genus is best separated from *Chloris* on the basis of having two (occasionally three) fertile florets per spikelet. *Chloris* regularly has a single fertile floret, though very occasionally individuals of certain species may produce a spikelet with two or more fertile florets. In addition, both glumes in *Tetrapogon* are thin, papery, or parchmentlike and (like the spikelets) are relatively large. The glumes in species of *Chloris* are not thin and papery, but are firmer and relatively smaller.

Several species in *Chloris* strongly resemble *Tetrapogon*. *Chloris mossambicensis*, an African species, is similar in many respects, but the bulk of material which this author has examined has spikelets with one fertile floret; only a few plants have spikelets with two or more florets. *Chloris bournei*, *C. wightiana*, and, to a lesser extent, *C. quinquesetica*—all from India—are similar to several *Tetrapogon* species, primarily in size of spikelets. However, they have just a single fertile floret and are best retained in *Chloris*.

The strikingly different *Chloris scariosa* from Australia could easily be given generic status, for its spikelets (with their several flabellate sterile florets) are unlike any other species in *Chloris*. *Chloris scariosa* has relatively large, papery glumes, in this respect strongly resembling *Tetrapogon*. I am maintaining this species in *Chloris* largely because of its single fertile floret. If *Chloris scariosa* were to be given generic rank, then a number of other somewhat unusual species are also deserving of such consideration—a process that could hopelessly fragmentize the genera in this complex.

Gymnopogon. The most striking difference between this genus and *Chloris* is vegetative. *Gymnopogon* is characterized by thick, sharp-pointed, distichous blades, the sheaths of which are more or less equitant and basal. Furthermore, many species of *Gymnopogon* have the spikes well separated and spreading, making the inflorescence quite open. *Chloris* generally has broader, more lax blades and sheaths that only partly overlap. While a few species have distant spikes, they are mostly borne in one or more radiating series.

Most species of *Gymnopogon* either lack sterile florets or they are very greatly reduced. In *Chloris* the sterile floret is generally well developed.

Overall, *Chloris mollis* is probably most similar to *Gymnopogon*, a fact reflected in its nomenclatural history. While the leaf blades of *C. mollis* are relatively short and sharp pointed,

the sheaths are not as strongly overlapping. The spikes are somewhat distant, but not as markedly so as in *Gymnopogon*. Sterile florets in *C. mollis* are well developed; in this respect they are unlike those in *Gymnopogon*.

Chloris clementis, *C. ekmanii*, *C. pycnothrix*, and *C. radiata* all have much reduced sterile florets; but in all other respects they fit *Chloris* well.

Cynodon. Clifford and Everist (1964) described a sterile intergeneric hybrid, which they named *Cynochloris macivorii*, which was found growing with *Cynodon dactylon* and *Chloris divaricata* on a lawn bowling rink at Ipswich, Queensland. The identification of this plant rests upon its intermediaity between the two putative parents with respect to a number of spikelet, habit, and behavioral characteristics, since experimental recreation of the hybrid has not been attempted. On the basis of the data, there is little doubt as to the correctness of Clifford and Everist's interpretation, however.

The existence of this bigeneric hybrid attests to the genetic proximity of these two genera; yet the two can ordinarily be separated readily by morphological features. Most species of *Cynodon* have obsolete or very poorly developed sterile florets, while in *Chloris* they are usually well developed. Likewise, in *Chloris* the callus is prominently short bearded, whereas in *Cynodon* it is less obviously pubescent.

Daknopholis. Described in 1967 by Clayton, this genus was erected to contain several anomalous species of *Chloris*: *C. boivinii*, *C. perrieri*, and *C. ramosissima*. Two features will separate the new genus from *Chloris*: (1) the lack of a well-defined sterile floret and (2) the presence of a truncate and erose second glume. In overall appearance *Daknopholis* is more suggestive of *Cynodon* than *Chloris*. The relationships were discussed in some detail by Clayton (1967).

Enteropogon. These Old World tropical perennials (as treated by Clayton [1957], for example) are easily separated from *Chloris* in having a single spike or, rarely, two; most *Chloris* species have three or more spikes. In addition, the fertile lemmas of *Enteropogon* are strongly, dorsally compressed and have a raised midnerve.

I do not believe that this difference in number of spikes accurately reflects the relationships. Two species with many spikes that are often treated in *Chloris*—*C. acicularis* from Australia and *C. dolichostachya* from southeastern Asia—have strongly dorsally compressed spikelets with a raised midnerve on the lemma. The similarity to *Enteropogon* is such that one would be hard

pressed to separate these two taxa of *Chloris* and various species of *Enteropogon* on the basis of spikelets alone. They could, of course, be separated readily on the number of spikes. But the differences do not end here. Tateoka (1962b) reported that starch grains were simple and angular in *Enteropogon*, while *Chloris* has only compound grains. Both *Chloris acicularis* and *C. dolichostachya* have *Enteropogon*-type starch grains, further reinforcing the removal of these species from *Chloris*. Accordingly, I have followed Lazarides (1972) in removing these two species from *Chloris* and referring them to *Enteropogon*.

Trichloris. This genus has been characterized as having three prominent awns on the fertile and sterile lemmas: one is an extension of the midnerve and the other two are of lateral nerves. The relative length of these awns varies between species.

The prominently three-awned lemmas of *Trichloris* will distinguish it readily from virtually all species of *Chloris* in the Western Hemisphere. *Chloris chloridea* and *C. halophila* have somewhat bilobed lemma apices, but these are mucronate, at most.

This same awn difference serves also for the Eastern Hemisphere, except in Australia. There are several Australian species, too, that have lateral nerves extended into awns (prominently so in *C. lobata* and *C. pumilio*; less obvious in *C. divaricata* and *C. pectinata*.) In all likelihood, of course, this resemblance is a result of parallel evolution and does not reflect a close genetic relationship. Nevertheless, it is ambiguous to continue to recognize *Trichloris* in the New World, while maintaining the three-awned species from Australia in *Chloris*. Clayton (1967) recognized this ambiguity and treated the two species of *Trichloris* as members of *Chloris*.

More recently, Sanchez (1971) resurrected *Trichloris* on the basis of anatomical studies of leaves. According to Sanchez, the bulliform cells of most Argentine species of *Chloris* have achlorophyllous cells lying immediately below them in the mesophyll. Such achlorophyllous cells are only rarely found in *Trichloris*.

While there are recognizable tendencies in the patterns of variation in these anatomical features, there is no reinforcement from spikelet morphology. Consequently, I am following the lead of Clayton (1967) in treating the two species of *Trichloris* as members of *Chloris*.

Neostapfiella. This genus from Madagascar is relatively poorly represented in most herbaria. The limited material available, however, shows the spikelets with either two basal fertile florets

or with the single terminal sterile floret identical to, or strongly resembling, the basal fertile floret. Additionally, the number of spikes (one to three) is fewer than that generally found in *Chloris*. *Neostapfiella* is probably more closely related to *Tetrapogon* than to any species in *Chloris*.

Relationships within *Chloris*

This synthesis is based primarily upon the gross morphology of the inflorescence and spikelet; but studies of the leaf epidermis, already discussed, provided important additional information. Chromosome number and structure have contributed virtually nothing, for the genus is essentially monobasic and the chromosomes very similar.

Some species complexes are well defined; i.e., there is a strong correlation of morphology, anatomy, and geography. Other species may resemble one another, but they are geographically isolated in such a way as to preclude a direct evolutionary connection. In still other complexes there may be little or no outward resemblance; yet the formation of hybrid swarms recombines those highly divergent characters and indicates strong evolutionary ties. Still other taxa are isolated entities, displaying no obvious relationships with any other species or complexes.

The formal recognition of a series of subgenera would be folly, not that some complexes are unworthy of it, but because the naming of these as subgenera will necessarily create a residue of species that cannot be grouped. The individual species in this remnant cannot be treated as a single subgenus, for such would be blatantly artificial and misleading. The other extreme would be to treat each as the single member of its own subgenus, a practice leading to rather hopeless fragmentation. I have tried to compromise in the following discussion. Those groups containing obviously closely related species—whether the basis is morphological, geographical, genetic, or all three—are treated as species complexes and discussed as such. The isolated species are discussed individually whenever this author feels that they have importance. In addition, discussions of relationships, especially within the various complexes, follow the descriptions provided later. A graphical synopsis of relationships within the genus is provided in Fig. 3.

The *Chloris inflata* complex.

Members of this complex are characterized by single-celled microhairs, by typical *Chloris*-type silica cells, and, in most, by a prominent

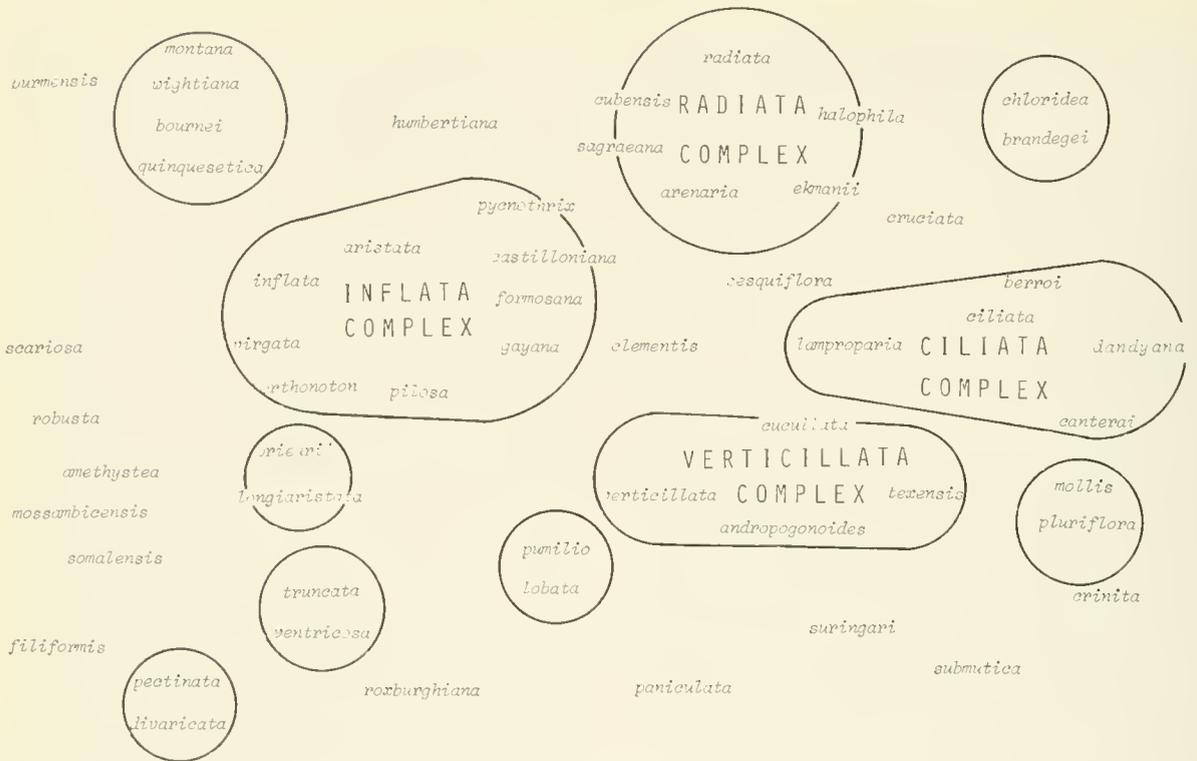


Fig. 3. Relationships of species and species complexes in the genus *Chloris*.

tuft of hairs on the upper margins of the fertile lemma. Included here are five very widely distributed species (*Chloris gayana*, *C. inflata*, *C. pilosa*, *C. pycnothrix*, and *C. virgata*), as well as several more restricted species (*C. aristata*, *C. castilloniana*, *C. formosana*, and *C. orthonotum*). Of these, *Chloris pycnothrix* is the most aberrant; if it were not for possession of unicellular microhairs, it would be placed confidently in the following complex.

The *Chloris radiata* complex.

Six similar species (*C. arenaria*, *C. cubensis*, *C. ekmanii*, *C. halophila*, *C. radiata*, and *C. sagracana*) make up this complex. All have comparatively narrow spikelets and reduced sterile florets; relatively long awns are also a common feature. The epidermal pattern includes bicellular microhairs and euboidal silicified cells. While most of the species have inconspicuously ciliate upper lemma margins, *C. cubensis* may approach the *C. inflata* complex in having more prominent pubescence. Though *Chloris cruciata* is not included here because of its somewhat unique short cells, it is similar in overall spikelet structure.

The *Chloris ciliata* complex.

While this group presents more interspecific taxonomic problems than any other group, it

is well defined as a whole. All species (*Chloris berroi*, *C. canterai*, *C. ciliata*, *C. dandyana*, and *C. lamproparia*, are characterized by having relatively short-awned, elliptic fertile lemmas that are prominently spreading-ciliate along most of the margin. Epidermal patterns are typical of *Chloris*. *Chloris sesquiflora* is similar, but the marginal pubescence is strongly appressed.

The *Chloris verticillata* complex.

Were it not for the extensive introgression between *Chloris andropogonoides*, *C. cucullata*, and *C. verticillata*, they would probably not be included in a single complex. Morphologically, there is considerable divergence, especially in *C. cucullata*, in which the broad fertile and sterile lemmas are distinctive in the genus. While introgression involving the very rare *C. texensis* has not been demonstrated, in spikelet and inflorescence morphology it is obviously similar to *C. andropogonoides*.

In *Chloris chloridea* and *C. brandegei* there is a strong tendency toward dorsal compression of the spikelet. In other respects the plants are similar to *C. halophila*, though considerably more robust. The development of underground spikelets in *Chloris chloridea* is unique in the genus.

Four Australian species have bilobed fertile

and sterile lemmas. In *Chloris pumilio* and *C. lobata*, this lobing is very prominent; the other two, *C. pectinata* and *C. divaricata*, are less so. The outward similarity to *C. pluriflora* and *C. crinita*, both formerly in *Trichloris*, an American genus, is probably the result of parallel evolution.

Another pair of Australian species, *Chloris truncata* and *C. ventricosa*, is notable for having very truncate or ventricose fertile lemmas. *Chloris truncata* is strikingly similar to the North American *C. verticillata*; again, the similarity seems best explained by parallel evolution.

Chloris longiaristata and *C. prieurii*, both primarily African in distribution, have several sterile florets and relatively narrow, long-awned lemmas. The glandular strip along the side of the lemma in *C. prieurii* is unusual in *Chloris*.

Chloris bournei, *C. quinquesetica*, and *C. wightiana* all have relatively large spikelets with obtuse lemmas, coarsely pubescent lemma margins, and several sterile florets. They bear a strong resemblance to species in *Tetrapogon* but have just a single fertile floret, whereas *Tetrapogon* has more than one.

The above discussion leaves unmentioned a rather large number of species which are quite isolated morphologically (Fig. 3). Unquestionably, these are best retained as a part of *Chloris*, for they have all of the features characteristic of the genus; and yet, the elaboration of some individual structural feature causes them to stand alone. None is truly widely distributed, and several are narrow endemics; this suggests adaptation to a particular climatic or edaphic regime.

Chloris Swartz

Chloris Swartz, Prodr. Veg. Ind. Occ. 25. 1788.

Rabdochloa Beauvois, Ess. Agrost. 84, 158, 176. 1812.

Placellaria Willdenow ex Steudel, Nom. Bot. ed. 2. 1:353. 1840. Herbarium name, given as a synonym.

Heterolepis Ehrenberg ex Boissier, Flora Orientalis 5:554. 1884. Herbarium name, given as a synonym of *Chloris*.

Trichloris Fournier, Mex. Pl. 2:142. 1856.

Chloropsis Kuntze, Rev. Gen. Pl. 2:771. 1891.

Leptochloris Munro ex Kuntze, Rev. Gen. Pl. 2:771. 1891.

Pterochloris Camus, Bull. Mus. Hist. Nat. (Paris). Ser. 2. 29:349. 1957.

Fibrous-rooted annuals or rhizomatous, stoloniferous, or caespitose perennials, ranging in

size from only a few cm to over 2 m tall; epidermal cells of root tips slightly different in size, giving rise to root hairs which project forward at about 60°; sheaths glabrous, scabrous, or villous; ligule often a ciliate crown, sometimes absent; blades narrow to wide, flat or rolled, deeply keeled and V-shaped, or with rounded keels and with several furrows, sclerenchyma girders complete or only on abaxial side, bulliform cells generally large and penetrating the mesophyll, bundle sheaths complete or incomplete; costal silica cells usually cuboidal-saddle- or axehead-shaped, very rarely somewhat cruciate, stomatal apparatus medium- to triangular-dome shaped, bicellular microhairs usually present, with relatively broad and short terminal cells, or, less commonly, single-celled; spikes¹ usually 5 to 25 (occasionally as few as 1 or 2, rarely more than 25), frequently digitately arranged, occasionally in several verticils, sometimes with a few isolated single spikes; spikelets borne in two staggered rows on one side of the rachis, sessile to pedicellate, commonly rather densely imbricate and appressed, sometimes sparsely so; glumes usually unequal, lanceolate, often glabrous with scabrous nerves, mostly acute, rarely acuminate, shorter than the florets; fertile lemmas one (very rarely two), lanceolate, occasionally elliptic, three-nerved, callus bearded, margins shortly to prominently pubescent, internerves usually glabrous, sometimes scabrous, rarely pilose, midnerves scabrous or glabrous, rarely long-pubescent, midnerve usually extended as an awn, either from the tip or from between two teeth, rarely only mucronate; palea shorter than the fertile lemma, with two scabrous nerves, otherwise glabrous; stamens three, anthers relatively small; pistil one, with two stigmas; lodicules two; sterile floret usually one (rarely two or three, mostly barren, very rarely staminate or perfect, varying widely in size and shape from highly reduced to well developed and similar to the fertile floret, rudimentary to cylindrical to obovoid, acute to truncate, awned or unawned; caryopsis ovoid, elliptic to obovoid, round to trigonous in cross section, the embryo relatively small, lower portions of scutellum separate from the rest of the embryo, epiblast present, vascular traces separated by an elongated area of vascular tissue, embryonic leaf margins usually not overlapping, very rarely overlapping; starch grains of endosperm compound; basic chromosome number $x=9$ (rarely), 10 (usually), the chromosomes relatively small.

¹The inflorescence branches of the various species bear spikelets that range from virtually sessile to obviously pedicellate, and thus may be called spikes or racemes, depending upon emphasis. In this study the main inflorescence branch is arbitrarily called a spike.

Widely distributed in tropical, subtropical, or warm temperate regions of both hemispheres, both north and south of the equator (Fig. 4).



Fig. 4. Worldwide distribution of the genus *Chloris*. (This map is a composite of the distribution maps of all of the species.)

Key to the species of *Chloris*

1. Inflorescence of many (30 or more) short spikes (6 cm or less) arranged along a central axis which is at least 1 cm in length, the spikes not in verticils..... 2
- Inflorescence of less than 30 spikes, the spikes arranged in one or more verticils..... 3
2. Sterile florets two or more; widely distributed in Africa, occasional in India *C. roxburghiana*, p. 22
- Sterile floret one; endemic to Cocos Island, off the west coast of Central America *C. paniculata*, p. 24
3. Spikes two to four, forming a cylindrical, spikelike inflorescence; the spikes attached to one another at least at the base and often for the full length, separable only with difficulty; Argentina, Uruguay..... *C. berroi*, p. 25
- Spikes neither attached to one another nor forming a cylindrical, spikelike inflorescence 4
4. Spikes one to three..... 5
- Spikes four or more..... 14
5. Sterile florets two or three..... 6
- Sterile floret one (See also *Chloris suringari*, which has a highly reduced upper sterile floret.) 10
6. Fertile lemmas 1.8 to 2.8 mm long..... 7
- Fertile lemmas 2.7 to 4.2 mm long..... 8
7. Inflorescence a single spike; lemmas awned from about the middle of the keel; Cuba, Curaçao) *C. suringari*, p. 39
- Inflorescence of more than one spike; lemmas awned subapically; southcentral United States, Caribbean Islands, Mexico, Central and South America *C. ciliata*, p. 27

- 8. Combined length of fertile- and sterile-floret awns 6.5 to 9 mm, usually more than 7 mm; annuals; Africa.....*C. lamproparia*, p. 30
 Combined length of fertile- and sterile-floret awns 4 to 8 mm, usually less than 7 mm; perennials; South America, Texas..... 9
- 9. Plants densely tufted, with basal, narrow, rolled, curved leaves; spikes 3 to 5 cm long..... *C. canterai* var. *grandiflora*, p. 32
 Plants not densely tufted; leaves cauline, up to 5 mm wide, not curled or curved; spikes 4 to 14 cm long..... *C. canterai* var. *canterai*, p. 30
- 10. Spikelets diverging from the rachis at nearly right angles; spikelets obviously pedicellate; Cuba, Haiti, Jamaica..... *C. cruciata*, p. 37
 Spikelets appressed or only slightly divergent from the rachis; spikelets sessile or nearly so 11
- 11. Awn of fertile lemma less than 1.5 mm long; internerves appressed-pubescent; Mauritius*C. filiformis*, p. 39
 Awn of fertile lemma more than 2 mm long; margins and keel spreading-pubescent; internerves glabrous or with inflated hairs..... 12
- 12. Awn of fertile lemma longer than 5 mm; Cuba, Jamaica, Hispaniola
*C. ekmanii*, p. 119
 Awn of fertile lemma less than 4.5 mm long 13
- 13. Internerves glabrous; Cuba, Curaçao*C. suringari*, p. 39
 Internerves densely covered with inflated hairs; Malagasy Republic
 *C. humbertiana*, p. 104
- 14. Sterile florets two or more, the uppermost floret sometimes represented only by the clavate rachilla joint..... 15
 Sterile floret one..... 41
- 15. Sterile florets greatly modified, commonly over 3 mm wide, flabellate, margins scarios, more or less inrolled and enclosing one another; Australia *C. scariosa*, p. 40
 Sterile florets neither greatly modified, flabellate, nor involute, seldom more than 1.5 mm wide 16
- 16. Fertile lemmas with a row of glands along the sides; Africa, India
*C. prieurii*, p. 42
 Fertile lemmas without a row of glands, though sometimes appressed-pubescent with nonglandular hairs..... 17
- 17. Fertile lemmas with a short mucro (less than 1 mm long); Africa *C. pilosa*, p. 58
 Fertile lemma with an awn more than 1 mm long 18
- 18. Sterile floret pubescent, either with a prominently appressed-pubescent callus, or densely pubescent on the midnerve, upper margins, or apex..... 19
 Sterile floret glabrous or, at most, with a few (10 or so) appressed hairs on the back 26
- 19. Callus of sterile floret bearded..... 20
 Callus of sterile floret not bearded..... 21
- 20. Sterile floret unawned, acuminate; rachilla joint not obvious; culms stout, bamboo-like; Africa*C. robusta*, p. 43
 Sterile floret obviously awned; rachilla joint prominent; culms not stout and bamboo-like; New World.....*C. mollis*, p. 45
- 21. Leaf sheath, blade, and spike rachis densely pustulose-pilose; sides of fertile and sterile lemma prominently and densely pustulose; India*C. wightiana*, p. 48
 Leaf sheath, blade, and spike rachis glabrous, scabrous, or sparsely pilose, but never pustulose; sides of lemma glabrous or occasionally appressed-pubescent, but not pustulose.. 22

22. Culms densely appressed-pubescent for several mm just below the points of attachment of the spikes.....	23
Culms glabrous or scabrous below the points of attachment of the spikes.....	24
23. Upper margins of lowermost sterile floret ciliate; sterile florets usually four (occasionally 3); uppermost sterile floret spherical and inflated; India ... <i>C. quinquesetica</i> , p. 48	
Upper margins of lowermost sterile floret usually not ciliate, occasionally sparsely pubescent; sterile florets usually three (rarely two or four); upper sterile floret resembling the lower, neither spherical nor inflated; Ceylon, India, Thailand ... <i>C. montana</i> , p. 51	
24. Awn of fertile lemma 2 mm long or less; Burma	<i>C. burmensis</i> , p. 125
Awn of fertile lemma more than 3.5 mm long	25
25. Midnerve of lowest sterile floret densely and prominently appressed-pubescent; fertile lemma longer than 3 mm; lowest sterile floret 1.5 mm or longer, its awn usually shorter than 4 mm; stoloniferous perennial; southern India	<i>C. bournei</i> , p. 53
Midnerve of lowest sterile floret sparsely appressed-pubescent; fertile lemma less than 3 mm long; lowest sterile floret less than 1.5 mm long, its awn over 5 mm; annual or weak perennial, sometimes rooting at the lower nodes; pantropical ...	<i>C. inflata</i> , p. 53
26. Awn of fertile lemma longer than 30 mm; Africa	<i>C. longiaristata</i> , p. 46
Awn of fertile lemma less than 15 mm long	27
27. Sterile florets two or three, only the lowermost awned, the others awnless	28
Sterile florets two or three; all are awned	34
28. Fertile lemmas prominently ciliate along most of the margin, the cilia spreading at nearly right angles; lemmas broadly elliptic	29
Fertile lemma margins glabrous or with strongly spreading hairs near the apex, but never along the lower margins	33
29. Fertile lemmas 1.5 to 2.8 mm long	30
Fertile lemmas 2.9 to 4.2 mm long	31
30. Spikes three to five (rarely six or seven), usually less than 8 cm long; Texas, Mexico, Central America, southern Brazil, Argentina ...	<i>C. ciliata</i> , p. 27
Spikes 7 to 40 (usually 10 to 20), usually more than 8 cm long, occasionally as short as 5 cm; Florida, West Indies, South America	<i>C. dandyana</i> , p. 34
31. Spikes one to four (often two); combined length of awns of fertile and sterile floret 6.5 to 9 mm (usually about 7 mm); annuals; Africa	<i>C. lamproparia</i> , p. 30
Spikes two to nine (usually three or more); combined length of awns of fertile and sterile floret 4 to 8 mm (usually less than 7 mm); perennials; South America, Texas	32
32. Plants densely tufted with basal, narrow, rolled, curved leaves; spikes 3 to 5 cm long	<i>C. canterai</i> var. <i>grandiflora</i> , p. 32
Plants not densely tufted; leaves cauline, up to 5 mm wide, not curled; spikes 4 to 14 cm long	<i>C. canterai</i> var. <i>caunterai</i> , p. 30
33. Annual plants arising from a fibrous root system, occasionally rooting at the lower nodes if culms are decumbent; Africa	<i>C. pilosa</i> , p. 58
Perennial plants, usually with prominent, aggressive stolons, occasionally tufted; widely distributed in the warmer parts of the world	<i>C. gayana</i> , p. 65
(NOTE: Occasional specimens of <i>Chloris ventricosa</i> having two sterile florets will key to this point.)	
34. Awn of fertile lemma less than 2 mm long; Burma	<i>C. burmensis</i> , p. 125
Awn of fertile lemma more than 3.5 mm long	35

35. Culms densely appressed-pubescent for several mm just below the points of attachment of the spikes; Ceylon, India, Thailand	<i>C. montana</i> , p. 51	36
Culms scabrous or glabrous just below the points of attachment of the spikes.....		
36. Upper sterile floret inflated, nearly spherical; widespread in warm regions	<i>C. inflata</i> , p. 53	37
Upper sterile floret cylindrical or very narrowly turbinate		
37. Rachis pilose; eastern China, Hong Kong, North Vietnam, Taiwan	<i>C. formosana</i> , p. 57	38
Rachis scabrous		
38. Fertile lemma with three awns, the lateral about equal to the central, or shorter....		39
Fertile lemma with only a single awn, lateral awns absent		40
39. Awns subequal, the lateral only slightly shorter than the central	<i>C. crinita</i> , p. 87	
Awns unequal, the lateral about one-tenth the length of the central	<i>C. pluriflora</i> , p. 89	
40. Fertile lemmas acute at the apex; margins not inrolled, densely ciliate, especially on the upper margins; spikelets tawny; robust, stoloniferous perennials more than 50 cm tall; widespread in warm regions	<i>C. gayana</i> , p. 65	
(NOTE: On rare occasions, specimens of <i>Chloris mossambicensis</i> , from southern Africa, and <i>C. sagraeana</i> , from the Caribbean region, both rarely having two sterile florets, will key to this point.)		
Fertile lemmas obtuse to rounded at the apex; margins inrolled and appressed-pubescent; spikelets dark brown to black at maturity; relatively short, tufted perennials; Australia		
.....	<i>C. truncata</i> , p. 78	
41. Sterile lemma bilobed for upper one-third to nearly all of its length, the lateral lobes usually awned		42
Sterile lemma not prominently bilobed		47
42. Fertile lemma margins pubescent to ciliate on upper half, the hairs usually prominent and spreading, especially toward the apex		43
Fertile lemma margins glabrous, scabrous, or strongly appressed-pubescent, but upper margins without prominent spreading hairs		44
43. Fertile lemma margins pubescent mostly on upper half; sterile floret bilobed nearly to the base, the lobes usually widely divergent at maturity; sterile lemma lobes gradually tapering into an awn; fertile lemma awns subequal; Australia	<i>C. lobata</i> , p. 82	
Fertile lemma margins pubescent along most of length (the hairs spreading apically, appressed basally); sterile floret bilobed to about the middle, very occasionally to the base, the lobes not widely divergent at maturity; sterile lemma lobes usually truncate to somewhat rounded, the awn arising laterally; median awn of fertile lemma usually about twice the length of the lateral awn	<i>C. pumilio</i> , p. 80	
44. Lateral and central awns of fertile lemma subequal to equal; southwestern United States, Mexico, and South America	<i>C. crinita</i> , p. 87	
Lateral awns of fertile lemma about one-tenth the length of the central awns		45
45. Spikelets densely pectinate, crowded, diverging at wide angles from the rachis; Australia	<i>C. pectinata</i> , p. 86	
Spikelets not densely pectinate, only slightly imbricate, appressed to the rachis		46
46. Spikes in two or more verticils; South America	<i>C. halophila</i> , p. 117	
Spikes in a single radiate series; Australia	<i>C. divaricata</i> , p. 83	
47. Fertile lemma awnless or with a short awn, generally less than 2 mm long		48
Fertile lemma prominently awned, the awn usually more than 3 mm long		52

48. Sterile floret very narrowly cylindrical, usually about 0.2 mm wide, usually sparsely pilose near the apex; Baja California, Mexico *C. brandegei*, p. 72
Sterile floret broader, usually more than 0.3 mm wide; at most merely scabrous at the apex 49
49. Sterile floret inflated-spherical, about 1 mm wide, usually as wide as long; Texas, New Mexico, Oklahoma, northeast Mexico *C. cucullata*, p. 91
Sterile floret not inflated-spherical, less than 0.5 mm wide, usually at least twice as long as broad 50
50. Fertile lemma margin glabrous, scabrous, or appressed-pilose for no more than one-half of its length; keel usually glabrous, occasionally scabrous near the apex, rarely sparsely appressed-pubescent; Mexico, Colombia *C. submutica*, p. 106
Fertile lemma margin and keel appressed-pubescent for most of length 51
51. Sterile floret elliptical, flattened, about 1 mm long; fertile lemma prominently spreading-pilose on margins and keel; South America *C. sesquiflora*, p. 104
Sterile floret cylindrical to narrowly turbinate, inflated, ca 2 mm long; fertile lemma margins and keel appressed-pubescent; Africa *C. amethystea*, p. 106
52. Fertile lemma broadly elliptic, prominently long-ciliate along most of the margin, the cilia spreading at nearly right angles 53
Fertile lemma margins glabrous or with appressed to widely spreading hairs near the apex, but never along the lower margins 54
53. Fertile lemma more than 3.5 mm long, gibbous; awn definitely subapical; Argentina *C. castilloniana*, p. 69
Fertile lemma less than 3 mm long, elliptic, not gibbous; arising only slightly subapically; Florida, Bahama Islands, Jamaica, South America *C. dandyana*, p. 34
54. Plants producing cleistogamous underground spikelets at the ends of thin rhizomes; southwestern United States, Mexico, Central America, and Venezuela *C. chloridea*, p. 74
Plants not producing cleistogamous underground spikelets 55
55. Spikes naked 2 to 5 cm from the base; endemic to eastern Texas; rare, possibly extinct *C. texensis*, p. 103
Spikes floriferous to near the base 56
56. Spikes borne in two or more verticils, these usually well separated. (See also *C. virgata* which may have two verticils, closely inserted.) 57
Spikes borne in a single terminal whorl 61
57. Sterile floret greatly reduced, usually less than 1 mm long; annuals; widely distributed in American tropics; Hawaii *C. radiata*, p. 110
Sterile floret longer than 1 mm, well developed; perennials, tufted or stoloniferous 58
58. Upper margins of fertile lemma with a prominent tuft of spreading white hairs, these usually longer than 1 mm; side of fertile lemma grooved, the groove usually with many glandular hairs (though these may be somewhat obscure or, rarely, absent); Brazil Ascension Island *C. orthotonon*, p. 69
Upper margin of fertile lemma scabrous or appressed short-pilose; side of fertile lemma without a groove or glandular hairs 59
59. Fertile lemma 2.0 to 3.5 mm long; widely distributed in central and southeentral United States *C. verticillata*, p. 93

(NOTE: Various introgressants of *Chloris verticillata*, *C. cucullata*, and *C. andropogonoides* may key to this point. See full discussion of this problem in the text.)

Fertile lemma longer than 3.8 mm	60
60. Awn of fertile lemma longer than 9 mm long; South America <i>C. halophila</i> , p. 117	
Awn of fertile lemma shorter than 5 mm long; Baja California, Mexico	<i>C. brandegei</i> , p. 72
61. Fertile lemma with a dense tuft of spreading hairs on the upper margins, the longest usually more than 1.5 mm long (see also <i>C. aristata</i> and <i>C. cubensis</i> , which occasionally have rather long hairs near the fertile lemma apex)	62
Fertile lemma without a dense tuft of long spreading hairs on the upper margins, though often with shorter (generally less than 1 mm), appressed hairs, occasionally scabrous or glabrous	64
62. Fertile lemma with a shallow lateral groove	63
Fertile lemma without a lateral groove; southern Africa <i>C. mossambicensis</i> , p. 123	
63. Annual plants; fertile lemma usually prominently carinate, gibbous; lateral groove of fertile lemma glabrous or appressed-pilose, not glandular; widely distributed	<i>C. virgata</i> , p. 60
Perennial, stoloniferous plants; fertile lemma rounded on the back, neither carinate nor gibbous; lateral groove of fertile lemma usually with many glandular hairs (though these are sometimes obscure, or, rarely, absent); Brazil, Ascension Island	<i>C. orthonoton</i> , p. 69
64. Spikelets bright green to olive green; Ethiopia, Somali Republic	<i>C. somalensis</i> , p. 109
Spikelets pale brown, tawny to black, but not greenish, at least at maturity.....	65
65. Fertile lemma usually less than 2 mm long; Phillippine Islands	<i>C. clementis</i> , p. 109
Fertile lemma more than 2 mm long	66
66. Spikes naked 2 to 5 cm from the base; endemic to eastern Texas; rare, possibly extinct	<i>C. texensis</i> , p. 103
Spikes floriferous to near the base	67
67. Sterile floret more than 0.6 mm wide, often nearly 1 mm wide.....	68
Sterile floret less than 0.6 mm wide	70
68. Upper fertile lemma margins densely ciliate or spreading-pilose, the margins not inrolled; Central America	<i>C. aristata</i> , p. 70
Upper fertile lemma margins glabrous, scabrous, or appressed-pilose, the margins inrolled, especially below	69
69. Margins of fertile lemma glabrous or sparsely pilose; fertile lemma apex generally acute, occasionally somewhat rounded; fertile lemma tawny to purple tinged, seldom dark brown or black; Australia	<i>C. ventricosa</i> , p. 76
Margins of fertile lemma appressed-pilose; fertile lemma apex broadly obtuse to rounded; fertile lemma dark brown to black at maturity. Australia	<i>C. truncata</i> , p. 78
70. Awn of fertile floret usually less than 5.5 mm long; southern Texas, northeastern Mexico	<i>C. andropogonoides</i> , p. 95
Awn of fertile floret usually more than 6 mm long	71
71. Sterile floret less than 1 mm long	72
Sterile floret more than 1 mm long	74
72. Culms slender, wiry; blades filiform or narrow, less than 1 mm wide (frequently less than 0.5 mm wide); Cuba, Jamaica, Hispaniola	<i>C. ekmanii</i> , p. 119
Culms stout, not wiry; blades (at least the wider) 5 to 10 mm wide	73

73. Awn of fertile lemma 6 to 13 mm long; fertile lemma margins sparsely pilose; leaf blade apex acute to subacute; widely distributed in American tropics; Hawaii *C. radiata*, p. 110
- Awn of fertile lemma 10 to 45 mm long; fertile lemma margin scabrous, rarely sparsely pilose; leaf blade apex obtuse, rarely acute; South America, Africa *C. pynothrix*, p. 114
74. Culms slender, wiry; blades filiform or very narrow, usually less than 1 mm wide, frequently less than 0.5 mm wide; Cuba, Hispaniola, Jamaica *C. ckmanii*, p. 119
- Culms stout, not wiry; blades, at least the larger, generally broader than 1.5 mm 75
75. Blades usually densely pubescent on both upper and lower surfaces; awn of fertile lemma 20 to 24 mm long; sterile floret narrowly cylindrical, 1.6 to 1.9 mm long, 0.2 to 0.3 mm wide; Cuba *C. arcuaria*, p. 119
- Blades usually glabrous or scabrous, occasionally sparsely pilose near the base; awn of fertile lemma less than 13 mm long; sterile floret comparatively broader, 0.3 to 0.6 mm wide, 0.7 to 1.9 mm long 76
76. Spikes strongly divergent from the vertical axis, becoming horizontally spreading or even somewhat reflexed at maturity; keel of fertile lemma glabrous, occasionally very sparsely appressed-pubescent; longest callus hairs 0.3 to 0.8 mm long; marginal hairs of fertile lemma strongly appressed, shorter than 0.5 mm long; Caribbean Islands, Cuba, Haiti, Jamaica *C. sagracana*, p. 121
- Spikes not divergent more than 45° from the vertical axis; keel of fertile lemma usually prominently appressed-pubescent, occasionally sparsely so, rarely glabrous; longest hairs of the callus 1.0 to 1.2 mm long; marginal hairs of the lemma somewhat spreading, especially toward the apex, the longest usually 1 mm or longer; Caribbean Islands, Cuba, Haiti, Jamaica *C. cubensis*, p. 123

1. **CHLORIS ROXBURGHIANA** Schultes, Mantissa 2:339. 1824. (Based on *Chloris polystachya* Roxburgh. See explanatory note in text.) Fig. 5, A-E.

Chloris polystachya Roxburgh, Hortus Bengalensis 82. 1814. *Nomen nudum*. *Non Lagasca*, 1816.

Chloris polystachya Roxburgh, Flora Indica 1:332. 1820. *Non Lagasca*, 1816. (See explanatory note in text.)

Chloris myriostachya Hochstetter, Flora 38:204. 1855.

(HOLOTYPE: "Hb. abyss. Buch. nr. 1416," not seen, but description is of this taxon.)

Chloris myriostachya var. *minor* Chiovenda in Pirota, Annuario Reale Ist. Bot. Roma 8:54. 1903. (Description is of a small variant of the species.)

Perennial to 125 cm tall, arising from a strongly stoloniferous, woody base; sheaths glabrous below, often pilose above; ligules pilose; blades up to 30 cm long, 5 to 6 mm wide, glabrous or scabrous; spikes many (usually 50 or more) attached along a short axis at the culm apex and forming a dense inflorescence up to 15 cm long and 4 to 6 cm wide;

spikelets densely imbricate, ca 17 per cm of the rachis length; glumes narrowly lanceolate, glabrous except for the slightly scabrous midrib; first glume 0.9 to 1.0 mm long, ca 0.1 mm wide; second glume 1.9 to 2.2 mm long, ca 0.2 mm wide; fertile lemma 1.7 to 2.1 mm long, ca 0.4 mm wide, ovate to elliptic, callus bearded, margins glabrous to sparsely ciliate, especially above; sides sparsely appressed-pilose to glabrous, apex acute, awn 10 to 15 mm long; sterile florets usually two (occasionally three) glabrous, shaped much like the fertile lemma, lower sterile floret 0.7 to 1.0 mm long, 0.2 to 0.3 mm wide, upper floret(s) progressively smaller, awn of lower sterile floret ca 10 mm long; caryopsis ca 1.1 mm long, 0.4 mm wide, ellipsoidal, trigonous; chromosome number $2n=20$.

Only *Chloris paniculata* has as large a number of spikes as *C. roxburghiana*. These two are most easily differentiated by the number of sterile florets, *C. roxburghiana* always having at least two, while *C. paniculata* always has one. *Chloris roxburghiana* is a stoloniferous perennial found in Africa and India. *Chloris paniculata* has a unique growth habit, with well-developed, short, vertical rhizomes bearing the frayed remnants of previous years' growth as well as many long, arching, basal leaves; it is endemic to



Fig. 5. *Chloris roxburghiana* and *C. paniculata*. (A-E) *C. roxburghiana*. (A) habit, x 1/5; (B) spikelet, partly dissected, x 15; (C,D) lower and middle sterile florets, respectively, x 10; (E) caryopsis, x 10. (F,G) *C. paniculata*. (F) habit, x 1/5; (G) spikelet, partly dissected, x 15.

Cocos Island, which is off the western coast of Panama.

Chloris myriostachya has been used as a name for this species for many years, especially in African floras. Part of this erroneous usage can be traced to the difficulty of typifying the Roxburgh names. William Roxburgh first used *C. polystachya* in 1814 (Hortus Bengalensis 82.), publishing it without a description. Identification of this name rests with its subsequent publication by Roxburgh (Flora Indica 1:332. 1820.), who included a fairly complete description. By that date, however, Lagasca y Segura (1816) had published the same name for a Mexican species (see under *C. submutica*). Shortly afterward, Schultes (Mantissa 2:339. 1824.) published a new name, *C. roxburghiana*, based upon *C. polystachya* Roxburgh. No plant specimen that may be connected positively with Roxburgh's name can be located; however, important clues may be obtained from the Roxburgh drawings at Kew and from the descriptions given by Roxburgh, both those of the published *Flora Indica* as well as the copy of the manuscript of that work in the Kew Library. The drawings, labelled "*C. polystachya*," show an inflorescence of sixteen spikes arranged along a short common axis, and a series of dissected spikelets showing broadly ovate-elliptic fertile lemmas and two similar sterile florets. While the inflorescence drawing does not portray accurately the more typical specimens of this taxon from Africa (though Indian collections bearing a strong resemblance are common) the spikelet drawings leave no question as to the identity of Roxburgh's *Chloris polystachya* and thus, indirectly, *C. roxburghiana* Schultes.

Chloris roxburghiana is common (sometimes dominant) in grasslands, brush, and disturbed areas, often on sandy loams from low to medium elevations (Fig. 6). Associates include *Cenchrus* sp., *Pennisetum* sp., *Sporobolus* sp., *Acacia mellifera*, *Blepharis* sp., *Commiphora* sp., and *Euphorbia spinescens*.

Representative specimens examined: ANGOLA: Mossamedes Dtr., Camucuo, *Azancot de Menezes* 363 (K). BOTSWANA: Maklautsi-Shashi Rivers, Palapye, *de Beer*, s.n., 9 May 1957 (K). ETHIOPIA: Harrar Prov., 40° 39' E, 10° 10' N, *Burger* 2,899 (K); Sidamo Prov., 20 mi N of Moyale (Kenya), *Mooney* 7,421 (K). INDIA: Nilgiri Dtr., Kitagin Ghat, *Fischer* 2,086 (K). KENYA: Kibwezi Plains, *Bally* 1,329, 8,090 (K); 25 mi SSW of Kitui, *Bogdan* AB 5,126 (K,US); Lugard's Falls Road, Tsavo National Park, *Greenway and Kanuri* 12,636 (K);

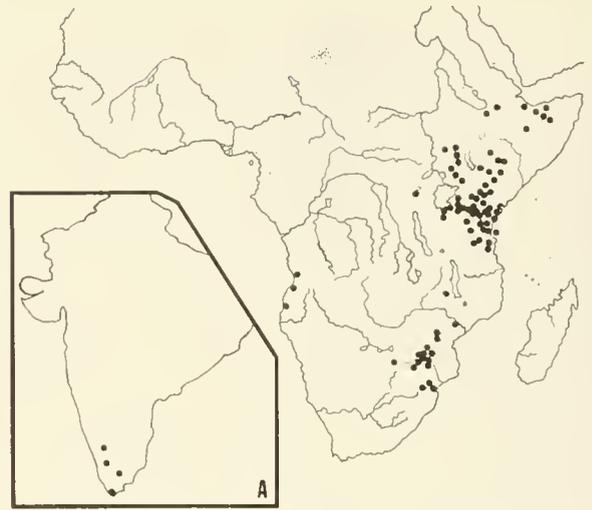


Fig. 6. Distribution of *Chloris roxburghiana*. Inset A: India.

Wei Wei 50 mi N of Kapenguria, *Trelawny* AB 4,325 (K,UC). MALAGASY REPUBLIC: Mombas, anon. (K). MALAWI: Lilongwe Dtr., *Salubeni* 428 (K). MOZAMBIQUE: Lourenço Marques Dtr., between Moambas and Sabie, *Torre* 2,237 (K). REPUBLIC OF THE CONGO: Plaine du Lac Edouard, Parc Nationale Albert, *Louis* 4,787 (K, US). SOMALI REPUBLIC: Boundary Pillar 93, 8°37'N, 45°09'E, *Gillett* 4,197 (K, US). SOUTHERN RHODESIA: 30-60 mi S of Ft. Victoria, *Rodin* 4,251 (K, UC, US); Sabi River Valley, Melsetter, *Whellan* 1,021 (K). SUDAN: Equatoria Prov., Kidepo resthouse, *Myers* 11,236 (K). TANZANIA: Tanga Dtr., Kange Estate, *Faulkner* 832 (K); SW of Uмба River, Kivingo, *Greenway* 1,996 (BM, K); Lake Manyara National Park, *Greenway and Kirrika* 11,089 (K, US). UGANDA: Kanamugit, *Eggeling* E 2,946 (K, US); Turkana Dtr., Oropoi Valley, *Liebenberg* 1,776 (K). UNION OF SOUTH AFRICA: Kruger National Park, between Punda Maria and Pafuri (Mozambique), *Godfrey* SH-1,729 (K, US); between Beauty and Ellisras, *Werdemann and Oberdieck* 1,801 (K).

2. **CHLORIS PANICULATA** Scribner in Robinson, Proc. Amer. Acad. Arts Sci. 38:262. 1902. (HOLOTYPE: "Nuez Isl . . . an islet near Cocos Isl.: Snodgrass and Heller, no. 968;" in GH. Not seen, but description is clear.) Fig. 5, F and G.

Perennial to 70 cm tall, arising from an upright, stout, underground stem bearing many rootlets and shreds of leaf sheaths; sheaths

glabrous; ligule lacking; blades very long and narrow, up to 50 cm long and 5 mm wide, arching, glabrous except for the scabrous margins; inflorescence paniclelike, made up of at least 50 spikes racemously arranged on the upper 10 to 12 cm of the culm; spikes about 5 cm long at lower part of inflorescence, becoming progressively shorter near the tip; glumes narrow to broadly lanceolate, glabrous except for the scabrous midnerve; first glume ca 1.2 mm long, 0.2 mm wide; second glume ca 3 mm long, 0.4 mm wide; fertile lemma ca 2.6 mm long, 0.6 mm wide, broadly lanceolate, glabrous except for the prominently bearded callus and scabrous keel, apex \pm obtuse, awn 2.5 to 2.8 mm long; sterile floret one, ca 1.5 mm long, 0.3 mm wide, glabrous, awn 1.5 to 1.8 mm long.

Only *Chloris roxburghiana* has as many spikes as *C. paniculata*. Differences between these two species have been discussed under *C. roxburghiana*.

Chloris paniculata is an endemic known only from Cocos Island and its associated islets—an archipelago lying about 300 miles southwest of Costa Rica, to whom it belongs. Robinson (1902) and Stewart (1912) both reported it as being abundant on rocky cliffs near the coast, both on the main island and on the islets. Most of the vegetation of the island area is made up of common Central American species or pantropical weeds. Only eight endemics in a total of about a hundred species were reported by Stewart. Fosberg and Klawe (1966) also report *C. paniculata* from Cocos Island.

I cannot suggest a species in *Chloris*, nor for that matter any other genus in the Chlorideae, that might be said to be closely related to *C. paniculata*. The previously discussed resemblance to *C. roxburghiana* is superficial, for there are many spikelet details in which they differ. Certain species of *Leptochloa* have a similar aspect because of the large number of spikes. *Leptochloa*, however, has spikelets which uniformly have a larger number of fertile florets, and the sterile floret is not as elaborated in structure and size as is generally the case in *Chloris*.

Specimens examined: COCOS ISLAND: exposed rocky cliffs near the ocean, Stewart 260 (F,MO,NY,US).

3. **CHLORIS BERROI** Arechavaleta, Anales Mus. Nac. Montevideo 5:388. 1896. (HOLOTYPE: "Berro, Uruguay, Estancia de Soriano, Estancia de Vera." This specimen was not seen, though specimens at K! and US! are labeled essentially the same

and are the species as commonly understood. The description and illustration accompanying the original description leave no question as to the identity of the taxon, however.) Fig. 7, A-D.

Chloris accumbens Hackel ex Arechavaleta, Anales Mus. Nac. Montevideo 5:391. 1896. *Nomen nudum, pro syn. C. berroi*.

Perennial from a fibrous root system, tufted, 15 to 80 cm tall; sheaths glabrous; ligule ciliate; blades narrow, 3 to 15 cm long, 1.5 to 2.0 mm wide, glabrous or sparsely pilose near the base; spikes two to four, 3 to 12 cm long, tightly appressed, adherent, and forming a narrow, cylindrical, spikelike inflorescence; spikelets densely imbricate, 9 to 12 per cm of the scabrous-hispid rachis; glumes glabrous, lanceolate; first glume 1.5 to 1.6 mm long, ca 0.3 mm wide; second glume 2.1 to 2.6 mm long, 0.3 to 0.6 mm wide; fertile lemma ovate, 2.7 to 3.5 mm long, 0.8 to 1.2 mm wide, margins and keel ciliate with hairs up to 2 mm long, awn 2.7 to 3.4 mm long; sterile florets usually three, up to 1.9 mm long, lowermost awned, upper unawned, glabrous; caryopsis 1.2 to 1.8 mm long, 0.5 to 0.7 mm wide, obovoid, trigonous; chromosome number $2n=40$.

Chloris berroi can be distinguished from all other species of the genus by its cylindrical inflorescence; this results from the interweaving of the spikelets on adjacent spikes and, more especially, from the hispid hairs of the rachises. The spikes remain interconnected past maturity, except for the very tips, and may be separated from one another only by actually tearing them apart.

Individual spikelets of *Chloris berroi* are very similar to the other species in which the lemmas have ciliate margins, especially those of *C. ciliata* and *C. dandyana*. Other than the inflorescence differences previously mentioned, there seem to be no other characteristics separating them.

Chloris berroi is restricted to the Río de la Plata region of Argentina and Uruguay (Fig. 8), where Parodi (1919) reported it to be abundant in the campo.

Specimens examined: ARGENTINA: Prov. Buenos Aires: La Plata, *Spegarrini* 1,433 (NY); Pergamino, *Niedfeld* 38 (US). Prov. Entre Ríos: camino de Puerto Constanza a Gualaguaychu, *Burkart* 10,529 (US); Dep. Federación: Estancia "Buena Esperanza," *Pedersen* 6,254 (US). URUGUAY: Dep. Canelones: Montevideo, *Sello s.n.* (MO). Dep. Florida: Arroyo Mansavillagra, *Gallinal* 5,790 (MO). Dep. Soriano,

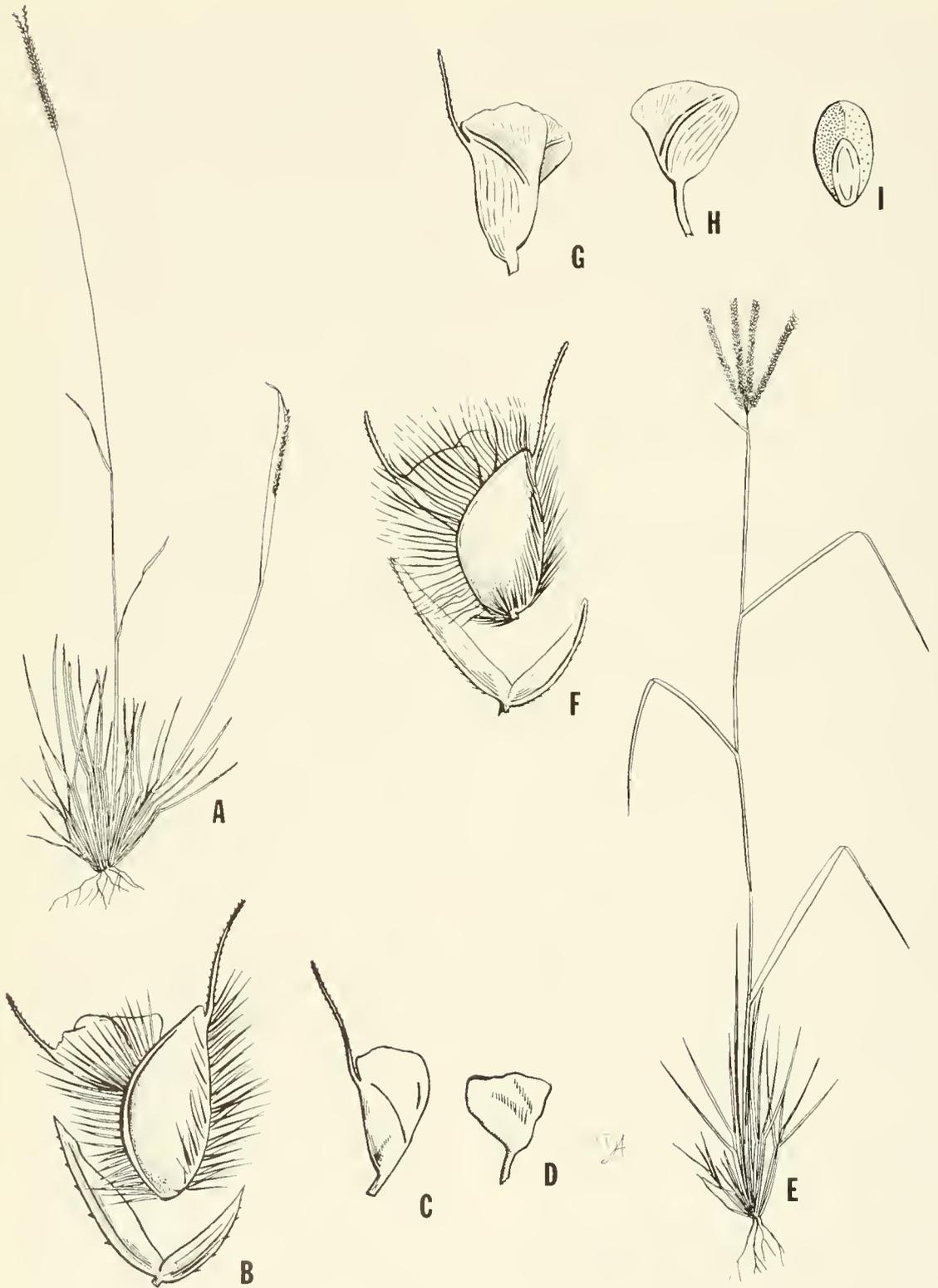


Fig. 7. *Chloris berroi* and *C. ciliata*. (A-D) *C. berroi*. (A) habit, x 1/5; (B) spikelet, x 10; (C) lower sterile floret, x 15; (D) upper sterile floret, x 15. (E-I) *C. ciliata*. (E) habit, x 1/4; (F) spikelet, x 10; (G) sterile florets, x 15; (H) upper sterile floret, x 15; (I) caryopsis, x 10.



Fig. 8. Distribution of *Chloris berroi* (southern South America).

Berro 6,385 (US). Dep. Tacuarembó, *Herter* 587a (MO).

4. **CHLORIS CILIATA** Swartz, Prodr. Veg. Ind. Oec. 25. 1788. (HOLOTYPE: Not seen. Swartz's original description in 1788 is clear; his amplification in 1797 leaves no doubt.) Fig. 7, E-I.

Andropogon pubescens Aiton, Hortus Kewensis 3:423. 1789. (Based on *Chloris ciliata* Swartz.)

Cynodon ciliatus (Swartz) Raspail, Ann. Sci. Nat. Bot. (Paris) 5:303. 1825. (Based on *Chloris ciliata* Swartz.)

Chloris propinqua Steudel, Syn. Pl. Glum. I:204. 1854. (HOLOTYPE: "Duchassaing legit in Guadeloupe." A fragment in US!, from the Steudel specimen in P, is badly shattered but would appear to be *Chloris ciliata*. The description seems to fit *Chloris ciliata* Swartz.)

Chloris ciliata var. *texana* Vasey, U. S. Dept. Agr. Div. Bot. Bull. 121. pl. 30. 1890. (HOLOTYPE: "Near Brownsville" US!)

Chloris texana (Vasey) Nash, Bull. Torrey Bot. Club 25:441. 1898. Based on *Chloris ciliata* var. *texana* Vasey.)

Chloris nashii Heller, *Muhlenbergia* 5:120. 1909. (Based on *Chloris ciliata* var. *texana* Vasey.)

Perennial 25 to 60 cm tall, tufted, erect; sheaths glabrous, ligule absent or reduced to a short ciliate crown (Northern Hemisphere) or densely and conspicuously pilose (Southern Hemisphere); blades 10 to 20 cm long, ca 5 mm wide, long-acuminate, glabrous or scabrous; spikes three to five (rarely six or seven), 3.5 to 6.0 cm long (occasionally up to 8 cm) somewhat flexuous and spreading, glumes narrowly lanceolate, glabrous except for the scabrous midrib, becoming hyaline near the margins; first glume 1.3 to 1.7 mm long, 0.2 to 0.4 mm wide; second glume 2.0 to 2.5 mm long, 0.2 to 0.4 mm wide; fertile lemma 1.8 to 2.8 mm long, 0.8 to 1.1 mm wide, strongly flattened, elliptic, margins and keel strongly ciliate, the cilia 0.5 to 1.5 mm long, awn 0.9 to 2.7 mm long; sterile florets two, lowermost enclosing the upper; lower sterile floret 1.3 to 1.8 mm long, 0.8 to 1.8 mm wide, truncate, glabrous, awn 0.9 to 1.4 mm long, upper floret similar but smaller, 0.8 to 1.1 mm long, 0.9 to 1.2 mm wide, membranous, awnless; caryopsis ca 1.4 mm long, ca 0.7 mm wide, obovoid to ellipsoid; chromosome number $2n=40$.

The species in this complex (*Chloris berroi*, *C. canterai*, *C. ciliata*, *C. dandyana*, and *C. lamproparia*) are characterized by elliptic to lanceolate lemmas, the margins of which are densely ciliate, usually along the entire length. *Chloris berroi* is easily distinguished, for it has spikes so interconnected by hispid hairs on the rachises that it appears to have but a single spike. The remaining species, however, present a more complex pattern. While most collections will fit a given species quite well, certain geographic areas (most often in South America) may have individuals which are somewhat intermediate with respect to the characteristics. Figure 9 illustrates selected features of a large number of specimens chosen at random from throughout the ranges of the species.

While this diagram reveals no distinct subpopulations, certain variation trends may be discerned. One trend is characterized by individuals with relatively short lemmas, short marginal cilia on the lemmas, short awns, and few spikes (six or less). These are the plants commonly called *C. ciliata* and are represented by the open circles situated roughly in the lower left quadrant of the diagram. A second trend, represented mostly by open circles with an upward line, is shown in the upper left quadrant. These collections had longer

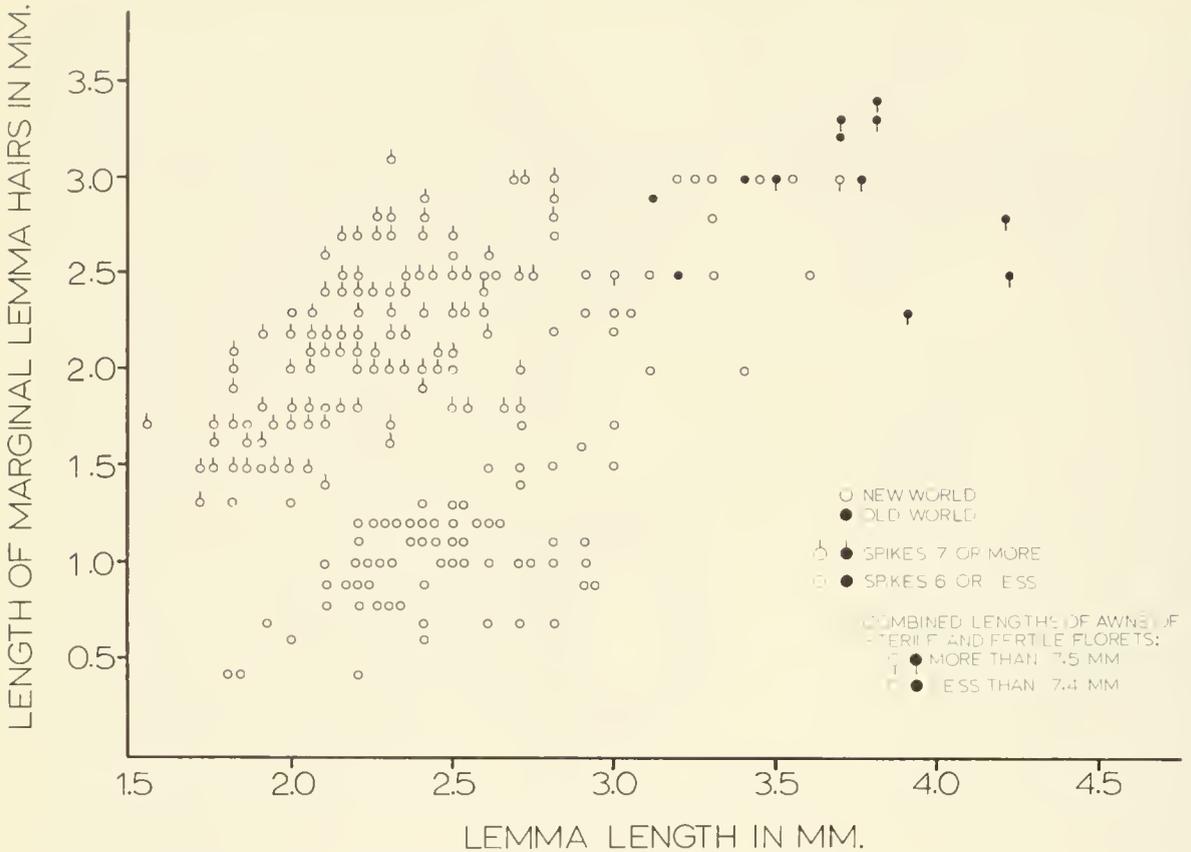


Fig. 9. Comparison of various morphological and geographical characteristics of *Chloris canterai* var. *canterai* and var. *grandiflora*, *C. ciliata*, *C. dandyana*, and *C. lamproparia*.

lemmas and marginal hairs, a larger number of spikes (often more than 20), but short awns; these are representative of plants commonly called *C. dandyana*. Extremes of these populations are easily separated, though individual plants may diverge considerably from the "average" member of each trend.

The third and fourth trends overlap more with respect to the morphological characteristics analyzed and are most easily separated geographically. These two groups are intermingled in the upper right quadrant and differ from both of the previous trends in length of the lemma and of its marginal cilia. Within this group, the New World collections are perennials with relatively short lemmas, marginal cilia, and awns. These are the plants commonly named *C. canterai*. The remaining specimens are Old World annuals and have, generally, longer lemmas, marginal cilia, and awns; these are commonly called *C. lamproparia*.

Well-defined discontinuities between the various populations have not been demonstrated, at least on the basis of the characteris-

tics employed. However, it does not seem that merging all of these into a single species is justified, for discernible variation trends are evident. Thus four species are recognized, each centering in one of the four trends discussed above.

Certain other characteristics were of value in differentiating elements *within* these taxa, but did not clarify the relationships *between* them; these are discussed individually under the appropriate species. All populations are deserving of further study, especially in areas of sympatry. Mass collections as well as cytological examination and genetic analysis will be especially valuable.

Table 7 compares all of the species in this complex with respect to a variety of characters. Figures 7, 11, 13, and 15 should also be used for comparison.

There are two recognizable geographic variants within *Chloris ciliata*: (1) a North American population with nonciliate ligules and (2) a South American group with prominently ciliate ligules. No other differences could be

Table 7. Comparison of *Chloris berroi*, *C. canterai*, *C. ciliata*, *C. dandyana*, and *C. lamproparia*.

Species	Annual or perennial	Culm type	Spikes		Length (in mm)	Fertile lemma	Awn length (in mm)
			Number	Length (in cm)		Marginal hair length (in mm)	
<i>C. berroi</i>	perennial	erect, 15-80 cm tall	2-4	3-12	2.7-3.5	up to 2.0	2.7-3.4
<i>C. canterai</i>	perennial	erect, to 1 m tall (except shorter and cespitose in var <i>grandiflora</i>)	2-9, often 3-6	4-14	2.7-3.7	1.5-3.0	2.4-5.5
<i>C. ciliata</i>	perennial	erect, tufted, 25-60 cm tall	3-5, rarely 6-7	3.5-6	1.8-2.8	0.5-1.5	0.9-2.7
<i>C. dandyana</i>	perennial	erect, usually tufted, rarely stoloniferous, up to 135 cm tall	4-28, usually more than 8	7-20	1.6-2.8	1.0-3.0	1.4-4.8
<i>C. lamproparia</i>	annual	erect to decumbent, 10-60 cm tall	1-4, often 2	ca 4	3.2-4.2	2.0-3.0	3.5-6.0

found, and the two are not given taxonomic status.

Chloris ciliata is widely distributed in open grasslands in the south central United States, Mexico, Central America, the Caribbean region, and in southern South America (Fig. 10).

Representative specimens examined: BAHAMA ISLANDS: Nassau, *Curtiss* 72 (F, MO, NY, US). ARGENTINA: Prov. Córdoba: Bell Ville, *Parodi* 3,055 (US); Prov. Entre Ríos: Dep. Federación, Estância "Buena Esperanza," *Pedersen* 6,197 (US); Prov. Formosa: *Jorgensen* 3,328 (US); Prov. Jujuy: camino a San

Pedro, *Parodi* 9,796 (US); Prov. Mendoza: Santa Rosa, *Jensen-Haarup s.n.*, 1904-5 (MO, US); Prov. Salta: N of Salta City, *Stephens and Hartley III* 57 (US). CUBA: Prov. Habana: Marianao, *Ekman* 1,192 (US); Prov. Pinar del Río: Bay of Mariel, *Britton and Earle* 7,570 (NY); Prov. Santa Clara Lomas de Banao, *Luna* 888 (NY). HAITI: Port-de-Paix, *Ekman* 4,324 (US); Massif de la Pelle, Port-au-Prince, *Ekman N. H.* 8,145 (US); Gonave Island: vicinity of Etroite, *Leonard* 3,371 (US); Tortue Island: Basse Terre, *Leonard and Leonard* 12,444 (NY, US); vicinity of Jean Rabel, *Leonard and*



Fig. 10. Distribution of *Chloris ciliata*. (A) Southern South America. (B) Puerto Rico, Leeward, and Windward Islands. (C) Central America and Caribbean Islands.

Leonard 12,934 (US). JAMAICA: Middlesex Co.: Clarendon Parish, Inverness, *Harris* 12,755 (F, MO, NY, US); Manchester Parish, *Harris* 12,689 (F, MO, NY, US); Cornwall Co., St. James Parish, Montego Bay, *Hitchcock* 9,671 (US). LEEWARD ISLANDS: Antigua: Dead-sands Bay, *Box* 31 (US); Guadeloupe Island, *Duss* 31,587 (NY, US); St. Barthélemy, *Questel* 337 (US). MEXICO: Coahuila: Castaños, *Reeder, Reeder and Soderstrom* 3,270 (US); Nuevo León: Monterey, *Kenoyer* 315 (MO); Oaxaca: Tomellin, *Hitchcock* 6,220 (US); San Luis Potosí, 7.5 mi N of El Naranjo, *McGregor et al.* 813 (US); Tamaulipas: 22 km S of Victoria, *Martinez and Luyando* F-2,283 (TEX, US); Yucatán: Chichen-Itza, *Swallen* 2,409 (US); Tizimín, *Swallen* 2,491 (US); Uxmal, *Swallen* 2,612 (US); Peto, *Swallen* 2,672 (US); Mérida, *Souza-Novelo* 15 (US). PUERTO RICO: Ponce, *A. Chase* 6,495 (NY, US). SANTO DOMINGO: Prov. Santo Domingo: Llano Costero, *Ekman* 12,486 (US); Barahona, *Fuertes* 308 (US). UNITED STATES: New York: Yonkers, mill yard, *Nash s.n.*, 24 July 1898 (NY). Texas: Aransas Co., Rockport, *Swallen* 10,297 (US); Bee Co., Pettus, *Tharp* 43,071 (TEX); Bexar Co., 20 mi S of San Antonio, *Silveus* 137 (TEX); Calhoun Co., 2 mi SW of Port Lavaca, *Rowell and Webster* 2,117 (TEX); Cameron Co., Laguna Atascosa Refuge, *Fleetwood* 3,800 (TEX); De Witt Co., near Edgar, *Owens* 155 (US); Jim Wells Co., 6 mi W of Alice, *Gould and Kapadia* 8,854 (UC); Karnes Co., 5 mi S of Kennedy, *Emery* 773 (TEX); Kleberg Co., King Ranch, *M. C. Johnston* 541,669 (TEX); Matagorda Co., near Palacios, *Rogers* 6,607 (TEX); San Patricio Co., 1 mi SE of Sinton, *Gould* 9,903 (TEX); Starr Co., Fort Ringgold, E of Rio Grande City, *Tharp and York* 51-84 (TEX); Travis Co., Zilker Park, *W. V. Brown s.n.*, 6 Oct 1957 (TEX); Wharton Co., 12 mi N of El Campo, *W. V. Brown* 3,265 (TEX); Willacy Co., Sauz Ranch, *M. C. Johnston and Davis*, 5,319.84 (TEX). URUGUAY: Dep. Montevideo, *Herter* 78,127 (US). VIRGIN ISLANDS: St. Croix: Bassin Yard, *Ricksecker* 42 (F, MO, NY, UC, US). WINDWARD ISLANDS: Barbados, *Hitchcock* 16,514 (US); Grenada: Richmond Hill, *Broadway* 1,869 (NY); Martinique, *Duss* 1,273 (MO, NY, US).

5. **CHLORIS LAMPROPARIA** Stapf in Chevalier, Bull. Bot. Soc. France Mem. IV. 8:220. 1912. (HOLOTYPE: Chad, "Baguirmi, emplacement de la ville de Massenia, 25-31 Aout 1903, no. 9633 bis." P! ISO-TYPE: K!) Fig. 11.

Annuals 10 to 60 cm tall, erect to decumbent; stems usually branched at the base, these sometimes rooting at the lower nodes; sheaths glabrous; ligule a short ciliate crown; blades 5 to 20 cm long, 3 to 5 mm wide, sparsely pustulose-pilose above, especially near the base, glabrous to scabrous below; spikes one to four (often two) ea 4 cm long, appressed or only slightly divergent; spikelets densely inserted on the rachis, usually divergent, ea 10 per cm of the long scabrous-hispidulous rachis; glumes lanceolate-ovate, thin, brown, glabrous (except for the scabrous midnerve); first glume 3.9 to 4.4 mm long, 0.6 to 0.9 mm wide, apex acute; second glume 6.5 to 8.0 mm long, ea 1 mm wide, apex acute to acuminate; fertile lemma 3.2 to 4.2 mm long, 0.8 to 1.7 mm wide, broadly ovate to elliptic, dark brown, keel appressed-pubescent, margins with spreading ciliate hairs, 2 to 3 mm long, internerves glabrous, apex acuminate, awn 3.5 to 6.0 mm long; sterile florets two or three; lowest sterile floret 1.3 to 1.6 mm long, 1.0 to 1.5 mm wide, triangular, apex truncate, awn 2.3 to 4.7 mm long, upper florets similar in shape, but progressively smaller, unawned; caryopsis 1.5 to 2.0 mm long, 0.8 to 1.0 mm wide, ovoid to obovoid.

Chloris lamproparia is the only species in the group with ciliate margins on the lemma that is distributed in the Old World, and it is also the only annual. It is most similar to *C. canterai*, differing from it in having larger spikelets, though occasional specimens are intermediate in spikelet size and can be assigned most easily by their geographic origin and habit.

Chloris lamproparia is distributed across central Africa (Fig. 12), where it is reported to be common in wet grasslands and savannas.

Representative specimens examined: CAMEROON: Tehabaol, 45 km ENE of Maroua, *Letouzey* 6,473 (K). MALI: Boré, *Demange* 14/1,957 (K). NIGERIA: Domaturu, *De Leeuw* 1,097a (K); Zaria Dtr., *Taylor H.* 2,624/32 (K). SUDAN: Darfur Prov.: 3 km NE of Kes, *Jackson* 4,040 (K); Jebel Marra, Zalingei, *Wickens* 2,304 (K); Equatoria Prov., 13 mi SW of Kapoeta, *Peers s.n.*, 29 Aug 1953 (K); Kordofan Prov.: El Muglad, *Andrews* 3,063 (K); near Hamadi, on El Obeid-Dilling road, *Harrison* 901 (K). TANZANIA: Tumba Rukwa, *Michellmore* C1,557 (K). UGANDA: Moroto, *Wilson* 15 (K). UPPER VOLTA: Ouagadougou, *Chevalier* 24,674 (K).

6a. **CHLORIS CANTERAI** Arechavaleta var. **CANTERAI**. Anales Mus. Nac. Montevideo

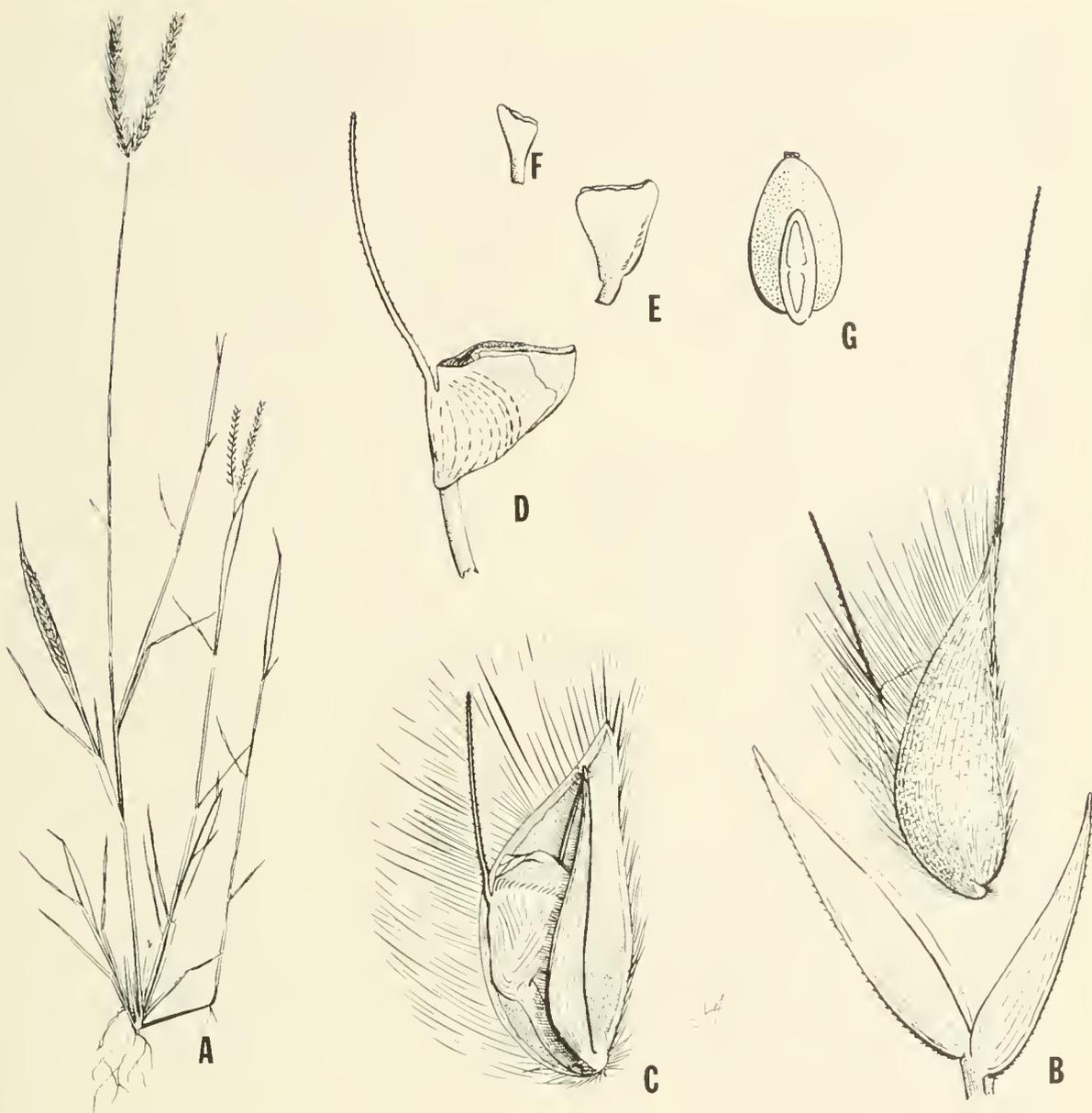


Fig. 11. *Chloris lamproparia*. (A) habit, $\times 1/4$; (B) spikelet, partly dissected; (C) lemma with one side removed, showing palea and sterile floret within; (D) sterile florets; (E-F) upper sterile florets; (G) caryopsis. (B-G) $\times 10$.

5:385. 1896. (HOLOTYPE: "Anderson . . . Montevideo." Not seen, but original description clearly identifies the plant.) Fig. 13, A, C-J.

Chloris parodiana Rosengurtt and Izaguirre, Bol. Soc. Argentina Bot. 12:128. 1968. (HOLOTYPE: "Paraguay, Paraguari . . . Rosengurtt B-5,979, MVFA." Not seen, but description and illustration are clear.)

Perennial up to 1 m tall, tufted and erect; sheaths glabrous; ligule long-ciliate, with cilia

up to 7 mm long; blades narrow, often rolled and appearing filiform, 1 to 5 mm wide, up to 25 cm long, glabrous to slightly scabrous, occasionally sparsely long-pilose; spikes two to nine (often three to six), 4 to 14 cm long, usually more than 7 cm long, erect to curving; spikelets densely imbricate, appressed, light to medium brown, ca 11 per cm of the scabrous rachis; first glume 1.6 to 2.4 mm long, 0.5 to 0.6 mm wide, narrowly lanceolate, markedly inequilateral; second glume 2.3 to 3.8 mm long, 0.4 to 0.6 mm wide, narrowly lanceolate, equi-



Fig. 12. Distribution of *Chloris lamproparia*.

lateral or inequilateral; fertile lemma narrowly ovate, 2.7 to 3.7 mm long, usually more than 3 mm, 0.6 to 1.1 mm wide, ovate, callus bearded, densely ciliate on keel and margins, marginal cilia 1.5 to 3.0 mm long, internerves glabrous, awn 2.4 to 5.5 mm long; sterile florets two (sometimes three), similar, turbinate-flattened; lower sterile floret 1.1 to 1.8 mm long, about half as wide, glabrous; awn 1.5 to 3.5 mm long; upper sterile floret(s) similar to lower in shape, but smaller, about 0.5 mm long, awnless; carpopsis ovoid-ellipsoid, 1.3 to 2.0 mm long, 0.8 to 0.9 mm wide; chromosome number $2n=36$.

6b. **CHLORIS CANTERAI** Arechavaleta var. **GRANDIFLORA** (Rosengurtt & Izaguirre de Artucio) Anderson, comb. nov. Fig. 13, B-J. *Chloris grandiflora* Rosengurtt and Izaguirre de Artucio, Bol. Soc. Argentina Bot. 12:127. 1968. (HOLOTYPE: "Uruguay, dep. Florida . . . Gallinal et Rosengurtt, PE-5,790 . . . MUFA." Not seen, but original description and illustration are clear.)

Perennial, densely caespitose, 5 to 30 cm tall (often about 20 cm) arising from a dense cluster of very narrow, often curved and rolled leaves; spikes three to five, ea 3 to 6 cm long; other characteristics as in var. *canterai*, except chromosome number unknown.

The most marked difference within *Chloris canterai* is a vegetative one. A group of specimens, primarily from Argentina (Fig. 14, open circles) is shorter than usual and has a well-defined, caespitose growth habit. No spikelet distinctions could be found. A few of these have been collected in the same precise location as specimens of var. *canterai*; but the collection data indicate that they are found in dry, rocky areas as opposed to the lower, wetter sites in which var. *canterai* is typically found.

While one immediately suspects that an environmental factor may be influential, or that the caespitose individuals are merely more heavily grazed, the morphological discontinuity is so well defined that it is felt that the population is worthy of being recognized taxonomically. Rosengurtt and Izaguirre de Artucio (1968) have given this population the name *Chloris grandiflora*. I feel that this overemphasizes the differences, however, and I have consequently reduced it to a varietal rank.

In addition, Rosengurtt segregated a second species from this variable population, naming it *Chloris parodiana*. It is based largely upon the relative length of lemma cilia. I do not feel that the differences emphasized are stable, at least on the basis of the data summarized in Fig. 9; and I, consequently, have treated it as a synonym under var. *canterai*. Further studies of a more experimental nature will be needed to determine the validity of all of these taxa.

While some specimens of *Chloris canterai* and *C. lamproparia* may be difficult to separate, there are ample differences. *Chloris canterai* is a tufted, South American perennial (Fig. 13) with relatively smaller and narrower spikelets and more spikes per inflorescence than *C. lamproparia*, which is an African annual (Fig. 11).

Chloris canterai var. *canterai* is restricted to northeastern Argentina, extreme southern Brazil, Paraguay, and Uruguay (Fig. 13, shaded circles), where it is reported as occurring on moist soils on the campo. *Chloris canterai* var. *grandiflora*, on the other hand, is found on dry sites, often rocky areas, most commonly in Argentina. A single specimen from BM! (collected by Gardner in 1839) is labeled "Banks of the Rio Gurgueia, Piaui," an area of Brazil far to the north of any existing collections and probably represents a labeling error. All North American plants are naturalized introductions.

Representative specimens examined: **CHLORIS CANTERAI** var. **CANTERAI**. ARGENTINA: Prov. Chaco: Tintina, *Parodi* 812 (US); Prov. Corrientes: Mercedes, *Parodi* 6,242 (US); Prov. Santa Fe: bajos del Río Salado, *Burkart* 9,077 (US); Prov. Formosa: Pileomayo, *Morel*, 6,569 (US). BRAZIL: Rio Grande do Sul, São Gabriel, *Rambo* 25,567 (US); Uruguaiana, Poste Zootecnieo, *Swallen* 7,617 (US). PARAGUAY: Dep. Paraguari: Caapueu, *Rosengurtt* 5,405 (US); Dep. Presidente Hayes: S of Villa Hayes, *Rosengurtt* 5,631 (US). UNITED STATES: Texas: Atascosa Co., 4.5 mi SE of Jourdanton, *J. C. Johnson* 2,044 (TEX); Jackson Co., 4 mi E of Edna, *Gould* 6,781 (TEX).

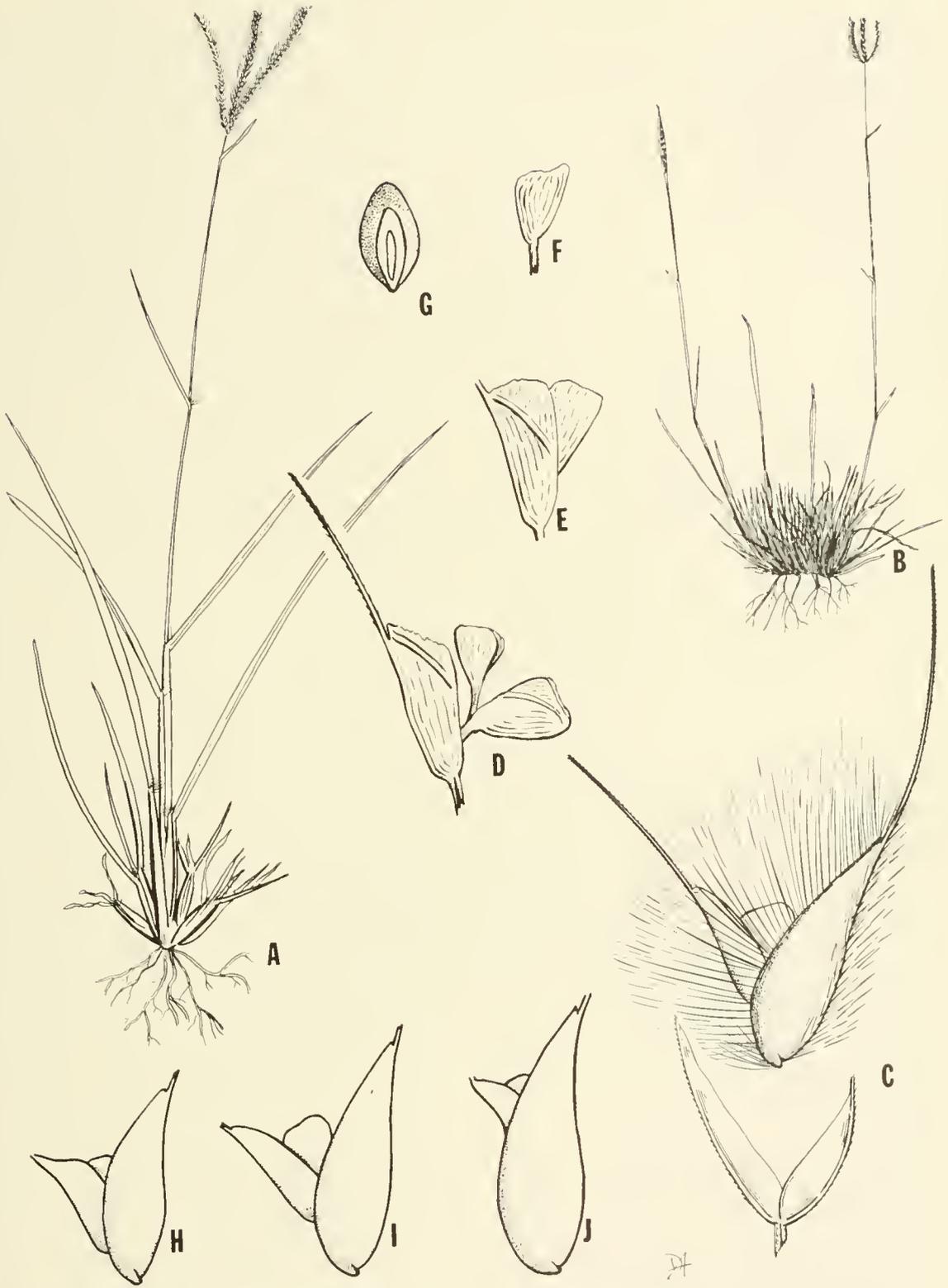


Fig. 13. *Chloris canterai* var. *canterai* and var. *grandiflora*. (A) habit, *C. canterai* var. *canterai*, x 1/6; (B) habit, *C. canterai* var. *grandiflora*, x 1/3; (C) spikelet, x 10; (D, E) sterile florets, partially dissected, x 15; (F) uppermost sterile floret, x 15; (G) caryopsis, x 10; (H-J) outlines of spikelets, showing variation, x 10.

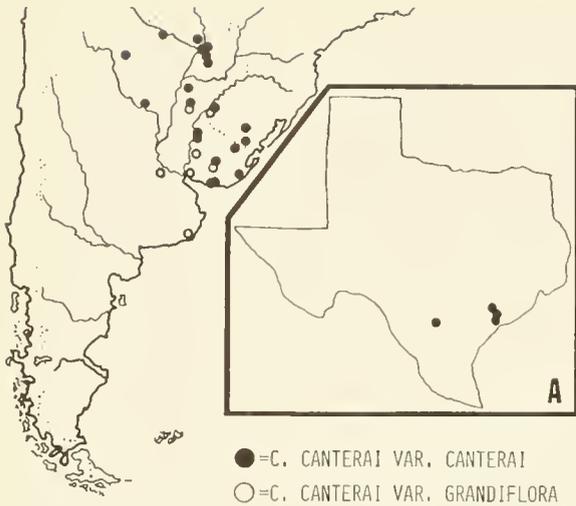


Fig. 14. Distribution of *Chloris canterai* var. *canterai* (dots) and var. *grandiflora* (open circles) in South America and Texas (Inset A).

UC); 14 mi NE of Port Lavaca, *Gould and Reeves* 8,208 (TEX, UC); La Ward, *Tharp et al.* 51-1,603 (TEX); 4 mi SE of Morales, *Turner* 3,276 and *Tharp* 53-430 (TEX); Milam Co., Buckholts, *Gould* 7,692a (TEX); Wharton Co., 6 mi S of El Campo, *Anderson* 3,288 (HSC). URUGUAY: Dep. Canelones: Pando, *Montaro* 709 (K); Dep. Cerro Largo: Río Negro, *Galinal et al.* PE-5,531 (MO, UC, US); Dep. Florida: Arroyo Mansavillagra, *Rosengurt* 5,852 (US); Dep. Paysandu, without precise locality, *Rosengurt* B-909 (US); Dep. Rocha: Camino de las Indios, *Rosengurt* B-6,938 (K); Dep. Salto: without precise location, *Del Puerto* s.n. in 1874 (US). **CHLORIS CANTERAI** var. **GRANDIFLORA**. ARGENTINA: Prov. Buenos Aires: Sierra de la Ventana, *Bartlett* 20,029 (US); San Nicolas, *Parodi* 1,023 (US). Prov. Corrientes: Dep. Mercedes, Estancia "Itacaabo," *Parodi* 6,118 (US). BRAZIL: Rio Grande do Sul, Uruguaiana, Poste Zootecnico, *Swallen* 7,656, 7,697 (US). URUGUAY: Dep. Colonia: San Juan, *Herter* 18,789 (US); Dep. Florida: Arroyo Mansavillagra, *Rosengurt* 5,790 (US).

7. **CHLORIS DANDYANA** C.D. Adams, *Phytologia* 21:408. 1971. (See discussion of this name below.) Fig. 15.

Andropogon barbatum Linnaeus, *Syst. Nat.* ed. 10. 2:1305. 1759. Non *A. barbatum* Linnaeus, 1771. (See discussion of this name below.)

Andropogon polydactylon Linnaeus, *Sp. Pl.*

ed. 2. 2:1483. 1763. (See discussion of this name below.)

Chloris polydactyla (Linnaeus) Swartz, *Prodr. Veg. Occ.* 26. 1788. (Based on *Andropogon polydactylon* Linnaeus.)

Chloris consanguinea Kunth, *Rév. Gram.* 1:89. 1829, published in key; *Enum. Pl.* 1:264. 1833, republished with full description. (HOLOTYPE: "Rio Janeiro," not seen, but description is clear.)

Chloris elata Desvaux, *Opuscules* 73. 1831. (HOLOTYPE: "Brasilio," not seen, but description is clear.)

Chloris arundinacea Nees ex Steudel, *Syn. Pl. Glum.* 1:207. 1854. (HOLOTYPE: "Sello. Brasil." Fragment of type in US! from B.)

Chloris barbata (Linnaeus) Nash, *Bull. Torrey Bot. Club* 25:443. 1898. Non *C. barbata* (Linnaeus) Swartz, 1797. (Based on *Andropogon barbatum* Linnaeus, 1759.)

Chloris polydactyla f. *stolonifera* Parodi, *Revista Argentina Agron.* 20:24. 1953. (PARATYPE: US! A stoloniferous form.)

Perennial to 135 cm tall, usually tufted, rarely stoloniferous, erect, arising from a thick fibrous root system; sheaths glabrous, becoming long-pilose at the ligule; blades up to 45 cm long, 1.5 cm wide, usually glabrous with scabrous margins, occasionally scabrous on both surfaces; spikes four to twenty-eight (usually more than eight), flexuous, to 20 cm long, usually more or less spreading, sometimes even drooping; spikelets densely imbricate, averaging 12 per cm of the scabrous to hispid-eiliate rachis; glumes pale, glabrous, with scabrous to short-hispid midnerves; first glume 1.0 to 2.5 mm long, 0.2 to 0.4 mm wide, ovate-lanceolate; second glume 1.9 to 3.5 mm long, 0.2 to 0.4 mm wide, narrowly lanceolate; fertile lemma 1.6 to 2.8 mm long, 0.5 to 0.9 mm wide, elliptic, prominently flattened, usually pale brown, margins prominently ciliate with hairs at least 1 mm long and often up to 3 mm long, keels densely appressed-pilose, awn 1.4 to 4.8 mm long; sterile florets usually two, the upper hidden in the lower; lower sterile floret cylindrical to narrowly turbinate, 1.0 to 1.6 mm long, glabrous, awn 1.7 to 4.0 mm long; upper sterile floret flattened and thin, 0.5 to 0.9 mm long, 0.3 to 0.7 mm wide, unawned; earyopsis ca 1 mm long, 0.5 mm wide, ellipsoidal.

Because of a complicated nomenclatural problem involving *Chloris dandyana* and *C. inflata*, it is necessary that a complete review of the history of these taxa be made.

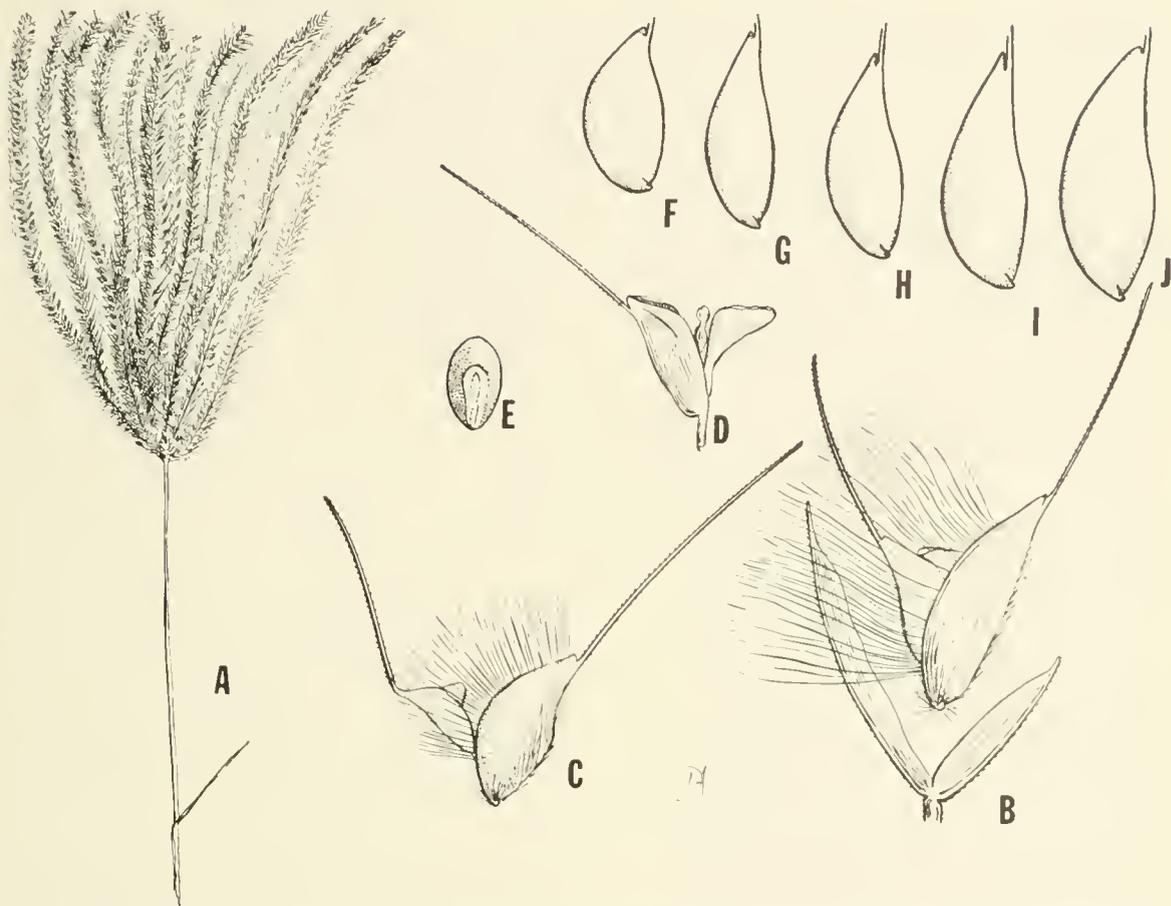


Fig. 15. *Chloris dandyana*. (A) Inflorescence, x 1/3; (B) spikelet from specimen with long lemma margin hairs; (C) spikelet from specimen with short lemma margin hairs; (D) sterile florets; (E) caryopsis; (F-J) outline of series of spikelets, showing variation. (B-J) x 10.

In 1759 Linnaeus described *Andropogon barbatus* (Syst. Nat. ed. 10. 2:1305), providing a brief description and a reference to "Sloane. hist. t. 65. f. 2." The protologue is inconclusive. The plate in Sloane is likewise not confirming, but the description of a Jamaican plant accompanying the plate (p. 111) would seem to fit best the plant described above. Reference will be made later in this discussion to a specimen labeled *Andropogon barbatus* in the Linnaean Herbarium.

Linnaeus again described *Andropogon barbatus* in 1760 (Amoen. Acad., p. 412), changing and amplifying the description and dropping the reference to Sloane, citing instead "Brown. jam. 364." The description again is not conclusive, but it would still appear to be the above-described species.

In 1763 the above names, references, and descriptions were tied together (Sp. Pl., ed. 2. 2:1483); but the name of the plant was changed to *Andropogon polydactylon*, no reason being

given for the change. There is no question of Linnaeus's intent, for he copied directly the description accompanying the 1759 publication of *Andropogon barbatus* and referred to Brown and Sloane, this time adding a direct reference to "p. 111" of the latter work. Reference was also made to the *Amoenitates* (1760).

In addition to the changes of names in the written descriptions, corroborative evidence is obtained from the Linnaean Herbarium, for there (in the *Andropogon* folder) is a specimen of the plant described above with three epithets written on it: "barbatus," "fasciculatum," and "polydactylon." The first two names are both lined through; the last is not. Nonetheless, *Andropogon polydactylon* is clearly a superfluous name and is illegitimate.

In 1771 Linnaeus again used the name *Andropogon barbatus* (Mantissa, p. 302), this time providing a clear description of a plant from the East Indies. There is no question about this description; it obviously refers to the

pan-tropical weed with inflated, truncate sterile florets, commonly called either *Chloris barbata*, *C. paraguayensis*, or (as in this study) *C. inflata*. There are two specimens—one immature, the other mature—of this taxon in the Linnaean Herbarium. One is labeled “barbatum”; the name is not lined through. Again, there is no explanation for Linnaeus’s second and different usage of *Andropogon barbatum*. The protologue is a description only; there are no references to previous publications. There is little question then about the species referred to; it is certainly not the same taxon which was given this name previously.

The transfer of *Andropogon barbatum* Linnaeus (1771) by Swartz cannot stand, for the basionym is a later homonym. It did, however, occupy *barbata* in *Chloris*, so that *Andropogon barbatum* Linnaeus (1759)—the first name applied to the species with ciliate margins on the lemmas described above—cannot be used as was proposed by Nash (1898).

Thus, all of the names used for this species are unacceptable and the new name *Chloris dandyana* Adams is adopted.

Chloris dandyana is distinguished from other members of this group primarily in spikelet size and lemma pubescence—characters in which it may approach *C. ciliata*, at least in South America. It is distinguished from *C. canterai* in usually having a relatively large number of flexuous spikes. There are, however, some specimens that differ from this pattern—these plants usually having relatively short hairs on the lemma margins and sometimes only seven to ten short spikes. In an attempt to learn more about this pattern of variation, many specimens were scored for these and other characters and various correlations were attempted. Fig. 16 shows the geographic origin of some of these specimens and their characteristics. No sharply defined patterns emerged, except that individuals with combinations of short lemma hairs and short spikes occurred randomly in South America but were neither found in the West Indies nor in Florida. In South America, however, these plants have no distinctive distribution pattern. If these variants were always found in areas of sympatry, a good case could be made for introgression with another species; but the presence of aberrant plants in Venezuela, for instance, where the nearest sympatric populations are in southern Brazil, virtually rules out all but the most ancient or fast-moving gene flows. Further studies, especially attempts at hybridizing various portions of the populations, may shed light

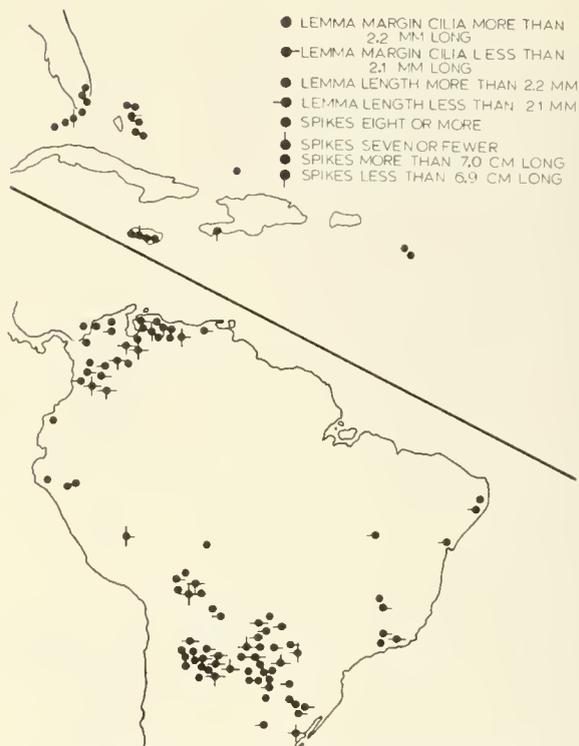


Fig. 16. Geographic distribution and morphological characteristics of *Chloris dandyana*.

on this problem. Since there are no sharp discontinuities in the variation pattern and only slight correlations of the characteristics with geographical distribution, I do not feel justified in naming the variants.

Representative specimens examined: ARGENTINA: Prov. Catamarca: Dep. Capital, Choya, *Castillon* 42,882 (US); Prov. Chaco, without precise location, *Asp* 21 (US); Prov. Córdoba, Río Tercero, *Stuekert* 13,689 (US); Prov. Corrientes: Isla Corrientes en el Río Uruguay, Cerca Monte Caseros, *Rosengurt* B-3,679 (US); Prov. Formosa: Costa Alegre, N de la Primavera, *Morel* 7,039 (US); Prov. Jujuy: 15 km SE of San Pedro, *Eyerdam and Beetle* 22,320 (UC, US); Prov. Misiones: San Javier, Oberá, *Schwindt* 4,779 (US); Prov. Salta: Dep. Orán, *Maldonado* 790 (F, US); Dep. Candelaria, Ruiz de los Llanos, *Montenegro* 322, 325 (US); Rosario de la Frontera, Los Baños, *Venturi* 7,974 (US); Prov. Santiago del Estero: between Forres and Robles, *Bartlett* 17,944, 19,744 (US); Beltrán, *Maldonado* 510 (US); Prov. Tucumán: Dep. Leales, Tres Pozos, *Descòle-Schreiter s.n.*, 5 Dec 1938 (NY, US); Río Chico, Escaba, *Monetti* 42,931 (US); Cruz Alta, *Schreiter* 3,987 (US); Burruyacu, *Venturi* 2,537, 2,661 (US), 7,536 (F, US). BAHAMA IS-

LANDS: Cat Island, Orange Creek, *Britton and Millspaugh* 5,733 (F, NY); Eleuthera Island, Governor's Harbor, *Hitchcock s.n.*, 14 Nov 1890 (F, MO); Long Island, vicinity of Clarence Town, *Britton and Millspaugh* 6,245 (F, NY); New Providence, Blue Hills, *Wilson* 8,247 (F, NY); Hog Island, near New Providence, *Wilson* 8,292 (F, MO, NY). BOLIVIA: Dep. Santa Cruz: among bushes in savanna, *Cardenas* 5,362 (US); Dep. La Paz: Coripata, *Hitchcock* 22,689 (US); Dep. Cochabamba: without precise location, *Spaggi* 26 (US). BRAZIL: Bahia: Cruz das Almas, *Pinto* 746 (UC, US); Matto Grosso: Corumba, *A. Chase* 11,136 (US); Aquidauana, *A. Chase* 11,046 (US); between Campo Grande and Dourados, *A. Chase* 10,915 (F, NY, US); Minas Geraes: Buritys, near Rio São Francisco, *A. Chase* 10,460 (US); Priapora, *Dorsett and Popenoe* 3,436 (US); Pernambuco: vicinity of Pernambuco, *A. Chase* 7,757 (NY, US); Rio de Janeiro: San Pedro, NW of Cabo Frio, *A. Chase* 10,158 (US); vicinity of São Leopoldo, *Leite* 471 (NY); Cerro Largo, near San Luiz, *Rambo* 53,116 (US); Santa Vitoria de Palmar, *Swallen* 7,416 (US). BRITISH GUIANA: Essequibo Co., Rupunini River, *Loxton s.n.*, 26 Sep 1955 (K). COLOMBIA: Dep. Antioquia: 1 km E of Puente de Occidente, *Pelaez and Barkley* 595 (US); Dep. Bolivar: Tierrabomba Island, Cartagena Bay, *Killip and Smith* 14,136 (NY, US); Dep. Torrecillo: near Turbaco, *Killip and Smith* 14,639 (F, MO, NY, US); Div. Boyaca, Soata, *Cuatrecasas* 1,094 (F, US); Dep. Cundinamarca: Route de Honda á Guaduas, *Humbert* 27,097 (US); Girardot, *Pennel* 168 (NY); Dep. Huila: 3°23'N, 74°49'W, *Fosberg* 19,589 (US); Dep. Valle: Hoya del Rio Sanjuniquin, *Cuatrecasas* 15,366 (US); Dep. Magdalena: E of Los Venadas, 10°N, 73°43'W, *Dugand* 5,829 (US); Dep. Santander: 12 km from Bucaramanga, *Langenheim* 3,198 (UC, US). ECUADOR: Prov. Imbabura: entre Parambas y Pajon, *Acosta-Solis* 12,667 (F, US). GRAND CAYMAN: *Hitchcock s.n.*, 19 Jan 1891 (MO). JAMAICA: Cornwall Co.: Santa Cruz Mts., *Britton* 1,172 (NY); Middlesex Co.: Lower Clarendon Parish, Inverness, *Harris* 12,743 (F, MO, NY, US); Leeward Islands: Antigua, road to Hermitage Bay, *Box* 26 (US). PARAGUAY: Dep. Boquerón: Puerto Casado, *Hartley* SH 141 (US); Puerto Sastre, *Ramirez* 5, 19 (US); Mariscal Estigarribia, *Rosengurt* B-5,813 (US); Dep. Concepcion: Estancia "Fanciere," *Ramirez* 193 (US); Dep. Paraguari: Caapucu, *Anderson* 1155A (US). PERU: Dep. Cajamarca: Jaen, *Hutchinson*, 1,422 (UC, US); Dep. San Martin: Pucayacu, 11 km S of Tarapoto, *Ferreira* 7,725 (US).

URUGUAY: Dep. Artigas: Santa Rosa del Cuareim, *Herter* 1,048 (US). UNITED STATES: Florida: Dade Co., Miami, *Tracy* 8,857 (F, MO, NY, TEX, US); Monroe Co.: Upper Matecumbe Key, *A. Chase* 3,914 (US); Long Key, *Silveus* 5,329 (TEX); Key Vaca, *Swallen* 5,189 (US); Plantation Key, *Swallen* 5,210 (US); Big Pine Key, *Swallen* 14,461 (US); Key Largo, *Weatherwax* 61,009 (UC). VENEZUELA: Carabobo, Valencia, *Carreno* 8,236 (US); Distrito Federal, vicinity of Caracas, *Bailey and Bailey* 200, 554 (US); Merida, Tovar, *Fendler* 1,854.5 (US); Miranda, between Los Teques and El Carrizal, *Pittier* 12,973 (NY, US); Tachira, La Mulera, *Tamayo* 2,296 (US); Trujillo, San Jacinto, *Tamayo* 1,698 (US); Zulia, savannas of Lagunillas, *Jahn* 658 (US).

8. **CHLORIS CRUCIATA** (Linnaeus) Swartz, *Prodr. Veg. Ind. Occ.* 25. 1788. (Based on *Agrostis cruciata* Linnaeus.) Fig. 17, A-E.

Agrostis cruciata Linnaeus, *Syst. Nat.*, ed. 10. 2:873. 1759. ("Sloan. jam. t. 69. f. I." cited by Linnaeus. The illustration cited is a good likeness of the species treated here. A specimen, in LINN!, labeled *Agrostis cruciata* is somewhat immature and does not have the spreading spikelets characteristic of the species. In all other respects the specimen fits the usual circumscription.)

Rabdochloa cruciata (Linnaeus) Beauvois, *Ess. Agrost.* 84, 158, 176. 1812. (Based on *Chloris cruciata* [Linnaeus] Swartz.)

Cynodon cruciatus (Linnaeus) Raspail, *Ann. Sci. Nat. Bot. (Paris)* 5:303. 1825. (Based on *Chloris cruciata* [Linnaeus] Swartz.)

Chloris humboldtiana Steudel, *Syn. Pl. Glum.* 1:205. 1854. ("C. cruciata H. B. [vix Swartz.] Ins. Cuba" cited. Description clearly of *C. cruciata* as commonly understood.)

Chloris brevigluma Wright, *Anales Acad. Ciencias Habana* 8:200. 1871. (HOLOTYPE: "1848. Canuela. . ." is cited in protologue. "1848" is evidently an error for "1548" for a photograph, in US!, of the type in GH has the latter number. Isotypes, also with the number "1548" are in BM! and G!.)

Tufted perennial up to 35 cm tall; sheaths glabrous; ligule shortly pilose; blades very narrow, usually less than 0.5 mm wide, up to 6

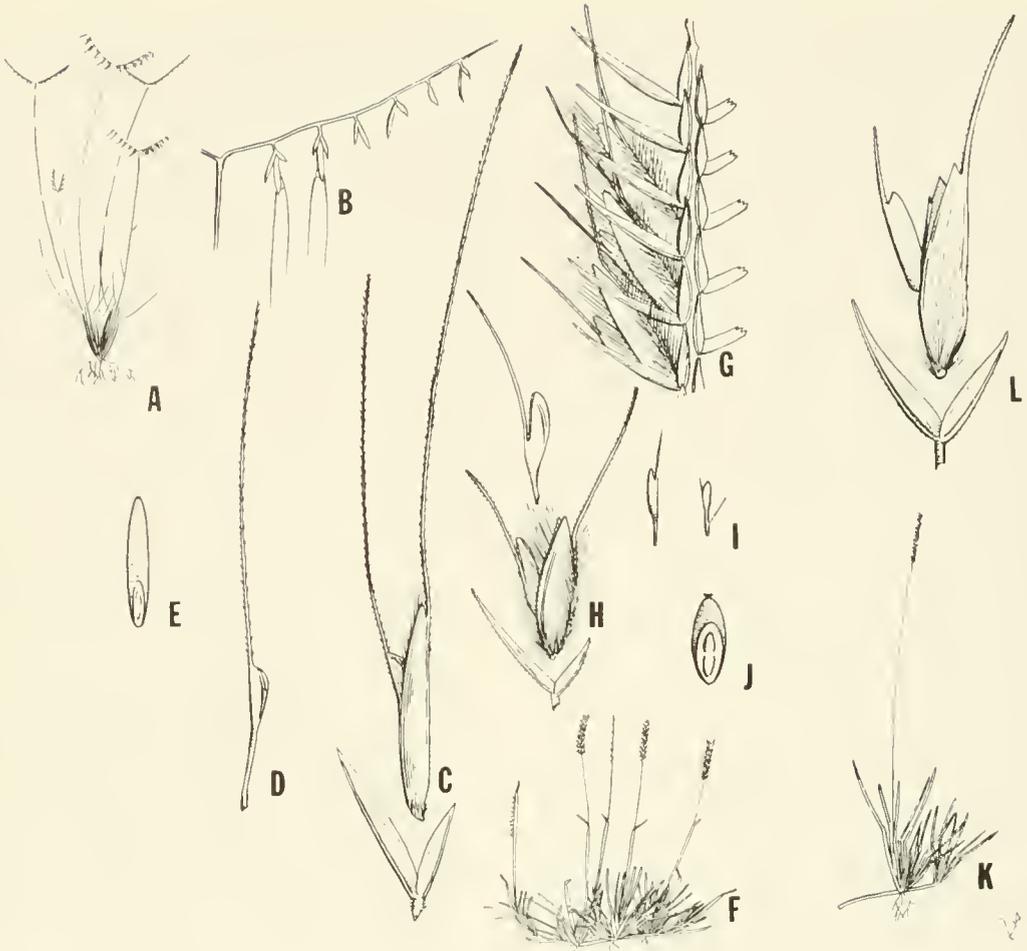


Fig. 17. *Chloris cruciata*, *C. filiformis*, and *C. suringari*. (A-E) *C. cruciata*. (A) habit, x 1/6; (B) portion of single spike, x 2; (C) spikelet, partly dissected, x 10; (D) sterile floret, x 10; (E) caryopsis, x 10. (F-J) *C. suringari*. (F) habit, x 1/5; (G) portion of spike showing rachis and attached spikelets, x 10; (H) spikelet, partly dissected to show lowest sterile floret, x 10; (I) upper two sterile florets, x 10; (J) caryopsis, x 10. (K-L) *C. filiformis*. (K) habit, x 1/3; (L) spikelet, partly dissected, x 10.

em long, involute; inflorescence of two or three radiate branches, spreading horizontally; spikes 1.0 to 2.5 cm long; spikelets somewhat appressed when immature, eventually spreading at nearly right angles to the rachis; spikelets only slightly (if at all) imbricate, averaging five or six per cm of the rachis length; first glume ovate-lanceolate, 0.7 to 1.3 mm long, 0.1 to 0.3 mm wide, glabrous, midrib sometimes slightly scabrous; second glume narrowly lanceolate, 1.6 to 2.2 mm long, 0.1 to 0.3 mm wide, glabrous, midrib occasionally scabrous; fertile lemma pale, narrowly lanceolate, 2.2 to 2.8 mm long, 0.3 to 0.5 mm wide, glabrous, occasionally the inrolled hyaline margins with a few short hairs, callus bearded, awn 7.5 to 17.0 mm long; sterile floret one, 0.5 to 1.4 mm long, 0.2 to 0.3 mm wide, narrowly truncate, borne on a fairly long rachilla joint, awn 3.7 to 7.0 mm long;

caryopsis narrowly cylindrical, 1.4 to 1.5 mm long, ca 2.0 mm wide.

Chloris cruciata is the only species in the genus with a tufted habit, very narrow leaves, two or three horizontally spreading spikes, and spikelets that are divergent from the rachis at right angles (Fig. 17). Other species from the Caribbean (especially *C. sagraana* and *C. ekmanii*) have similar, though appressed, spikelets; they also lack the other features.

Epidermal studies of this species (Rogers, 1967, and those reported earlier in this paper) revealed the presence of somewhat cruciate short cells, a feature not found elsewhere in *Chloris*. All inflorescence and spikelet characteristics are typical of *Chloris*, however, and I do not feel that taxonomic recognition of this species as a distinct genus is warranted.

Chloris cruciata has been collected in stony

soils (often of serpentine origin) from Cuba, Haiti, and Jamaica (Fig. 18).

Representative specimens examined: CUBA: Prov. Habana: Guanabacoa, Lomas de Jatas, *Ekman 279* (US); San Miguel de Casuora, Loma de la Vita, *Leon 11,753* (US); Prov. Las Villas: 10 km S of Santa Clara, *Howard et al. 100* (UC); vicinity of Sancti Spiritus, *Leon 1,497* (US); Oriente Prov.: Bazate, banks of Río Canto, *Ekman 3,016* (K, NY, US). HAITI: Massif du Nord, between Cerca-Carvijal and Bois-Charles, *Ekman 11607* (US). JAMAICA: Cornwall Co., Troy, *Harris 12,647* (F, K, MO, NY, US); St. Elizabeth Parish, between Ipswich and Black River, *Hitchcock 9,597* (US); Middlesex Co., vicinity of Mandeville, *Britton 1,029* (NY); Surrey Co., St. Andrew Parish, Stony Hill, *Harris 11,341* (F, K, NY, US); Clifton, *Harris 11,375* (F, NY, US); near Kingston, along Stony Hill Road, *Hitchcock 9,276* (F, NY, UC, US); Blue Mountains, Yallahs Valley, *Perkins 1,481* (US).

9. **CHLORIS FILIFORMIS** (Vahl) Poiret in Lam. Encycl. Method. Bot. Suppl. 2:238. 1811. (Perhaps based on *Cynosurus filiformis* Vahl.) *Non Chloris filiformis* Poiret. Fig. 17, K-L.

Cynosurus filiformis Vahl, Symbolae Bot. 2:20. 1790. (HOLOTYPE: Photograph, in US!, of type from Vahl Herbarium, C.)

Chloris filiformis Poiret, in Lam. Encycl. Meth. Bot. Suppl. 2:237. 1811. (TYPE MATERIAL: P! There are several specimens at P, in the Herbarium Richard, labeled "Chloris filiformis Poiret. Ile. de France." While Poiret did not designate a type as such, they probably represent authentic material. The specimens fit the description closely; and this is, unquestionably, the same taxon first described by Vahl under *Cynosurus*, though Vahl is not cited by Poiret in the protologue of this name.)

Chloris distachya Kunth, Rév. Gram. 1:291. pl. 57. 1830. (HOLOTYPE: "Chloris distachya Kunth, Insula franeiae. Ex Museo



Fig. 18. Distribution of *Chloris cruciata*.

Paris." Not seen, but description and accompanying plate are clear.)

Stoloniferous or tufted perennial, 10 to 30 cm tall; sheaths glabrous to sparsely pilose, compressed, keeled; ligule a very short ciliate crown, often with a few longer hairs near the margins; blades narrow, 1 to 6 mm long, about 1 mm wide, folded, often curved, sparsely pilose near the base, becoming apically glabrous, acute; spikes one or two, 1 to 3 cm long, erect; spikelets rather densely imbricate, ca 12 per cm of rachis length, more or less appressed; glumes lanceolate, glabrous; first glume 1.7 to 2.0 mm long, ca 0.4 mm wide; second glume 2.5 to 2.8 mm long, ca 0.4 mm wide; fertile lemma 2.6 to 2.8 mm long, 0.5 to 0.6 mm wide, lanceolate-elliptic, apex acute, callus bearded, internerves densely appressed-pubescent, awn 1.0 to 1.2 mm long; sterile floret 1.3 to 2.0 mm long, 0.2 to 0.5 mm wide, narrowly lanceolate to linear, acute, sparsely appressed-pubescent, awn 0.5 to 1.1 mm long; earyopsis not seen.

Known only from Mauritius and nearby islets, *Chloris filiformis* is easily distinguished from the similar *C. suringari* (from Cuba and Curaçao) by having considerably shorter awns and lemmas with appressed pubescence on the internerves rather than spreading pubescence on the margins and keels (Fig. 17, K-L, F-J, respectively).

Specimens examined: MAURITIUS: Montagne Longue, dry regions, *Bouton s.n.*, without date (K); Round Island, rocky hillside, 520 ft., *H. H. Johnston s.n.*, 28 Nov 1889 (K); Round Island, *Wiene s.n.*, Nov 1937 (K). Hubbard and Vaughn (1940) reported this species also from the islets of Gunners Quoin and Le Morne.

10. **CHLORIS SURINGARI** Hitchcock in Urban, Symb. Antill. 7:167. 1912. (HOLOTYPE: "Curaçao ad Brakkeput . . . W. F. R. Suringar, Jan 14, 1885" Type fragment, in US!, from Krug and Urban Herbarium.) Fig. 17, F-J.

Densely tufted, very shortly stoloniferous, diminutive perennial up to 15 cm tall; sheaths very short, about 1 cm or less, striate, sparsely to densely pilose below, becoming glabrous above on some culms; ligule a short tuft of hairs; blades highly reduced, less than 0.5 mm wide and 2 cm long, usually somewhat curved; apex blunt to acute, glabrous to sparsely pilose; inflorescence a single spike 1.0 to 2.5 cm long; spikelets imbricate, about 15 per cm of the rachis; first glume 1.0 to 1.5 mm long, 0.4 to 0.5 mm wide, lanceolate, appressed to the

rachis, one-nerved, glabrous, marginal areas thin and hyaline; second glume very narrowly lanceolate, diverging from the rachis at about 70° , 2.3 to 3.0 mm long, ca 0.3 to 0.4 mm wide, one-nerved, glabrous, margins hyaline; fertile lemma ovate-lanceolate, 1.7 to 2.5 mm long, 0.4 to 0.6 mm wide, densely pubescent on the callus, margins and keel with hairs about 0.7 mm long, awned from about the middle of the keel, the awn 2 to 3 mm long, straight or slightly geniculate; sterile florets three, the lowest about 1 mm long, 0.3 to 0.4 mm wide, awned from about the middle, the awn 1.5 to 2.0 mm long; upper sterile florets much reduced, awned; caryopsis ca 1.2 mm long, 0.5 mm wide, ovoid, flattened to slightly trigonous.

This unique species, endemic to Cuba and Curaçao, may be immediately separated from the similar species, *C. filiformis*, in having relatively long awns and a single spike (Fig. 17, F-J). Additional notes on the relationships of these species have been presented under *C. filiformis*.

Collection labels indicate that *Chloris suringari* grows on limestone benches and rocks not far from the seashore. Only four specimens were seen in all herbaria consulted.

Specimens examined: CUBA: Oriente Prov., El Guanabaco, *Leon 11,564*, Jan 1940 (US). CURAÇAO: without precise location, *Boldingh 9,281*, 1909-1910 (US); limestone bench near Willemstad, *Britton and Shafer 3,058*, 20-27 Mar 1913 (US); Kleine Berg, *Mordant 251*, 23 Nov 1966 (P).

11. **CHLORIS SCARIOSA** F. von Mueller, *Fragm. Phyt. Australiae*, 6:85. 1867. (HOLOTYPE: MEL, not seen. There are two specimens at Kew, collected by von Mueller in 1879, both of this species as commonly understood. One is labeled "Chloris scariosa F. Muell. Gracemere. Bowman. Herb. F. Mueller. 1879." The other is labeled "Chloris lativalvis Muell. Sturt's Creek. M. Gregory." Lazarides [1972] says that the latter specimen is an isotype of the holotype at MEL. The protologue, which is very short, refers to "glumis latis scariosis insignis." Since von Mueller, as evidenced by other descriptions on the same page, was familiar with the species of *Chloris* in Australia, there is no doubt as to the taxon to which he referred and Lazarides's designation of the Gregory specimens as the type is reasonable. *Chloris lativalvis* was apparently never published.) Fig. 19, A-D.

Erect caespitose or stoloniferous perennial, 25 to 50 cm tall; sheaths glabrous to very sparsely spreading pubescent; ligule a short ciliate crown; blades up to 20 cm long, 5 to 8 mm wide, glabrous to scabrous or very sparsely pilose; spikes four to six, 3 to 5 cm long, virgate to somewhat spreading; spikelets imbricate, ca 7 per cm of the scabrous rachis; glumes unequal, purplish, membranous, glabrous except for the scabrous midrib; first glume elliptic to linear, 4.0 to 4.7 mm long, ca 0.5 mm wide, rounded at the apex; second glume 5 to 7 mm long, ca 1 mm wide, narrowly oblanceolate to obovate or elliptical, apex bifid; fertile lemma highly modified and differing from any other species in *Chloris*, callus narrow and elongated at the base of the lemma, 1.0 to 2.5 mm long, densely bearded, sharp-pointed, body of lemma ovate to ellipsoid, 1.0 to 2.5 mm long, 0.5 to 1.2 mm wide, margins membranous, prominently winged, glabrous below, becoming densely spreading ciliate above, keel sparsely to densely pilose, especially below, awn 5.8 to 8.5 mm long; sterile florets three to five, broad, membranous margined, with prominent veins; lowermost floret broadly cordate or even amplexicaulous at the base and partly surrounding the corky rachilla, tapering to a narrow tip above, ca 4.5 mm long, ca 5 mm wide, awn 5 mm long, upper sterile florets progressively reduced; caryopsis 1.3 to 1.5 mm long, 0.8 to 1.0 mm wide, broadly obovoid-ellipsoid, trigonous; chromosome number $2n=40$.

No other species in the genus has such highly modified spikelet parts as *Chloris scariosa*. The broadly winged fertile lemmas and sterile florets at once set this species apart from all others. This unique character was recognized by Thellung (1919), who erected the section *Hackelochloris* to include it.

Furthermore, there is a strong overall resemblance between *C. scariosa* and various species of *Tetrapogon*. Certainly, the two genera approach closely at this point and must be rather arbitrarily separated on the basis of fertile floret number. Both epidermal and anatomical features have been studied; no significant differences between the two genera can be demonstrated. On these bases it does not seem desirable to erect a new genus for this single species.

Chloris scariosa has been collected from a variety of soils, most commonly in arid regions of Queensland and Northern Territory, Australia (Fig. 20).

Representative specimens examined: AUSTRALIA: Northern Territory: 5 mi S of Yam-



Fig. 19. *Chloris scariosa* and *C. pricurii*. (A-D) *C. scariosa*. (A) habit, x 1/4; (B) spikelet, partly dissected, x 5; (C) sterile florets, partly dissected, x 5; (D) caryopsis, x 10. (E-H) *C. pricurii*. (E) habit, x 1/4; (F) spikelet, partly dissected, x 10; (G) sterile florets, partly dissected, x 15; (H) caryopsis, x 10.



Fig. 20. Distribution of *Chloris scariosa*.

bah Station, *Perry* 3,368 (K); near coast, 60 mi N of Wollongong Station, *Perry* 1,218 (K, US); 8 mi N of Tennant Creek, *Perry* 551 (K); Burtwell, *Cleland* 349 (K). Queensland: Burke Dtr., Cloncurry, *Allan* 20 (K); Forest Home Station, *Brass* 1,790 (K); near Normantown Township, flood flats of Norman River, *Lazarides* 4,248 (K, US); Charters Towers, *Michael* 1,299 (K); Antil Plains, near Townsville, *White* 8,909 (K, NY, US); Warrego Dtr., claypans near Cunnamulla, *White* 11,566 (K, US). South Australia: Cordillo (Downs), *Cleland* s.n., 5-24 (May, 1924?). Western Australia: between Gascoyne and Fortescue River, *King* s.n. 1885 (K). SWITZERLAND: Derendingen, Kammgarn Fabrik, *Probst* s.n., 25 Oct 1919, *adventive* (K).

12. **CHLORIS PRIEURII** Kunth, Rev. Gram. 1:89. 1829. (HOLOTYPE: ". . . Ile St. Louis [Senegal] Roger Dedit, Major 1825." P! ISOTYPE: K! Fig. 19, E-H.)

Chloris cryptostachya Steudel ex J. A. Schmidt, Beitr. Flora Cap Verdischen Inseln 148. 1852. (HOLOTYPE: ". . . C. punctulata Hochstetter hrbr. u. it. nubie. nr. 23 Cordofan." P! ISOTYPE: K!)

Chloris punctulata Hochstetter ex Steudel, Syn. Pl. Glum. 1:205. 1854. (HOLOTYPE: "Hrbr. un. it. nubie. nr. 23." P! ISOTYPE: K!)

Chloris subtriflora Steudel, Syn. Pl. Glum. 1:208. 1854. (HOLOTYPE: "LaPrieur in Senegambia." No collection that can be identified positively as the holotype can be found, though there are specimens in the Herbarium Richard in P! that were collected by Le Prieur in Senegal in 1829. These are not labeled as *Chloris triflora*, and there are no other data on the labels.

Dr. W. D. Clayton, in a personal communication, says that the type cannot be found at CN. Under these circumstances, it must be presumed lost. The description, while not detailed enough for positive identification, suggests strongly that the plant referred to is *C. prieurii*.)

Chloris multiradiata Hochstetter, Flora 38:204. 1855. (The original description seems to refer to *C. prieurii*. There are possible isotypes in K! and P! The K specimen is *C. virgata*; the P specimen, *C. prieurii*.)

Stoloniferous perennial up to 80 cm tall; sheaths glabrous, occasionally becoming pilose near the ligule; ligule variously short-ciliate to long-pilose; blades narrow, 10 to 14 cm long, up to 5 mm wide; lower surface glabrous, upper surface scabrous to pilose; spikes appressed to slightly diverging, three to seven, 6 to 11 cm long, spikelets imbricate, 8 to 11 per cm of the scabrous-hispidulous rachis; glumes thin and delicate, narrowly lanceolate, glabrous with slightly scabrous midnerves; first glume 2.1 to 2.2 mm long, 0.2 to 0.3 mm wide; second glume 3.7 to 4.0 mm long, 0.2 to 0.3 mm wide; fertile lemma narrowly elliptic, 3.3 to 4.7 mm long, 0.4 to 0.7 mm wide, with a row of clavate glandular hairs along the middle of the lemma side, awn 10 to 18 mm long; sterile florets four or five, the lower successively enclosing the upper and becoming progressively more reduced; lowermost sterile floret cylindrical, 1.5 to 2.5 mm long, 0.2 to 0.4 mm wide, awn 8 to 17 mm long, uppermost sterile floret more or less flabellate, ca about 0.3 mm long, 0.1 mm wide, awn 1.5 to 2.0 mm long, intermediate sterile florets gradually changing from cylindrical to flabellate; caryopsis 2.0 to 2.5 mm long, 0.5 mm wide, ellipsoid, strongly flattened, light brown.

Only two species of *Chloris* have a row of glandular hairs on the side of the lemma—*C. prieurii* and *C. orthonoton*. The two are easily separated. *C. prieurii* is limited to the Old World (Fig. 21) and has four or five sterile florets (Fig. 19, E-H); *C. orthonoton* is, on the other hand, from South America and has a single sterile floret (Figs. 33, A-D; 39).

Representative specimens examined: BOTSWANA: between Kapupahedi and Tamso, Okavango National Territory, anon. (K). CHAD: Biltine, *Rossetti* 39 (BM). CAPE VERDE ISLANDS: Boa Vista, *Chevalier* 44,423 (K). ETHIOPIA: Nario Dikeno, *Schimper* 1,607 (MO). GHANA: Accra, *Irvine* 3,023 (MO).

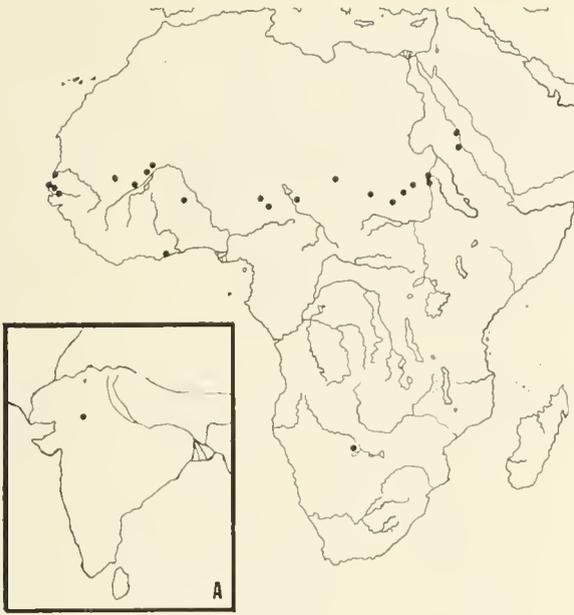


Fig. 21. Distribution of *Chloris plicurii*. Inset A: India.

INDIA: Rajasthan Prov., Jaipur, *Raizada* 2/53 (K). MALI: Sansanding, *Chevalier* 24,958 (P); Nara, *Chudeau s.n.*, 26 Aug 1918 (P); Timbuktu, *Hagerup* 239 (US). NIGERIA: Bornu Prov., 48 mi N of Damaturu, *De Leeuw* 1,150 (K). SENEGAL: Kaolack, *Berhaut* 456 (P); Mbambey, *Chevalier* 33,795 (P); Pointe Louis, *Roberty* 149.16.2 (K). SUDAN: Blue Nile Prov., Bagein, 50 mi S of Khartoum, *Jackson* 2,336 (K); Darfur Prov., Jebel Marra, *Blair* 140 (K); Khartoum Prov., Khartoum, *Schweinfurth* 813 (US); Kordofan Prov.: El Muglad, *Andrews* 3,062 (K); El Obeid, *Harrison* 76 (K). UNITED STATES (adventive): Alabama: Mobile, Mobile and Ohio wharf, *Mohr* 44 (US); North Carolina: Wilmington, *McCarthy* 90 (US). UPPER VOLTA: Gourma, *Rossetti* 110 (K).

13. **CHLORIS ROBUSTA** Stapf in *Chevalier*, Bull. Soc. Bot. France Mem. IV 8:221. 1912. (DUPLICATES OF SYNTYPES: "Haut-Chari, Ndelle, 20-25 Dec 1902, *Chevalier*, 6,991; Nigeria du Nord, Borgu, *Barter*, 878." K1) Fig. 22, A-D.

Robust perennial to 3 m tall, aquatic to subaquatic with very strong, heavy culm bases, and often dense rooting at the lower nodes, stoloniferous with stolons up to 7 m long; sheaths glabrous; ligule a minute naked crown; blades up to 40 cm long and 20 mm wide, glabrous and glaucous or scabrous; spikes seven

to twenty-eight, 6 to 10 cm long, erect, somewhat flexuous; spikelets imbricate, ca nine per cm of rachis length; first glume ovate-lanceolate, glabrous except for the slightly scabrous midnerve, 1.6 to 2.5 mm long, ca 0.2 to 0.3 mm wide; second glume linear-lanceolate, arcuate, glabrous except for the scabrous midnerve, 4.0 to 5.5 mm long, 0.4 to 0.5 mm wide; fertile lemma 3 to 4 mm long, 0.4 to 0.5 mm wide, narrowly elliptic, apex long-acuminate, tapering into the awn, upper $\frac{2}{3}$ of the margin with long hairs, these up to 2.5 mm long; callus bearded, awn ca 0.5 to 1.0 mm long; sterile florets two; lower sterile floret similar to the fertile floret in shape, staminate, often with a rudimentary pistil, 2.5 to 3.5 mm long, ca 0.3 mm wide, margins with cilia up to 2.5 mm long, callus bearded, upper lemma sides sparsely pubescent, palea present, about as long as the sterile lemma; upper sterile floret clavate, less than 1 mm long, pilose. Caryopsis not seen.

Chloris robusta is unique in many respects, including the bamboolike growth habit, preference for aquatic to subaquatic habitats, and spikelets with sterile florets that are regularly staminate. These features, together with the overall morphological aspect of the spikelets, suggest that this species should be separated from the rest of *Chloris*. Epidermal and anatomical characters, however, are those typically found in other species of *Chloris*; and, therefore, there seems to be little justification for segregating it.

This species has been collected throughout equatorial Africa (Fig. 23). Its tall, bamboolike, elastic culms form large colonies along and in rivers and streams. Associated grasses include *Phragmites communis* and species of *Andropogon*.

Representative specimens examined: CAMEROON: riverain forest of Sanaga River, near Goyoum, 20 km W of Deng Deng, *Breteler* 980 (K). DAHOMEY: entre de Lac Ozri et Zagnando, *Chevalier* 23,054 (K). GHANA: 3 mi from Yendi, Kufapindi River, *Adams and Akpabla* 4,101 (K); 30 mi from Navrango, Tumu Road, *Adams and Akpabla* 4,361 (K); Sakogu-Shishe Road, old Morago River bridge, *Ankrah* 20,507 (K); Daka River near Yendi, *Brand* 444 (US); Weija, near Accra, *Hall* 2,552 (K); Wenchi, between Banda and Menji, *Morton GC* 25,256 (K); near Daboya, *Thorold* 288 (K). IVORY COAST: Marabadiassa, along Bandama Blanc River, *Assi* 7,178 (K); entre Sanlo and Kalepui, *Assi* 9,291 (K); bords du Bandama River, Dume, *Roberty s.n.* (MO 1640174). NIGERIA: between Oyo and Iseyin,



Fig. 22. *Chloris robusta* and *C. mollis*. (A-D) *C. robusta*. (A) lower and middle portions of stem, $\times 1/3$; (B) upper stem and inflorescence, $\times 1/4$; (C) spikelet, partly dissected, $\times 10$; (D) sterile florets, $\times 15$. (E-J) *C. mollis*. (E) habit, $\times 1/4$; (F) spikelet from type of *C. mollis*, partly dissected, $\times 10$; (G) floret from type of *C. anisopoda*, $\times 10$; (H) sterile florets from spikelet with two sterile florets, $\times 20$; (I) sterile floret from spikelet with single sterile floret, $\times 15$; (J) caryopsis, $\times 5$.



Fig. 23. Distribution of *Chloris robusta* (equatorial Africa).

Brenan and Keay, 8,959 (K); Yola, *Dalziel* 269 (K); Lagos, *Foster* 2 (K); Jebba, on Niger River, *Hagerup* 692 (K, US); Onitsha Prov., near Nzam Anambra Forest Reserve, Oramili Creek, *Jones* 6,888 (K); Oyo Prov., Dtr. Ibadan, Awba Hills Forest Reserve, *Onochie and Jones* 14,666 (K); by Chinchaga River, near Muina, *Meikle* 736 (K); Kaiama, *Ward* 35 (K, US). REPUBLIC OF THE CONGO: Prov. Equateur, Baugui, Ubangi River, *Meruillan* 209 (K). SIERRA LEONE: Moa River, Mafindo Falls, near Kailahun, *Deighton* 4,004 (K, US). SUDAN: Equatoria Prov., 40 mi NW of Yei, *Myers* 7,865, 8,496 (K); Bahr Ghazal Prov., Mvolo, *Schweinfurth* 2,843 (US). UGANDA: Kitgum, Chua, *Thomas* 4,346 (K).

14. **CHLORIS MOLLIS** (Nees) Swallen, North Amer. Flora 17:596. 1939. (Based on *Gymnopogon mollis* Nees.) Fig. 22, E-J; 24.

Gymnopogon mollis Nees, Agrost. Bras. 427. 1833. (FRAGMENT OF TYPE?: US! Labeled "Gymnopogon mollis Nees. Type. Campi Mimoso dicit. Prov. Piauhy." The name of the herbarium from which the fragment was obtained is illegible. While the information on the label is sketchy, it does match exactly the collection location noted by Nees. This, together with the very complete original description, leave no question as to the typification of this name.)

Gymnopogon rupestre Ridley, Jour. Linn. Soc. Bot. (London) 27:73. 1891. (HOLOTYPE: BM! ISOTYPE: US! "Fernando do Noronha. Cliffs on Portuguese Bay. Ridley, Ramage, Sept. 14, 1887.")

Chloris luetzelburgii Hitchcock, Proc. Biol. Soc. Washington 36:197. 1923. (HOLO-

TYPE: "Serra do Borborema, State of Parahyba do Norte, Brazil, April, Lutzburg, No. 12451" US!)

Chloris anisopoda Scribner in Robinson, Proc. Amer. Acad. Arts Sci. 38:118. 1902. ISOSYNTYPES: [Galápagos Islands] "Charles Isl., Baur, 333; Snodgrass and Heller, 459" US! SYNTYPES: GH, not seen.)

Chloris angustiflora Arcschoug, Kongl. Svenska Fregatten Eugenies Bot. III. 118. 1910. (TYPE: not seen, but description of specimen, collected on the island of Puna, by Andersson is conclusive.)

Chloris leptantha Hitchcock ex Urban, Symb. Antill. 7:166. 1912. (HOLOTYPE: "Hab. in insulis orae Venezuelensi adjacentibus Bonaire, 19 Feb 1885. W. F. R. Surinagar." US!)

Chloris rupestris (Ridley) Hitchcock, U. S. Dept. Agric. Misc. Publ. 243:126. 1936. (Based on *Gymnopogon rupestre* Ridley.)

Annual 40 to 60 cm tall from a fibrous, rather poorly developed root system; sheaths usually densely appressed- to spreading-pilose, especially near the apex, occasionally enclosing cleistogamous spikelets; ligule long-pilose; blades variable in size, ranging from short and very narrow up to 30 cm long and 1 cm wide, appressed-pilose on both upper and lower surfaces; inflorescence of three to seven spikes, 6 to 9 cm long, mostly radiate at the apex of the culm, sometimes with one or two single spikes inserted separately just below; spikelets imbricate, seven to ten per cm of rachis length; glumes thin, transparent, narrowly lanceolate, glabrous except for the seabrous midnerve; first glume 3 to 4 mm long, 0.2 to 0.3 mm wide,

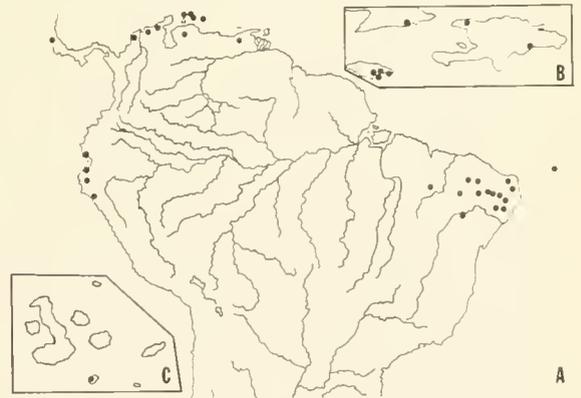


Fig. 24. Distribution of *Chloris mollis*. Insets: (A) northern South America. (B) eastern Cuba, Jamaica, Hispaniola. (C) Galápagos Islands.

glabrous; second glume 3.1 to 4.6 mm long, ca 0.3 mm wide, glabrous; fertile lemma very narrow, 2.5 to 6.8 mm long, ca 0.3 mm wide, glabrous except for the prominently bearded callus and the short-ciliate upper margins, awn 4.0 to 7.5 mm long; sterile floret usually one (occasionally two), and then the lowermost bearing rudimentary flower parts; lowermost sterile floret cylindrical, 1.2 to 1.6 mm long, 0.1 to 0.2 mm wide, awn 3.7 to 5.8 mm long, callus prominently pubescent with spreading hairs, margin ciliate above; upper sterile floret, when present, ca 1 mm long, 0.1 mm wide, callus bearded, awn ca 2.5 mm long; earyopsis ca 3.3 mm long, ca 0.5 mm wide, narrowly cylindrical.

Chloris mollis is unique in the genus in having sterile florets with a prominently pubescent callus and long awns.

As may be seen from the synonymy, this species has been placed in both *Gymnopogon* and in *Chloris*. In some respects it does have characters of both genera. Many species of *Gymnopogon* are characterized by having short, stiff, sharp-pointed leaf blades, which appear crowded at the base of the culm because of their short, overlapping sheaths. *Chloris mollis* has these characters, except that the leaves are not crowded at the base. *Gymnopogon* tends to have inflorescence branches somewhat staggered at the culm apex rather than in the verticillate arrangement so common to *Chloris*. In this respect, *Chloris mollis* is intermediate between the two genera, with the upper spikes more or less radiate but occasionally with a few remote lower spikes. In *Gymnopogon* the sterile floret is usually much reduced, often being represented only by a swollen area at the junction of rachilla and awn. One species, *G. foliosus*, however, does have a reasonably well-developed sterile floret and bears a remarkable resemblance to *Chloris mollis*. Essentially then, we are faced with the problem of which characters to accept. I believe that by emphasizing primarily the rather unusual vegetative characteristics and inflorescence of such species of *Gymnopogon* as *G. floridanus*, *G. chapmannianus*, etc., that the highest degree of homogeneity may be established in the resulting group. In such a system, *Chloris mollis* is still essentially unclaimed, for its outward vegetative appearance and inflorescence type do not fit well with *Gymnopogon*. However, the well-developed sterile florets of *C. mollis* are certainly more like the majority of *Chloris* species rather than most of the *Gymnopogon* taxa.

Representative specimens examined: BRA-

ZIL: Bahia: Juazeiro, *Dorsett and Popenoe 411b* (US); Ceará: Crateús, *Swallen 4,481* (US); Iguatu, *Swallen 4,399* (K, US); Fernando de Noronha: Morro Francez, *Simmons 9,263* (US); Maranhão: Município de Loreta, between Balsas and Paraiaba Rivers, *Eiten and Eiten 4,503* (K, US); Paraiba: Pombal, *Pickel 3,804* (US); Soledade, *Pickel 3,851* (US); Pernambuco: Serra do Genipapo, *A. Chase 7,686* (US); Pesqueira, *Pickel 1,662, 3,675* (NY, US); Piauí: Fazenda Nacional, *Swallen 4,179* (NY, US), *4,196* (K, US); Picos, *Swallen 4,228* (US); Rio Grande do Norte: Santa Cruz, *Swallen 4,558* (US); Angicos, *Swallen 4,714* (K, US). COLOMBIA: Bolívar Div.: Cartagena, *Hitchcock 9,906* (US); Magdalena Div.: Santa Marta, *H. H. Smith 2,752* (F, K, MO, NY, US). COSTA RICA: Boruca, *Pittier 3,675* (BR). CUBA: Oriente Prov.: Cañanera Naval Station, *Hioram and Ramsden s.n.*, 6 Feb 1919 (US). CURAÇAO: near Willemstad, *Britton and Shafer 2,906* (US). DOMINICAN REPUBLIC: Prov. Barahona: Las Salinas, *Fuertes 1,921* (US). ECUADOR: Prov. Guayas: Chanduy, in littore Maris Pacifici, *Spruce 6,436*, Apr 1862 (K, NY, US); between Guayaquil and Salinas, *Hitchcock 20,056* (US); Chongón, *Asplund 7,671* (US). GALÁPAGOS ISLANDS: Charles Island: near Black Beach, *Howell 9,355* (NY, US), *Svenson 184* (US); Post Office Bay, *Howell 8,801* (US). GUATEMALA: Dep. Zacapa: 1 mi W of Teculután, *Steyermark 29,192* (US). HAITI: Anses-à-Pitre, *Ekman 6,999* (G, K, US); Jean Rabel, *Leonard and Leonard 12,551* (US). JAMAICA: Gordontown, *Harris 11,515* (F, K, MO, US); near Kingston, *Harris 12,212* (K, US). LESSER ANTILLES: Bonaire Island, *Boldingh 7,208B* (US); Aruba, *Suringar 12* (US). PERU: Prov. Lambayeque: entre Motupe y Olmos, *Lopez 1,238, 2,463* (US); Prov. Tumbes: entre Pocitos y Una de Gato, *Ferreyra et al. 10,634* (US). VENEZUELA: Dep. Federal, Gran Roque, *Gines 4,615* (US); Anzoátegui, 14 km S of San Mateo, *Garroni 53* (US).

15. **CHLORIS LONGIARISTATA** Napper, *Kirika 3:117*. 1963. (ISOTYPE: "Tanganyika. Ngudu. R. R. Staples. 382. 1/4/1935." K!) Fig. 25, E-H.

Stoloniferous perennial 30 to 70 cm tall; sheaths somewhat compressed, glabrous; ligule a short ciliate crown; blades up to 15 cm long, 3 to 6 mm wide, acute, glabrous below, sparsely long-pilose above and on the margins, especially near the base; spikes three to five, 3.5 to 12.0 cm long, appressed to slightly divergent; spike-



Fig. 25. *Chloris quinquesetica* and *C. longiaristata*. (A-D) *C. quinquesetica*. (A) habit, x 1/4; (B) spikelet, partly dissected, x 10; (C) sterile florets, x 10; (D) caryopsis, x 10. (E-H) *C. longiaristata*. (E) habit, x 1/4; (F) spikelet, partly dissected, x 5; (G) sterile florets, x 5; (H) caryopsis, x 5.

lets slightly divergent, ca four per cm of the scabrous rachis; glumes very narrowly lanceolate, pale, membranous, tapering to a delicate point or a short awn; first glume 3.7 to 4.9 mm long, 0.2 to 0.4 mm wide; second glume 5.5 to 6.7 mm long, 0.3 to 0.5 mm wide; fertile lemma dorsally compressed, 7.5 to 8.1 mm long, 0.8 to 0.9 mm thick, 1.0 to 1.5 mm wide, narrowly lanceolate to elliptic, callus well developed, tapering, sharp pointed, densely bearded, margins, sides, and keel glabrous except coarsely scabrous near the apex, awn 30 to 35 mm long, subtended by two short teeth; sterile florets two or three, lowermost sterile floret narrowly cylindrical, 2.0 to 2.7 mm long, 0.3 to 0.4 mm wide, glabrous below, sparsely scabrous above, gradually narrowing into the awn, awn 20 to 35 mm long, subtended by a pair of deltoid teeth, rachilla joint well developed; upper sterile florets progressively reduced; caryopsis ca 3 mm long, ca 0.7 mm wide, dorsally flattened, shallowly trigonous.

Chloris longiaristata is most closely related to *C. prieurii*, from which it may be separated by its very long awns, longer than those on any other species of *Chloris*, and lack of ciliate hairs on the upper lemma margins.

Specimens examined: TANZANIA: Mwanza, Lloyd 4 (K).

16. **CHLORIS QUINQUESETICA** Bhide, Jour. Proc. Asiatic Soc. Bengal n.s. 8:311. pl. 24. 1912. (HOLOTYPE: "Papadi Bassein, growing on the bounds of rice fields in semisalt lands. R. W. Bhide. 30-8-1911." K!) Fig. 25, A-D; 30.

Perennial, culms erect to strongly stoloniferous and rooting at the lower nodes, to 50 cm tall; sheaths glabrous; ligule a tuft of hairs; blades to 15 cm long, 2 to 4 mm wide; upper surface glabrous to scabrous, lower surface glabrous to loosely pilose; spikes three to eight (rarely two, occasionally up to eighteen, as indicated in original description), only slightly divergent, 1.5 to 5.0 cm long, decurrent at the base and united into a common axis bearing a few spikelets; culms villous for 5 to 6 mm below the spikes; spikelets densely imbricate, averaging ca 20 per cm on the prominently hirsute rachis; glumes linear-lanceolate to ovate, membranous, glabrous except for the scabrous midnerve; first glume 1.5 to 1.8 mm long, 0.2 to 0.3 mm wide; second glume 2.2 to 2.5 mm long, 0.5 to 0.6 mm wide; fertile lemma 2.0 to 3.1 mm long, 0.8 to 0.9 mm wide, ovate, keel and lateral nerves usually appressed-pubes-

cent, sometimes glabrous, margins densely spreading-pubescent with hairs about 1 mm long, callus densely bearded, awn 4 to 8 mm long; sterile florets three or four; lowest sterile floret truncate, 1.3 to 1.6 mm long, 0.5 to 0.6 mm wide, glabrous below but with a prominent fringe of hairs along the upper margin, awn 3.5 to 6.0 mm long; upper florets enclosed by the lower and progressively reduced, becoming more inflated; caryopsis 1.4 to 1.6 mm long, 0.5 to 0.7 mm wide, ellipsoid.

Only two species of *Chloris*—*C. quinquesetica* and *C. montana*—have a dense feltlike pubescence just below the points of attachment of the spikes. *Chloris quinquesetica* usually has four sterile florets (occasionally three); the lowermost sterile floret is ciliate along the upper margin, and the upper sterile floret is spherical and inflated (Fig. 25, A-D). On the other hand, *Chloris montana* usually has three sterile florets. These are commonly all glabrous, though occasionally sparsely pilose; and the upper sterile floret resembles the lowest and is not spherical and inflated (Fig. 27, F-I). A comparison of *C. quinquesetica* and similar species is shown in Table 8.

Specimens examined: INDIA: Kistna Dtr.: Vijayarion, Barber 8,243 (K); Kannefalli, Bourne s.n., without date, (K); Jubi, near Cawnpore, Duthie 7,759 (K); Cawnpore, Makldompur, Mobbs s.n., Aug 1933 (K); Sindi, Hooper s.n., without date (K); Madh Island, Santapau 21,284 (K); Andra Pradesh, Secunderabad, without collector or date (K).

17. **CHLORIS WIGHTIANA** Nees ex Steudel, Syn. Pl. Glum. 1:206. 1854. (ISOTYPES: There are three sheets with apparently four different collections mounted upon them at K!, among which are undoubtedly duplicates of the syntypes cited by Nees and, subsequently, Steudel. Among these is a specimen labeled "Herb. Wight. 1766.

Chloris wightiana NE. Wall s.n. 3809." The label corresponds in many respects to the specimen cited in the original description.) Fig. 26.

Chloris incompleta Wight ex Steudel, Syn. Pl. Glum. 1:206. 1854. *Pro syn. Non C. incompleta* Roth, 1821.

Tufted to somewhat stoloniferous perennial, 10 to 30 cm tall; sheaths densely pustulose-pilose; ligule a densely ciliate crown; blades up to 4 cm long, ca 4 to 6 mm wide, densely pustulose-pilose on both surfaces; spikes three or four, 1.0 to 2.5 cm long, appressed or only slightly

Table 8. Comparison of *Chloris bournei*, *C. formosana*, *C. inflata*, *C. montana*, *C. quinquesetica*, and *C. wightiana*.

Species	Root system duration, habit	Culm pubescence	Leaf blade pubescence	Number of spikes; rachis pubescence	Sterile florets
<i>C. bournei</i>	perennial, stoloniferous from a tufted base	glabrous	glabrous, scabrous, or pilose above; pilose below	3-9; rachis scabrous	2 or 3, somewhat inflated, glabrous to sparsely pilose
<i>C. formosana</i>	perennial, stoloniferous	glabrous	glabrous	5-9; rachis pilose	2, not or only slightly inflated, glabrous
<i>C. inflata</i>	annual, occasionally rooting at lower nodes or stoloniferous	glabrous	glabrous to pilose	7-15; rachis scabrous	usually 2, occasionally 3, upper sterile floret strongly inflated, glabrous to short pubescent
<i>C. montana</i>	perennial, stoloniferous	glabrous, except pilose just below spike attachment points	glabrous to scabrous, rarely pilose	2-5; rachis scabrous to sparsely pilose	usually 3, occasionally 2, usually not inflated, usually glabrous, occasionally sparsely pilose
<i>C. quinquesetica</i>	perennial, strongly stoloniferous	glabrous, except felty pubescent just below spike attachment points	glabrous to scabrous to loosely pilose	usually 3-8, rarely 2 or more than 8; rachis pilose, especially at base	usually 4, occasionally 3, lower not inflated, upper inflated, glabrous except upper margin ciliate
<i>C. wightiana</i>	perennial, tufted to shortly stoloniferous	densely pustulose-pilose	densely pustulose-pilose	3 or 4; rachis pustulose-pilose	3 or 4, uppermost somewhat inflated, pustulose-pilose

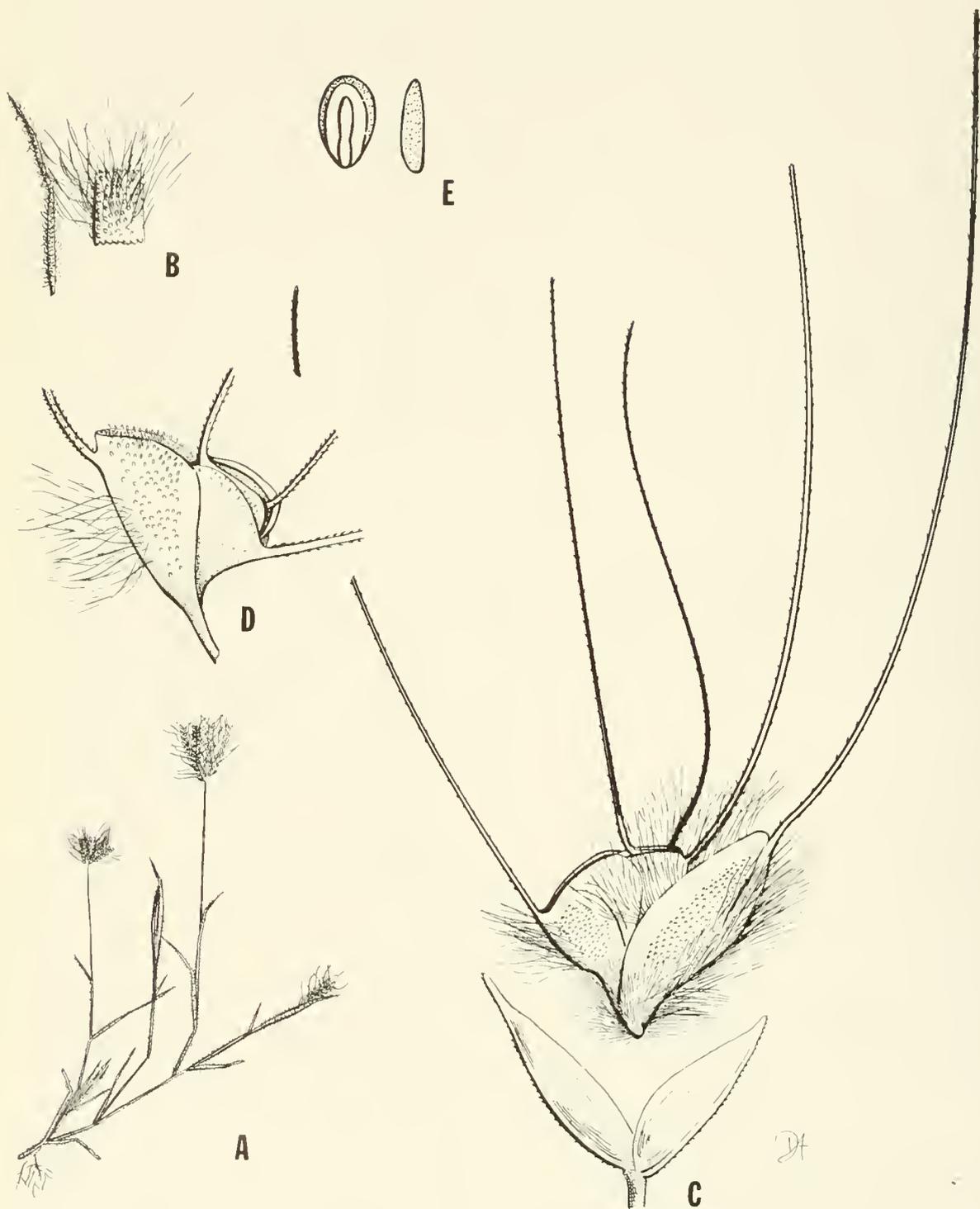


Fig. 26. *Chloris wightiana*. (A) habit, $\times 1/4$; (B) leaf (left) and enlargement of blade (right) showing pustulose-based hairs; (C) spikelet, partly dissected, $\times 10$; (D) sterile florets, $\times 15$; (E) caryopsis, dorsal view (left) and lateral view (right), $\times 10$.

divergent; spikelets densely imbricate, spreading widely from the pustulose-pilose rachis, ca 12 per cm of rachis length; glumes broadly lanceolate, thin, membranous, glabrous except for the midnerve, which is sometimes scabrous; first glume 2.0 to 2.5 mm long, 0.2 to 0.3 mm wide; second glume 2 to 3 mm long, 0.3 to 0.4 mm wide; fertile lemma 2.7 to 3.1 mm long, 0.9 to 1.0 mm wide, elliptic, callus, margins, and keel densely and prominently spreading-pilose, lemma sides pustulose, awn 7.5 to 10.0 mm long; sterile florets three or four, lowest sterile floret broadly triangular, 1.4 to 1.5 mm long, 1.9 to 2.0 mm wide, pustulose, midrib densely pilose, awn 6 to 7 mm long, upper sterile florets progressively reduced; caryopsis ca 1.3 mm long, ca 0.9 mm wide, ca 0.5 mm thick, ovoid-elliptic, strongly dorsally flattened.

Chloris wightiana may be easily separated from all other species in the genus by its pustulose pubescence; this is especially noticeable on the sheaths and blades. Only *Chloris arenaria* is as pubescent, but it is not pustulose. A comparison with other similar species is presented in Table 8.

Only two collections in addition to the isotypes mentioned above were studied in the herbaria. One label indicated the plant was collected on alkaline soil.

Specimens examined: INDIA: Peninsula Indiae Orientalis, *Wight* without precise locality, date, or collection number (K); Tinnevely Dtr., Tamparaparani River delta, *Lundararaj s.n.*, 28 Dec 1943 (K).

18. **CHLORIS MONTANA** Roxburgh, *Flora Indiae* ed. Carey 1:331. 1820. (Type not found. There is, however, a colored plate at K!, number 882 in the *Roxburgh Flora Indiae* drawings labeled "Chloris montana Roxb." This plate clearly shows a villous upper culm and a good spikelet dissection, leaving no question about the plant to which Roxburgh was referring.) Fig. 27, F-I, 28. *Andropogon tetra-aristatus* Roxburgh, ex Hooker, *Flora British India* 7:292. 1896. *Pro syn.*

Chloris montana Roxburgh var. *glauca* Hooker f. in Trimen, *Flora Ceylon* 5:276 1900. (ISOTYPE?: "from the herbarium, Ceylon, Jaffna, abundant. II. Trimen 22. 2 ii 90." US! The collection data correspond with those given in the original description, but no collection number or date was given. The plant is small, possibly only a seasonal dwarf; no spikelet differences were noted.)

Stoloniferous, occasionally tufted, perennial from 20-50 cm tall; sheaths glabrous; ligule a short ciliate crown; blades up to 12 cm long, 2-4 mm wide, glabrous below, glabrous to scabrous above; spikes two to five, 1.5 to 6.5 cm long, slightly divergent; upper culms puberulent; spikelets densely inserted, appressed, averaging ca 15 per cm of the scabrous to sparsely pilose rachis; glumes narrowly lanceolate, pale, translucent, glabrous except for the scabrous midnerve; first glume 1.5 to 1.7 mm long, ca 0.2 mm wide; second glume 2.2 to 2.7 mm long, 0.2 to 0.4 mm wide; fertile lemma 2.1 to 3.5 mm long, 0.5 to 0.7 mm wide, elliptic, upper margins ciliate with hairs up to 1 mm long, keel glabrous, sides glabrous to sparsely appressed-pilose, callus bearded, awn 4.2 to 9.5 mm long; sterile florets usually three (rarely two or four); lowest sterile floret 0.9 to 1.7 mm long, 0.4 to 0.6 mm wide, truncate, usually glabrous, rarely with a few appressed hairs in the midnerve region, awn 3.9 to 9.5 mm long; upper sterile florets progressively reduced, terminal sterile floret elongated to subspherical, usually only slightly inflated; caryopsis 1.7 to 2.0 mm long, ca 0.3 to 0.4 mm wide, ellipsoid, trigonous.

Some specimens of *Chloris montana* have the sterile lemma apex quite ciliate, though not as densely as *C. quinquesetica*, which they may resemble in other respects (Figs. 27, F-I; 25, A-D).

Occasional specimens may approach *C. inflata*, particularly in the number of sterile florets. *Chloris montana* usually has three sterile florets, though sometimes only two. Likewise, *C. inflata* usually has only two sterile florets, though some plants from the South Pacific island archipelagoes regularly have three. However, *C. montana* is a stoloniferous perennial with puberulous upper culms and without inflated upper sterile florets (Fig. 27, F-I). *Chloris inflata* is usually a tufted annual though occasionally stoloniferous, and has glabrous upper culms and inflated upper sterile florets (Fig. 30, A-M). Additional differences between these and other similar species are presented in Table 8.

Representative specimens examined: INDIA: Nellore Dtr., Tada, *Bourne 2,471* (K); Kistna Dtr., Manilapatam, Madras, *Gamble 17,396* (K); Madras Dtr.: Dugarazpatam, *Gamble 20,389* (K); Adzar, *Gamble 20,784* (K); Chingleput Dtr., Aradi, anon. 18 Sept 1917 (K); Chittoor Dtr., Panappakkam, without collector or date (K); Pondicherry, *Perrottet s.n.*, 1839 (K). MAURITIUS: Round Island, Barkley?, without



Fig. 27. *Chloris bournei* and *C. montana*. (A-E) *C. bournei*. (A) habit, x 1/4; (B) spikelet, partly dissected, x 10; (C,D) sterile florets, showing variation, x 10; (E) caryopsis, x 10. (F-I) *C. montana*. (F) habit, x 1/4; (G) spikelet, partly dissected, x 10; (H) sterile florets, dissected, x 10; (I) caryopsis, x 15.

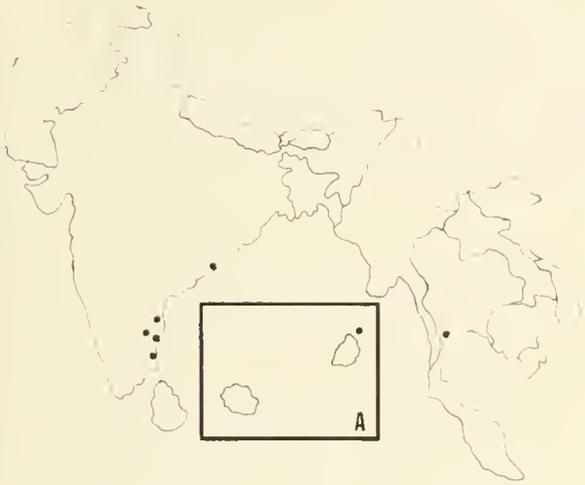


Fig. 28. Distribution of *Chloris montana*. Inset A: Mauritius, Reunion, and Round Island.

collection number or date (K). THAILAND: Hua Hin, Kerr 13,477 (K).

19. **CHLORIS BOURNEI** Rangachariar and Tadulingam, Jour. Indian Bot. Soc. 2:189. 1921. (TYPE: MH, not seen. Original description and accompanying illustration are clear.) Fig. 27, A-E.

Stoloniferous perennial up to 1 m tall, with geniculate culms ascending from a tufted base; sheaths glabrous, ciliate near the membranous ligule; blades up to 10 cm long, 5 mm wide, glabrous, scabrous, or sparsely pilose above, pilose on lower surface, especially at base; spikes three to nine, 6 to 9 cm long; spikelets imbricate, ca six per cm of the scabrous rachis; glumes broadly lanceolate to ovate, glabrous and membranous except for the scabrous to hispid midnerve; first glume 1.8 to 2.5 mm long, 0.3 to 0.4 mm wide; second glume 3.2 to 3.7 mm long, 0.4 to 0.5 mm wide; fertile lemma elliptic to obovate, 3.0 to 3.7 mm long, 0.8 to 1.3 mm wide, densely appressed-pubescent along callus, margins, and keel, awn 3.5 to 7.0 mm long; sterile florets two or three; lowest sterile floret obovate, 1.5 to 2.8 mm long, ca 1 mm wide, glabrous to sparsely pubescent on the midnerve, somewhat inflated, often containing rudiments of the palea, stamens, and pistil, occasionally apparently fertile, somewhat inflated, awn 3 to 4 mm long; caryopsis ca 1.7 mm long, 0.7 mm wide, ellipsoid-ovoid; chromosome number $2n = 40$.

Chloris bournei and *C. inflata* are similar, though *C. bournei* has much larger spikelets

(Table 8; Fig. 27, A-E). Also, *Chloris bournei* is a stoloniferous perennial, while *C. inflata* is a tufted or stoloniferous annual.

Representative specimens examined: INDIA: Coimbatore Dtr.: Talamalai Forest Reserve, Jacob 100 (K); Coimbatore Botanical Garden, Janaki-Ammal 1,172 (K); Bombay, Hubb, Koelz 19,901 (US); Arcot Dtr.: Ammapettai, banks of Uppanera, Narayanaswami 4,171 (K); Tanjore Dtr.: Ponnakani Meda, Narayanaswami 5,141 (K); Bellary Dtr.: Tornagallu, Rangachari s.n., 11 Aug 1901 (K); Madras Presidency: near Ahmednagar, Shattuck s.n., (K, US 879426); prope Palamaltah, Wight 3,316 (US); Godaveri Dtr.: Samalkot, anon., 19 Jan 1918 (K).

20. **CHLORIS INFLATA** Link, Enum. Pl. I:105. 1821. (FRAGMENT OF TYPE?: "Chloris inflata Link. Hb. Link. Sem. ex California." US! It is uncertain whether this is a fragment of the type, but the original description does refer to seed having been sent by Dr. Chamisso and that the origin was California. The locality must be an error. Fortunately, the original description clearly applies to the species described below.) Fig. 30, A-M.

Andropogon barbatum Linnaeus, Mantissa 302. 1771. Non *A. barbatum* Linnaeus Syst. Nat. ed. 10. 2:1305. 1759. (For a full explanation, see below and also under *Chloris dandyana*.)

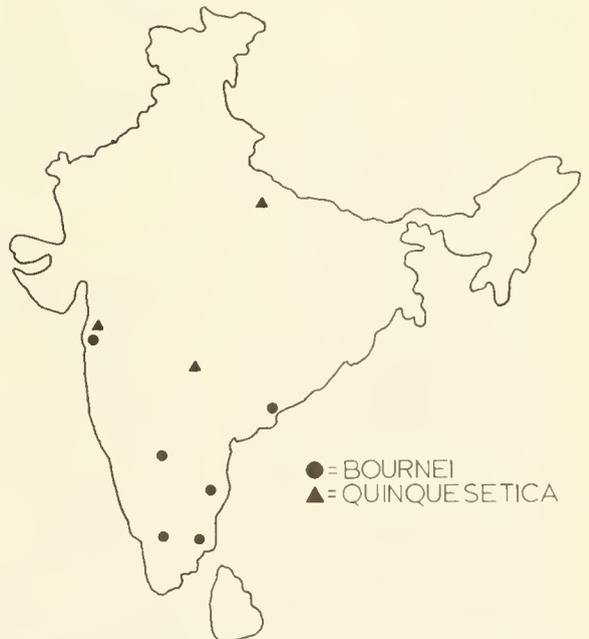


Fig. 29. Distribution of *Chloris bournei* (circles) and *C. quinquesetica* (triangles).

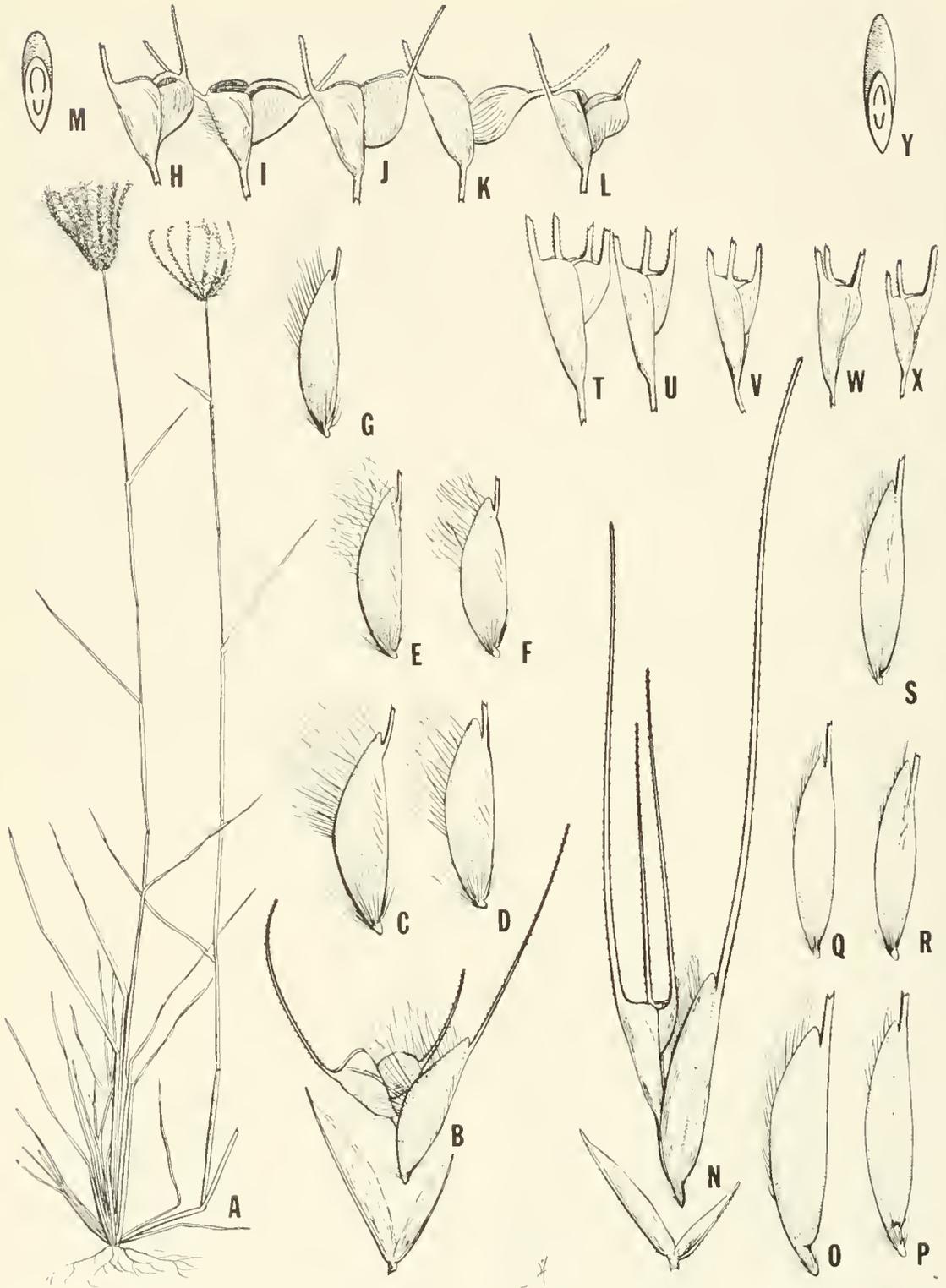


Fig. 30. *Chloris inflata* and *C. formosana*. (A-M) *C. inflata*. (A) habit, x 1/3; (B) spikelet, partly dissected, x 10; (C-G) fertile florets, showing variation, x 10; (H-L) sterile florets, showing variation, x 10; (M) caryopsis, x 10. (N-Y) *C. formosana*. (N) spikelet, partly dissected, x 10; (O-S) fertile florets, showing variation, x 10; (T-X) sterile florets, showing variation, x 10; (Y) caryopsis, x 15.

Chloris barbata (Linnaeus) Swartz, *Flora Indiae Occ.* 1:200. 1797. (Based on *Andropogon barbatus* Linnaeus, 1771, but not *Andropogon barbatus* Linnaeus, 1759.) *Non Chloris barbata* (Linnaeus) Nash, 1898. *Chloris longifolia* Steudel, *Syn. Pl. Glum.* 1:205. 1854. (HOLOTYPE: "Hrb. Cum- ing, nr. 696." P! FRAGMENT OF TYPE: US!)

Chloris paraguayensis Steudel, *Syn. Pl. Glum.* 1:204. 1854. (TYPE: "Rengger legit in Paraguay." Not seen. Original description clearly fits the above species.)

Chloris barbata Swartz var. *divaricata* Kuntze, *Rev. Gen. Pl.* 2:771. 1891. (ISO-TYPE: "Turong, Anam. Com. 2/1889." K!) *Chloris rufescens* Steudel, *Syn. Pl. Glum.* 1:206. 1854. (TYPE: "Urville legit in Ins. Maurit." Not seen. The original description is not conclusive, but it seems to fit this species best.) *Non Chloris rufescens* Lagasca, 1805.

Annual 15 to 95 cm tall, erect to decumbent and rooting at the lower nodes; sheaths glabrous; ligule short, pilose, occasionally merely shortly ciliate; blades flat, up to 15 cm long, 0.3 to 0.6 mm wide, glabrous, occasionally pilose at the base; spikes seven to fifteen, 3 to 8 cm long, digitate, \pm erect, often somewhat flexuous and purplish; spikelets densely imbricate, about 14 per cm of the scabrous rachis; glumes lanceolate to narrowly ovate, hyaline, glabrous except for the scabrous midnerve; first glume 1.2 to 2.1 mm long, 0.1 to 0.3 mm wide; second glume 2.3 to 2.7 mm long, 0.2 to 0.3 mm wide; fertile lemma 2.0 to 2.7 mm long, 0.4 to 0.7 mm wide, ovate to elliptic, callus and upper margins spreading to appressed-pilose, with hairs up to 1 mm long, keel glabrous to pilose, sides of lemma occasionally sparsely appressed-pilose, awn 4.0 to 7.7 mm long; sterile florets usually two (rarely three), lowest sterile floret 0.9 to 1.3 mm long, 0.4 to 0.9 mm wide, narrowly turbinate, truncate, inflated, usually glabrous, occasionally sparsely appressed-pilose on back, awn 5 to 7 mm long; upper sterile floret obovoid to subspherical, markedly inflated, about $\frac{2}{3}$ the length and width of the lower; carvopsis 1.1 to 1.4 mm long, 0.4 to 0.5 mm wide, ellipsoid to obovoid; chromosome number $2n=20, 40, ea 50$.

Chloris inflata varies greatly in several characters, including size, growth habit, spikelet pubescence, and number of sterile florets. Neither discernible geographic patterns nor consistent correlation of characters can be dis-

tinguished, except that specimens from the island archipelagoes of the southwest Pacific show a high frequency of plants with three sterile florets. One collection with three sterile florets was named *C. barbata* var. *divaricata* by Otto Kuntze (1891), though he mentioned only that the awn of the sterile floret was divaricate to reflexed. The plant is essentially identical to other populations of *C. inflata* in all other respects.

Chloris inflata is similar to *C. formosana* (Fig. 30, N-Y), *C. montana* (Fig. 21, F-1), and *C. quinquesetica* (Fig. 25, A-D). It is readily separated from the last two by being annual and lacking a felty pubescence at the apex of the culm just below the point of attachment of the spikes. In addition, it has more spikes (7-15) than *Chloris montana* (2-5). *C. quinquesetica* usually has four sterile florets; *C. inflata*, two or three.

Detailed differences and a short key, separating *Chloris inflata* and *C. montana*, are given under the latter species. Table 8 presents a comparison of this and other related species.

Considerable confusion has been evident as to whether *Chloris barbata* (Linnaeus) Swartz, *C. inflata* Link, or *C. paraguayensis* Steudel should be the accepted binomial. Certainly, the last name is predated by the other two and must be rejected. A full discussion of the relationship of *Andropogon barbatus* Linnaeus (both 1759 and 1771), *Chloris polydactyla* (Linnaeus) Swartz, and *Chloris barbata* (Linnaeus) Swartz, has been presented in the treatment of *C. dandyana* and should be consulted (p. 34). Essentially, I am rejecting *C. barbata* (Linnaeus) Swartz, for the basionym (*Andropogon barbatus* Linnaeus, 1771) is a later homonym. Swartz clearly referred to *Andropogon barbatus* Linnaeus, 1771, when making the transfer; and thus, *C. barbata* cannot be accepted as a new name as proposed by previous authors. The next available name is *Chloris inflata*.

Chloris inflata has been collected in a wide variety of habitats throughout the warm temperate, subtropical, and tropical regions of the world (Fig. 31). *Chloris inflata* is often a weed in waste areas, but it may be found also in cultivated fields, along beaches, etc. It appears to be very salt-tolerant: one gathering from La Salinas, Dominican Republic (*Howard and Howard 8,411*, NY! US!), was growing on pure salt rock. Still other collections are from sand dunes, loams, or limestone derivatives.

Representative specimens examined: (Note: *Chloris inflata* is very well represented in major herbaria and over 700 individual specimens



Fig. 31. Distribution of *Chloris inflata*. Inset A: Hawaiian Islands.

were examined. The following list represents only a small fraction of these collections. A complete list is available from the author in mimeographed form.) ADMIRALTY ISLANDS: Bismarek Arch., Goodenough Island, Milne Bay Dtr., *Brass* 24,419 (K). ANTIGUA: near St. John, *Rose et al.* 3,377 (NY, US). ARGENTINA: Buenos Aires, Isla Manel, *Parodi* 740 (US). AUSTRALIA: Northern Territory: near Darwin, *Black* 1,270,200 (K); Queensland: South Kennedy Dtr.: 13 mi SE of Eaglefield Station, *Adams* 1,079 (K). BAHAMA ISLANDS: Grand Turk Island, *Millspaugh and Millspaugh* 9,002 (F, NY); Inagua, *Hitchcock s.n.*, 3 Dec 1890 (F, MO). BARBADOS: Bridgeton, *F. W. Johnson* 1,194 (NY). BORNEO: Balikpapan, *Frost* 1 (K). BRAZIL: Bahia: 46 km WSW of Joazeiro, *A. Chase* 7,939 (F, US); Pernambuco: Bello Jardim, Serra do Genipapo, *A. Chase* 7,698 (F, MO, US). BRITISH GUIANA: Georgetown, *Graham* 345 (K). BURMA: Mandalay, *White* 132-237 (US); Sagaing, *Huk s.n.*, 5 July 1890 (K). CANTON ISLAND: without precise location, *Degener and Hathaway* 21,251 (MO, NY). CELEBES ISLAND: Manado, *Egman* 1,732 (K, US). CEYLON: Trincomalee coast, *Kingdon-Ward* 23,064 (K). COCOS KEELING ISLAND: *St. John* 26,465A (K). COLOMBIA: Dep. Atlantico: entre Palmar de Varelay Pondera, *Dugand* 4,428 (US). CUBA: Havana Prov.: without precise location, *Baker* 1,441 (F, US); Oriente Prov.: Guanta-

namo Bay, *Britton* 2,032 (NY, US); Isla de Pinos, *Curtiss s.n.*, Apr. 1904 (NY). CURAÇAO: near Willemstad, *Curran and Haman* 63 (NY, US). DOMINICA ISLAND: near Morne Daniel, *Hodge* 3,893 (NY). DOMINICAN REPUBLIC: Prov. Barahona: Neiba Valley, *Howard and Howard* 8,360 (NY, US); Prov. Monte Cristo: Guayubin, *Abbott* 876, 878 (US); Prov. Santo Domingo: vicinity of Ciudad Trujillo, *Allard* 14,626 (NY). FERNANDO DE NORONHA: Quixaba, *Cuyler* 9,395 (US). FIJI ISLANDS: Viti Levu Island, *Greenwood* 1,213 1,308 (US). FRENCH GUIANA: Cayenne, *Hook s.n.*, 2 Jun 1962 (NY). GHANA: near Labadi, *Adams* 3,835 (K). GRAND CAYMAN: without precise location, *Moggs* 61 (K). GRENADINES: Petit Martinique, *Howard* 10,917 (NY). GUADELOUPE: Basse Terre, *Duss* 3,158 (NY, US). HAITI: Gonave Island, vicinity of Etroite, *Leonard* 3,339a (F, NY, US); Tortue Island, vicinity of LaVallee, *Leonard and Leonard* 11,262 (UC). HONDURAS: Dep. Atlantida, *Standley* 56,587 (F, US). INDIA: Madura Dtr.: Pulney Hills, Dindigal, *Anglade* 1,109 (K); Chingleput Dtr.: Madras, *Gamble* 16,415 (K); Calcutta, *Helfer s.n.*, 1836-38 (BR, NY); Coimbatore Dtr.: Anai Katti, *Rapi and Naganathan* 4,802 (K). IVORY COAST: Abidjan Plateau, *Adjanohoun* 428A (K). JAMAICA: between Portland Point and Rocky Point, limestone plain, *Britton* 1,903 (NY); Kingston, *Harris* 9,049 (F, K, NY, US).

JAVA: Ambarawa, *Brooks s.n.*, Mar 1909 (BM). KENYA: Voi Dtr., Tsavo National Park, E of Lugard Falls, *Greenway and Kanuri 12,874* (K); Kwale, SW of Mombasa, *Bogdan AB 3,194* (K). LINE ISLANDS: Christmas Island, *Pearson P22* (K). LIBERIA: Cape Palmas, *Hale 157* (US). MACAU: vacant lot, *Hitchcock 19,153* (US). MALAGASY REPUBLIC: Nossi Bé, *Hildebrandt 2,939* (US), *2,932* (K). MALAYSIA: Singapore, *Bor 561* (K); Selonger State, Port Swettenham, *Buckill 12,839* (K). MARSHALL ISLANDS: Guam, *Fosberg 25,334, 31,223* (US); Pagan Island, *Bonham 33* (US); Saipan Island, *Fosberg 31,287* (US); Tinian Island, *Fosberg 24,798* (US); Bikini Atoll, *Taylor 1,500* (UC); Eniwetok Atoll, *Fosberg 24,407* (US); Kwajalein Atoll, *Fosberg 31,202* (US); Majura Atoll, *Fosberg 31,193* (US). MARTINIQUE: St. Anne, S of Dunkerque-Catherine mangrove, *Egler 39-73* (NY). MAURITIUS: Batterie Dauphine, *Sauer 2,701* (F). MEXICO: Tamaulipas: N of Ciudad Mante, *Beetle M-521* (UC); Yucatán: Mérida, *Swallen s.n.*, Aug 1932 (US). MOLLUCA ISLANDS (HALMAHERA): Morotai, *Main and Aden 1,477* (US). NEW CALEDONIA: Anse Vata, *McKee 4,063* (K). NEW PROVIDENCE: Nassau, *Matthews 61* (K). NIGERIA: Lagos, *Ward 9* (K). PALAU ISLAND: Arakabesan Island, *Hosaka 3,354* (US); Peleliu Island, *Fosberg 31,952* (US). PANAMA: near Miraflores, Locks, *Allen 1,752* (F, K, MO, NY). PAPUA: Daru Island, *Brass 6,403* (BM, US); Fairfax, 9°55'S, 147°20'E, *Gillison NGF 22,211* (K); SW base of Mt. Lawes, *Eucalyptus savannah, Schodde 2,644* (K, US). PEMBA ISLAND: *Vaughn 252* (BM). PHILIPPINE ISLANDS: Luzon: Manila, *Clemens s.n.*, Sep 1924 (UC, US); Corregidor, *Cuming 696* (K, MO). PUERTO RICO: Mona Island, Sardinera, *Britton et al. 1,831* (NY, US); Isla de Culebra, *Brown and Wheeler 141* (NY, US); Guanica Bay, *A. Chase 6,529* (US). RYUKYU ISLANDS: Okinawa, *Amano 6,800* (US). ST. KITTS: *Hitchcock 16,369* (US). ST. LUCIA: *Brooks 20* (US). SAMOA EAST: Tutuila Island, *Collarnio 508* (US). SERAM (CERAM) ISLAND: Amboina, *Robinson 1,647* (BM). SEYCHELLES ISLANDS: Mahé Island, *Boivin s.n.*, 17 Nov 1855 (K). TAIWAN: Chiayi, *Devol 7,095* (UC). TANZANIA: Dar Es Salaam, *Hitchcock 24,424* (US); Tanga Prov.: Sakura Sec.: Panyani Dtr., *Tanner 2,027* (K, UC). THAILAND: Bangkok, *Kerr 3,761, 7,853* (BM); Wangka, Kwae Noi River basin, *Wichian 330* (K). TIMOR: Kupang, *R. Brown s.n.*, Apr 1803 (BM). TOBAGO: Speyside, *Purseglove P. 6,358* (K).

TRINIDAD: Woodbrook, *Broadway 7,177* (F, MO). UNITED STATES: Hawaii: Oahu, N of Koko Head, *Degener 10,835* (NY); Texas: Hidalgo Co., McAllen, roadside, *Anderson 3,875* (HSC). VENEZUELA: Lara, Palmasola, *Pittier 6,385* (US). VIRGIN ISLANDS: St. Croix, *Thompson, 5 Oct 1921* (NY, US); St. Thomas, *Hitchcock 16,320* (US); Tortola, *Velez 3,123* (K). WAKE ISLAND: Peale Islet, *Fosberg 34,928* (US). WEST IRIAN (IRIAN BARAT): Merauke River, Kelapi Lima, *McKee 1,705* (K). ZANZIBAR: *Cooke s.n.*, 1861 (MO).

21. *CHLORIS FORMOSANA* (Honda) Keng, *Claves Gen. Sp. Graminearum Primarum Sinicarum* 197. 1957. (Based on *Chloris barbata* Swartz var. *formosana* Honda.) Fig. 30, N-Y.

Chloris barbata Swartz var. *formosana* Honda, *Bot. Mag. Tokyo* 40:437. 1926. (SYNTYPES: "Taiwan: Takao, G. Nakahara, no. 635, anno 1905." "Bachu, B. Hayata anno 1919." Not seen. Description refers to species as commonly understood.)

Perennial often stoloniferous, 30-75 cm tall, erect to decumbent; sheaths glabrous, rarely sparsely pilose; ligule a very short ciliate fringe; blades up to 20 cm long, usually folded, glabrous, acute; spikes five to nine, 4 to 8 cm long, erect to somewhat lax; spikelets densely imbricate, ca fourteen per cm of the pilose rachis; glumes lanceolate, glabrous, except for the scabrous midnerve; first glume 1.0 to 1.5 mm long, ea 0.2 mm wide, acute; second glume 2.2 to 2.5 mm long, 0.2 to 0.3 mm wide, apex obtuse, mucronate; fertile lemma 2.3 to 3.0 mm long, 0.5 to 0.7 mm wide, with a lateral groove, which is occasionally appressed-pilose, upper margins densely pilose with hairs up to ca 1 mm long, keel glabrous, slightly gibbous, awn 2.0 to 5.7 mm long; sterile florets two; lower sterile floret oblanceolate to truncate, 1.6 to 1.9 mm long, 0.6 to 0.7 mm wide, flattened or only slightly inflated, awn 2.3 to 5.0 mm long; upper sterile floret of same shape as lower, but smaller, 0.5 to 0.7 mm long, 0.4 to 0.5 mm wide, glabrous, awn 1.5 to 2.5 mm long; carvopsis 1.2 to 1.6 mm long, 0.3 to 0.4 mm wide, ellipsoid.

Chloris formosana is most easily confused with *C. inflata*. The following key will separate the two:

- I. Lower sterile floret 1.6 to 1.9 mm long, flattened or only slightly inflated; upper sterile floret about one-third the size of

the lower, scarcely inflated; upper sheaths, ligules, and lower portions of leaves glabrous, rarely sparsely pilose; perennials.

C. formosana (Fig. 30, N-Y)

1. Lower sterile floret 0.9 to 1.3 mm long, usually inflated; upper sterile floret two-thirds to about the same size as the lower, usually inflated and spherical; upper sheaths, ligule, and lower portions of the leaves usually loosely pilose, though sometimes sparsely so; annuals, occasionally rooting at the lower nodes.

C. inflata (Fig. 30, A-M)

Other species that might be confused with *C. formosana* are compared in Table 8.

Collected from sandy or gravelly soils, often near the ocean in China, Hong Kong, Taiwan, and Vietnam (Fig. 32).

Representative specimens examined: CHINA: Fukien Prov.: Amoy, *Chung* 6,055 (US), *Price* 1,363 (K); Kwangtung Prov.: Taio, *Chun* 3,114B, 3,123 (NY); Pakhoi, *Hitchcock* 19,255 (US); Hainan Island: Hoihow, *Hitchcock* 19,547 (US), *McClure* 10,451 (BM, K), *Tsang* 986 (NY). HONG KONG: *Bor* H.K. 76 (K), *Ford* s.n., 25 Aug 1893 (K, NY), *Hance* 1,943 (BM); Quarry Bay, *Sampson* 851 (BM). NORTH VIETNAM: Tonkin, route de Haiphong á Doso, bords des chemins, *Petelot* 425 (NY, US). TAIWAN: Takao, *Henry* s.n., 1893-4 (BM), *Henry* 1,023 (K), *Playfair* 53 (K); without precise location, *Tanaka* 10,352 (BM, NY, UC).

22. **CHLORIS PILOSA** Schumacher, Beskr. Guineiske Planter 75. 1827. (PHOTOGRAPHS OF HOLOTYPE: K! US! Type specimen, in Isert and Thonning Herbarium, C, has mucronate lemmas.) Fig. 33, E-K.



Fig. 32. Distribution of *Chloris formosana* (southeast China, Hainan, and Taiwan).

Chloris breviseta Benth in Hooker f., Niger Flora 566. 1849. (SYNTYPES: "Cape Coast, Don" BM! "Cape Coast, Vogel" K!)

Chloris nigra Hackel, Bol. Soc. Broteriana 21:179. 1906. (TYPE: "Insula S. Jacobi Prom Viridis, pr. Trinitate, leg. A. Barjona" not seen, but description is clear.)

Chloris virgata Swartz var. *breviseta* (Benth) Pilger ex Peter, Beih. Repert. Sp. Nov. 40:262. 1931. (Based on *Chloris breviseta* Benth.)

Annual often weakly rooted, sometimes shortly stoloniferous, erect or in stoloniferous specimens somewhat decumbent, usually 30 to 70 cm tall, occasionally to 2 m; sheaths glabrous to densely pilose; ligule densely and prominently pilose; blades 2 to 10 mm wide, up to 30 cm long, scabrous; spikes five to nine, 3 to 5 cm long; spikelets loosely imbricate, ca five to seven per cm of the scabrous rachis; glumes membranous, unequal; first glume 1.1 to 1.6 mm long, 0.2 to 0.3 mm wide, narrowly lanceolate, glabrous except for the scabrous midnerve; second glume 1.9 to 2.3 mm long, 0.3 to 0.4 mm wide, glabrous with scabrous midnerve, rounded at the apex and bearing an awn ca 0.3 mm long; fertile lemma 2.3 to 3.5 mm long, 0.7 to 1.5 mm wide, broadly ovate or elliptic in overall outline, prominently gibbous on the keel; varying from pale to dark gray or black, often mottled when mature, callus bearded, sides with a prominent glabrous or appressed-pilose furrow, apex acute to blunt, mucronate, or with an awn up to 6 mm long; sterile florets two (very rarely one) glabrous, becoming scabrous at the apex, lower sterile floret 1.5 to 2.2 mm long, 0.7 to 1.1 mm wide, narrowed at the base, becoming inflated at the truncate apex, glabrous below, apex scabrous, mucronate, or with an awn up to 3.0 mm long, upper sterile floret a triangular inflated rudiment less than 1 mm long, ca 1 mm wide, usually hidden in the lower sterile floret, awnless; anthers ca 0.4 to 0.5 mm long; caryopsis 1.3 to 1.5 mm long, ca 0.5 to 0.6 mm wide, obovoid, trigonous; chromosome number $2n=20, 30$.

Awn length in this species varies widely. Most specimens fall in one of two groups, those with awns less than 1 mm long, generally only mucronate (represented on the map in Fig. 34 by unshaded circles) and those with longer awns, usually from 2 to 6 mm (indicated on the map by shaded circles). No strong correlations of awn length can be made with geographic origin, nor with other morphological characters. While the variation in awn length



Fig. 33. *Chloris castilloniana* and *C. pilosa*. (A-D) *C. castilloniana*. (A) habit, x 1/5; (B) spikelet, partly dissected, x 10; (C) sterile floret, x 15; (D) caryopsis, x 10. (E-K) *C. pilosa*. (E) habit, x 1/3; (F) spikelet of awned variant, partly dissected, x 10; (G) spikelet of unawned variant, x 10; (H) sterile florets of awned variant, x 15; (I) sterile florets of unawned variant, x 15; (J) upper sterile floret, x 15; (K) caryopsis, x 10.

produces plants with somewhat diverse appearances, their nomenclatural recognition is not warranted.

Chloris pilosa most closely resembles *C. virgata*, from which it may be separated in having prominently pilose ligules and broader lemmas which have shorter marginal cilia.

Widely distributed in equatorial Africa, *Chloris pilosa* has been collected in weedy areas and as a native in savannahs. It is occasionally cultivated as a forage grass. The natural distribution is shown in Fig. 34.

Representative specimens examined: BELGIUM (adventive): Dunquerque, anon. (US). CAMEROUN: Boro, 35 km ENE of Maroua, *Bounougou* 13 (K); Darga, 30 km ESE of Maroua, *Koechlin s.n.*, May 1965 (K); Victoria Dtr.: roadsides, weedy, *Maitland* 9 (K). CAPE VERDE ISLANDS: San Nicalao, *Lowe s.n.*, 22 Feb. 1864 (BM); São Tiago, *Grandvaux-Barbosa*, 5,755 (K). CONGO: Leopoldville, *Fasseaux* 1,019 (K). DAHOMEY: Parakou, *Risopoulos* 1,197 (K). ETHIOPIA: Seriba, Ghattas, *Schweinfurth* 2,283 (K, US). FERNANDO PO: Mann 118 (K). GAMBIA: Sankuli-Kunda, *Pirie s.n.*, Sept 1933 (K). GHANA: Nungua, Accra Plains, 5°40'N, 0°06'W *Ankrah* 20,150 (K); 2.5 mi SW of Kpetehu Ferry, 7°55'N, 0°22'E, *Ankrah* 20,387 (K); Baikpa, 6°51'N, 0°26'E, *Rose-Innes* 31,189 (K); Axim, *Vigne* 395 (NY, US). GUINEA: Nzerekore, *Baldwin* 9,722 (K, US); Kouroussa, *Pobéquin* 546 (K). IVORY COAST: Kouibly, *Adjanohoun* 413A (K). LIBERIA: Grand Bassa Co.: Timbo, *Baldwin* 11,223 (K); 10 mi inland from River Cess, *Baldwin* 11,228 (K); Sinoe Co.: Sasstown, *Baldwin* 11,603 (K). MAURITANIA: Dahr, 16°30'N, 7°W, *Rossetti* 61 172 (K). NIGERIA:

Prov. Oyo: Ibadan, *Brenan* 9,601 (K, US); Prov. Zaria: Samaru, *Freeman* S. 116 (K); Jebba, *Hagerup* 739 (K, US); Jos Plateau, along Delimi River, Naraguta, *Lawlor and Hall FHI* 46,540 (K); Toro, 20 mi S of Jos, *Seiple* 176 (US). REPUBLIC OF THE CONGO: Musa, *De Giorgi* 1,299 (K); Eala, *Germain* 1,695 (K); Kasenye, *Johnston* 1,042A (K); Bukama, *Shantz* 565 (K). SUDAN: Cordofan Prov.: El Obeid, *Harrison* 75 (K); Darfur Prov.: Jebel Marra, *Wickens* 2,279 (K); Equatoria Prov.: Lado Dtr., *Cartwright* 27 (K); Upper Nile Prov.: Zerat Island, *Harrison* 1,005 (K). SIERRA LEONE: Mano, *Deighton* 674 (K); Musaia, *Deighton* 5,386 (K); Freetown, *Deighton* 2,029 (K). SENEGAL: Dakar, *Baldwin* 5,714 (K). TANZANIA: Tanga Dtr.: Kange Estate, *Faulkner* 808 (K); Rufiji Dtr.: Utete boma, *Milne-Redhead and Taylor* 7,537 (K); Morogoro Dtr.: Duturi, *Nicholson* 29 (K). TOCO: Palime, *Stage* 73 (K). UGANDA: Buganda Dtr., *Hitchcock* 24,934 (K); Lango Dtr.: Amugo, *Johnston* 1,037 (K); Ankole Dtr.: Kiruhara, *Thornton* 39 (K); near Mt. Elgon, *Snowden* 1,207 (K).

23. *CHLORIS VIRGATA* Swartz, Flora Indiae Occ. 1:203. 1797. (Holotype not seen, but description clearly refers to the species as commonly understood.) Fig. 35.

? *Chloris pubescens* Lagasca, Var. Cienc. Lit. Artes (Madrid) 4:143. 1805. Description recopied in Lagasca, Gen. Sp. Pl. 5 Nov. 1816. (A specimen, at G!, labeled "*Chloris pubescens* Lagasca, ex Peruvia, Lagasca 1807" is *Chloris virgata*. The original description is not conclusive, and this name is included here provisionally.)

Rabdochloa virgata (Swartz) Beauvois, Ess. Agrost. 84, 155, 176. 1812. (Based on *Chloris virgata* Swartz, but *Rabdochloa* not validly published.)

Chloris elegans Humboldt, Bonpland, Kunth, Nov. Gen. Sp. Pl. 1:166, pl. 49. 1816. (HOLOTYPE: "Mexico, Queretaro. M.A. Bonpland n. 4194." P! Fragment in US!)

Chloris alba Presl, Rel. Haenke 1:289. 1830. (Description clearly refers to *Chloris virgata*. Scribner, 1899, examined and described the presumed type in the Bernhardt Herbarium, saying it was the same as *C. elegans*.)

Chloris caudata Trinius ex Bunge, Mém. Savans Étr. Acad. Pétersburg 2:144. 1835.



Fig. 34. Distribution of *Chloris pilosa*. Dots represent specimens with awned lemmas; open circles represent specimens with unawned or merely mucronate lemmas.

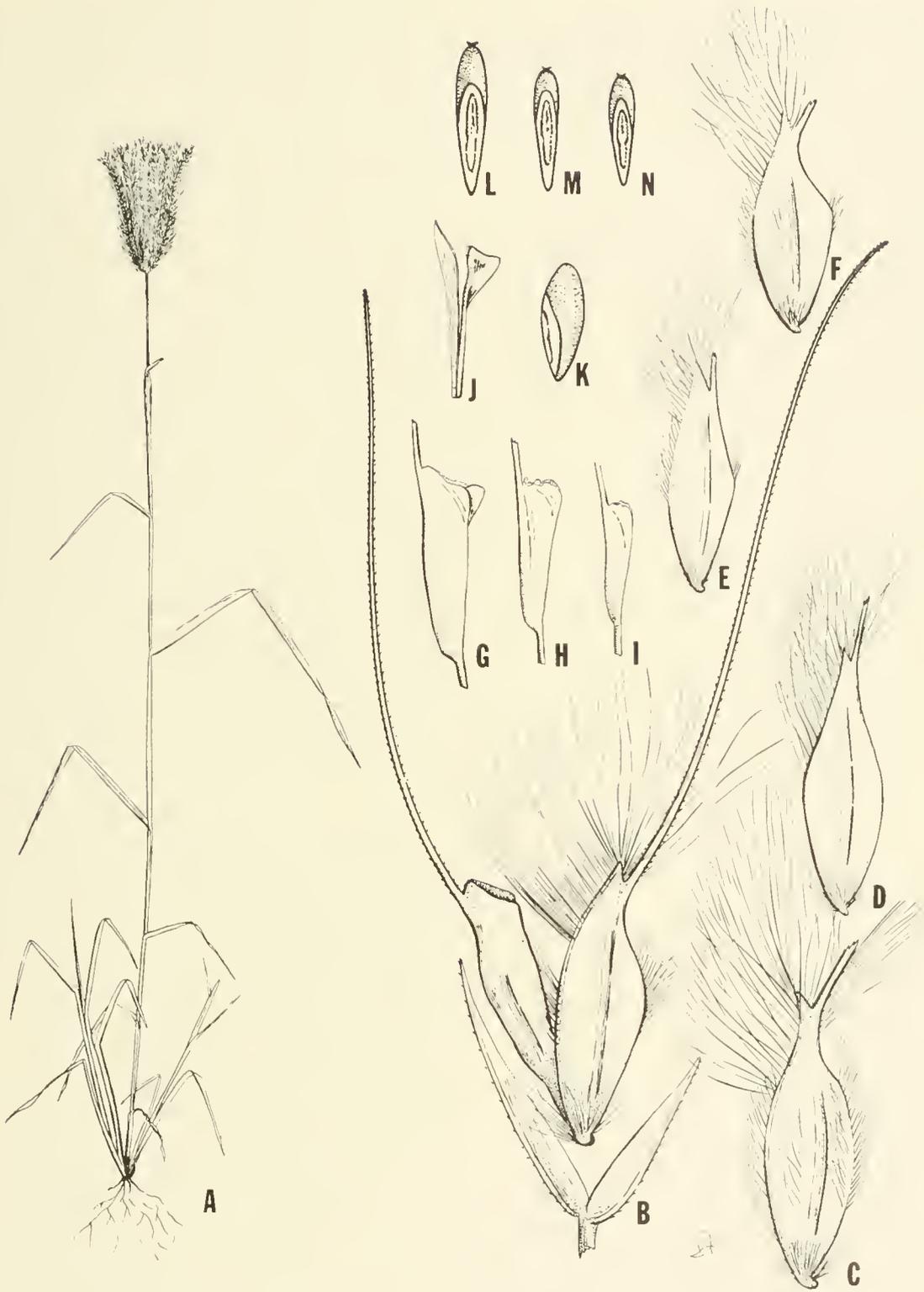


Fig. 35. *Chloris virgata*. (A) habit, x 1/4; (B) spikelet, partly dissected; (C-F) fertile lemmas, showing variations; (G-I) lower sterile florets, showing variation; (J) rudimentary palea of lower sterile floret (left) and attached upper sterile floret (right); (K) caryopsis, lateral view; (L-N) caryopses, dorsal views, showing variations. (B-N) x 10.

(Description, combined with geographical citation, "Hab. propre Pekinum," seems to refer to *C. virgata*. A specimen in the Cosson Hb., at P!, collected by Bunge in 1835, and labeled "*Chloris caudata*," perhaps in Bunge script, is *C. virgata*.)

Chloris penicillata Willdenow ex Steudel, Nom. Bot. ed. 2. 1:353. 1840. *Pro syn.*

Chloris decora Nees ex Steudel, Syn. Pl. Glum. 1:205. 1854. First published as *nomen nudum* by Nees in Royle, Illust. Bot. Himalayan Mts. and Flora Cashmere 1:416. 1840. (HOLOTYPE: "Royle Herbr. nr. 87" K!)

Chloris meccana Hochstetter ex Steudel, Syn. Pl. Glum. 1:205. 1854. (ISOTYPES: "802. Chloris meccana Hochst. ex Steudel . . . d. II Febr. 36, leg. W. Schimper" G! US!)

Chloris madagascariensis Steudel, Syn. Pl. Glum. 1:203. 1854. (HOLOTYPE: ". . . Le Jolis legit 1849 . . ." P!)

Chloris notocoma Hochstetter, Flora 38:204. 1855. (ISOTYPES: "Hb. abyss. Hohenacker nr. 2125" G! P!)

Chloris multiradiata Hochstetter, Flora 38:204. 1855. (Description is of *C. virgata*. Type, "Hb. abyss. Buch. nr. 486" in P! is *C. prieurii*; a duplicate at K! is *C. virgata*.)
Chloris alba Presl var. *aristulata* Torrey, Rept. Expl. Survey Mississippi River Pacific 4:155. 1857. (A short-awned variant.)

Chloris brachystachys Andersson in Peters, Naturwiss. Reise Mossambique 556. 1864. (Based on *Chloris alba* Presl.)

Agrostomia barbata Cervantes, Naturaleza (Mexico City) 1:346. 1870. (TYPE: Cuernavaca, Mexico, not seen, but description fits *C. virgata*.)

Chloris barbata var. *decora* (Nees) Bentham, Flora Australiensis 7:613. 1878. (Based on *C. decora* Nees.)

Chloris alberti Regel, Acta Horti Petropolitani 7:650. 1881. (TYPE: "Mongolia occidentali prope Takiansi, A. Regel," not seen. Geographic origin and description seem to suggest *C. virgata*.)

Chloris tetrastachys Hackel ex Hooker f., Flora British India 7:291. 1896. *Pro syn*
Chloris virgata var. *elegans* (Humboldt Bonpland Kunth) Stapf in Thistleton-Dyer, Flora Capensis 7:642. 1900. (Based on *C. elegans*.)

Chloris polydactyla Swartz ssp. *multiradi-*

ata (Hochstetter) Chiovenda in Pirota, Annuario Reale Ist. Bot. Roma 8:54. 1903. (Based on *C. multiradiata* Hochstetter).

Chloris gabrielae Domin, Biblioth. Bot. 85:368, Fig. 83. 1915. (HOLOTYPE: "Queensland; am Flinders River bei Hughenden, haufig, Domin, II. 1910." K!, on extended loan from PR.)

Chloris rogeoni Chevalier, Rev. Bot. Appl. Agric. Trop. 14:127. 1934. (SYNTYPES: "Dire. 43,871, El Oualadjü 43,937 et 42,357." All except the last at P! Fragments of last two at K!)

Chloris tibestica Quezel, Bull. Soc. Hist. Afrique Nord 48:84. 1957. (TYPE: "Emi Koussi," not seen. Description and subsequent illustration in Quezel, 1958, leave no doubt as to identity.)

Annual, extremely variable in size, ranging from a few centimeters to over a meter; culms usually tufted, several arising from one root system, occasionally stoloniferous; sheaths usually glabrous, occasionally rather densely pilose toward the apex; ligule glabrous, or with a ciliate fringe of hairs up to 4 mm long; blades up to 30 cm long and 1.5 cm wide, usually glabrous with scabrous margins, occasionally pilose; spikes four to twenty, 5 to 10 cm long, usually more or less erect; spikelets densely imbricate, averaging 10 per cm of the scabrous or hispid-ciliate rachis; glumes pale brown, lanceolate, glabrous with scabrous midnerves; first glume 1.5 to 2.5 mm long, 0.2 to 0.4 mm wide; second glume 2.5 to 4.3 mm long, 0.3 to 0.5 mm wide; fertile lemma 2.5 to 4.2 mm long, 0.7 to 1.3 mm wide, pale brown, occasionally purplish or blotched with dark brown spots, keel usually prominently gibbous, keel, midnerves, and lower margins glabrous to prominently pilose, margins long-ciliate, with spreading hairs near the apex, awn 2.5 to 15.0 mm long, usually more than 5 mm long; sterile floret one, on robust specimens, occasionally two; lower sterile floret 1.4 to 2.9 mm long, 0.4 to 0.8 mm wide, awn 3.0 to 9.5 mm long; upper sterile floret, when present, usually borne on a short rachilla and greatly reduced, sometimes absent, leaving only the naked rachilla; caryopsis 1.5 to 2.0 mm long, ca 0.5 mm wide, ellipsoid-trigonous; chromosome number $2n=20, 26, 30, 40$.

Without doubt, *Chloris virgata* is the most variable of all of the annual species in the genus. Great variation is shown in many traits, including such vegetative features as height, leaf size, tomentum, and habit, as well as spikelet

characters (especially various pubescence on the lemma, such as presence or absence of hairs on the keels, midnerves, and margins). In addition, the lemmas themselves may be variously gibbous, keeled, or merely folded at the midnerve. Only two attributes seem constantly correlated: (1) the conspicuous tuft of spreading hairs on the upper lemma margins and (2) the appressed to erect or only slightly divergent spikes.

No well-marked patterns of variation can be identified, though several somewhat cryptic populations are noticeable. Most specimens from Australia and some from Asia and Africa have relatively narrow lemmas that are not conspicuously gibbous, though other collections from the same general area may show the typical prominently gibbous keel. Some of the populations, especially those from Tibet and Nepal, may eventually prove to be distinct; but presently, so few specimens are available for study that it seems advisable to treat the entire variable population as a single species. By contrast, western hemisphere material seems to be quite uniformly gibbous, usually conspicuously so.

Occasionally novelties, such as a specimen collected by Dr. T. L. Bancroft at Palm Island, Queensland (K!), may be very different. This particular specimen was unique in having densely pilose glumes. In other respects it is similar

to typical specimens of *C. virgata* and is considered here as merely an aberrant individual.

Chloris virgata closely resembles *C. gayana* and *C. pilosa* in spikelet characters. It may be easily separated from the former in being an annual and from the latter in having relatively long awns.

Chloris virgata has been widely collected from many habitats, primarily in warm temperate to tropical areas, but extending well into temperate areas where hot summers are common (Fig. 36). Over 1,300 different specimens were examined in this study. The following list represents only a small fraction of the total.

Representative specimens examined: AFGHANISTAN: Helmand River Valley, irrigated field, Long 326 (US). ANGOLA: Kaoko veld, N of Ohopoho, ca 18°E x 14°S, *de Winter and Leistner* 5,177 (K). ARGENTINA: Prov. Buenos Aires: Pergamino, *Parodi* 834 (US); Prov. Catamarca: 6 mi SW of Andalgalá, *Bartlett* 20,226 (US); Prov. Córdoba: Dep. de Santa María, *Hunziker* 1,294 (MO); Prov. La Rioja: Patguía, *Lahitte y Castro* 2 (US); Prov. Mendoza: Santa Rosa, *Jensen-Haarup* s.n., 1904-05 (US); Prov. Salta: Dep. Rosario de Lerma, Las Tres Acquias, *Montenegro* 455 (US); Prov. Tucumán: Dep. Trancas, Río Tipainago, *Venturi* 4,354 (NY, US). AUSTRALIA: Queensland: Darling Downs, *Ashcroft* s.n., May 1916 (K); Petrie, *Blake* 170 (K); Western Australia: Wan-



Fig. 36. Distribution of *Chloris virgata*. Inset A: Hawaiian Islands.

dagee, Minitlya River, *Gardner* 3,234 (K). BOLIVIA: Cochabamba Dep.: without precise location, *Buchtien* 2,512 (US); Dep. Tarija, near Entre Ríos, *West* 8,250 (MO, US). BOTSWANA: Kgalagedi, without precise location, *Leistner* 3,103 (K); Ngwato, Bokalaka area, Francistown, *McClintock s.n.*, 18 Dec 1966 (K). BRAZIL: Bahia: near Rio São Francisco, Joazeiro, *A. Chase* 7,946 (F, US); Ceará: Campo Salles, *Swallen* 4,288 (US, Piauí: between Floriano and Oeiras, *Swallen* 4,171 (US); Rio Grande do Norte: Santa Cruz, *Swallen* 4,849 (US). BURMA: Mingaladon, *Pokhant* 1,375 (K). CHINA: Honan Prov.: Cheng-Chou, *Chiao* 18,500 (F); Hopeh Prov.: near Peking, *Cheng* 2,038 (US); Inner Mongolia: Ordos, Tapuchan, *Hsiu II* 3,799 (US); Kansu Prov.: Yao Kai, near Lichen, *Ching* 258 (US); Kiangsu Prov.: Nanking, *Chiao* 12,916 (K, NY, UC); Manchuria: Darien, *Juliana* 59a (NY); Harbin, *Dorsett and Dorsett s.n.*, (US); Shungari River, *Komarov* 167 (BM, K); Shansi Prov.: Sui Guan Dtr., *Han Ngan* 32 (UC); Shantung Prov.: Chingtao, Li Chuan, *Chiao* 2,864 (F, K, NY, UC, US); Shensi Prov.: Chou-chih-hsien, *Kung* K3,734 (US); Yunnan Prov. La-Kov, *Maire* Apr 1914 (BM, F). CURAÇAO: Sovonet, *Suringar* 9 (US). ECUADOR: Prov. Guayas: W of Guayaquil, *Asplund* 15,369 (K); Puntilla, Salinas, 2 13'S, 81 W, *Svenson s.n.*, 1 Mar 1941 (F, MO); Prov. Loja: between La Toma and Loja, *Hitchcock* 21,493 (US). EL SALVADOR: vicinity of San Salvador, *Standley* 19,234 (NY). GALAPÁGOS ISLANDS: Charles Island, Post Office Bay, *Howell* 8,838 (US); Chatham Island: Wreck Bay, *Howell* 8,595 (US), *Stewart* 1,254 (K, MO); Indefatigable Island, *Howell* 9,917 (US); North Seymour Island, *Howell* 9,967 (US); South Seymour Island, *Howell* 9,924 (US). GUATEMALA: near Jalapa, *Kellerman* 7,975 (F, NY); vicinity of Zacapa, *Standley* 74,606 (F). HONDURAS: 5 km N of Talanga, *Johannessen* 892 (UC); Dep. Morazan: vicinity of El Zamorano, *Standley s.n.*, 27 June 1949 (F). INDIA: Allahabad, *Dudgeon s.n.*, 1 Nov 1919 (MO); Bombay, *Gamble* 21,028 (K); Central Prov.: Nagpur, *Haines* 3,609 (K); Assam, 21 mi marker on Ledo road, 27° 20'12"N, 96°2'55"E, *Juan LSC93* (US); Bihar Prov.: Ranka Koelz 18,971 (K, US); Shimoga, Mysore, *Meebold* 10,495 (K); Gwalior St.: *Wisner* 35 (US). KENYA: Esageri Station, Nakuru to Eldama Ravine Road, *Bogdan* AB2,014 (K); 12 mi N of Magadi, *Clayton* DC56 (K); 20 mi E of Isiolo, *Stewart* 474 (K); Nairobi, *Webster* K33 (K). KOREA: in campis Chinampo, *Faurie* 1,244 (BM); Pyengyang, *Smith s.n.*, 5 Sept 1935 (US). LESOTHO: Leribe, *Dieterlen* 6,326 (K). MEXICO: Aguascalientes: 2 mi S of Aguascalientes-Zacatecas line, *Emery* 182 (TEX); Baja California: Magdalena Island, *Brandegee s.n.*, 21 Jan 1889 (UC); 57 km NW of San Ignacio, *Carter, Alexander, and Kellogg* 1,950 (K, UC, US); Chihuahua: 2 mi N of Lucero, *Weber and Charette* 11,604 (UC); Coahuila: W of Puerto de las Monjas, *I.M. Johnston* 8,640 (MO, US); Colima: Alzada, *Hitchcock* 7,054 (US); Distrito Federal: Ixtapalapan, *Matuda* 25,685 (MO); Durango: 3 mi N of Donato Guerra, *Emery* 337 (TEX); Jalisco: Guadalajara, La Barranca, *M.E. Jones s.n.*, 19 Nov 1930 (MO, UC); Guanajuato: Acambaro, *Hitchcock* 6,932 (US); Guerrero: near Iguala, Cañon de la Mano Negra, *Rose* 9,385 (NY, US); Michoacán: 26 mi SE of Sahuayo, *Pratt* 699 (TEX); Morelos: Cuernavaca, *Hitchcock* 6,835 (US); Nayarit: Tepic, Acaponeta, *Rose* 14,248 (NY, US); Oaxaca: Ixtepec, *Fisher* 35,311 (F, MO, NY); Puebla: Tehuacán, *Hitchcock* 6,073 (US); Querétaro: 5 mi from Querétaro, *Pratt* 774 (TEX); San Luis Potosí: 6 mi S of Matehuala, *McGregor et al.* 516 (US); Sinaloa: San Ignacio, *Ortega* 4,468 (US); Sonora: 25 mi W of Angostura, *Santos* 1,831 (F, K); Tamaulipas: near Aldama, *Martinez and Luyando* F-2,177 (TEX); Veracruz: 6 to 7 km N of Tierra Blanca, *Santos* 3,313 (NY); Yucatán: Izamal, *Gaumer* 1,085 (F, MO, NY, US); Zacatecas: 30 mi N of Zacatecas, *Emery* 307 (TEX). MADEIRA ISLANDS: near Funchal, *Sledge s.n.*, 14 Apr 1949 (BM). MALAWI: Zomba, *Cormack* 176 (K); Domasi, between Zomba and Ncheu, *Jackson* 132 (K). MARIANAS ISLANDS: Saipan, Kagman Peninsula, *Fosberg* 31,288 (NY, US). MAURITANIA: Atar Parielle, *Adam* 21,799-1 (K). MOÇAMBIQUE: Prov. Moçambique: Mocuba, Namozoa, *Faulkner* 29 (K); Lourenço Marques Dtr.: near Costa do Sul, *Gomes e Sousa* 3, 438 (K). MONGOLIA: Shabarakh Usu, *Chaney* 407, 537 (NY, UC, US); 110 mi NW of Ila Hiu, *Eriksson* 478 (US). NEPAL: Rohagan, Suli Gad, *Polunin, Sykes and Williams* 3,373, 3,376 (BM). NICARAGUA: road to Granada, *Hitchcock* 8,706 (US). NIGERIA: Bormu, Gudumbali, *Rains s.n.*, Oct 1961 (K). PAPUA: 9 mi NW of Oro Bay, *Reeder* 831 (US). PARAGUAY: chaco boreal, *Rojas* 7,124 (US). PERU: Prov. Apurima: 20 km N of Abancay, *Stork et al.* 10,539 (UC, US); Prov. Lima: Huarochiri, *Weberbauer* 5,287 (F); Prov. Ayacucho: entire Puquio y Nazca, *Ferreya* 5,523 (K, US); Prov. Piura: 1 km W of Talara, *Beetle* 26,197 (F, K, UC, US); Prov. Tumbes: Contramirante Villar, *Ferreya* 12,214 (US). REPUBLIC OF THE CONGO: Kasenye,

Johnston 1,042, 1,084a (K); Katanga, Tumbwe, *Symoens 8,382* (K). SAUDI ARABIA: 80 to 90 km N of Aden, *Wahab 1,904* (US). SENEGAL: without precise location, *Adanson 74* (BM). SEYCHELLES ISLANDS: Long Island, *Squibbs 611* (K). SOCOTRA ISLAND: *Balfour 341* (K). SOMALI REPUBLIC: Ga'ad Forest Reserve, 7 mi W of El Afwein, *Boaler B 130* (K); Erigavo Dtr.: Hubera, *McKinnon S249* (K, US). SOUTHERN RHODESIA: Shangani Dtr.: Gwampa Forest Reserve, *Goldsmith 48,828* (K); Lower Sabi Dtr.: *Rattray 1,230* (K); Miami Dtr.: termite mound, K.34 Experimental Farm, *Wild 1,773* (K). SOUTHWEST AFRICA: Avis Dam, Windhoek, *Liebenberg 4,446* (UC, US); Grootfontein, *Schoenfelder 88 5494* (K). SUDAN: Darfur Prov.: Nyorlete, 12°58'N, 24°4'E, *Blair 11* (K); Wadi Toro, 13°6'N, 23°56'E, *Blair 144* (K); Jebel Mara, Zalingei, *Wickens 1,786* (K); Kassala Prov.: between Berber and Suakin, *Schweinfurth 399, 572* (US). TANZANIA: Tumba, *Bullock 2,415* (US); Mwanza Township, *Carmichael 1,160* (K); Mbulu Dtr.: near Mdala River, Lake Manyara National Park, *Greenway and Kanuri 11, 239* (K); Dar-es-Salaam, *Marshall 50A* (K); Monik Plateau, above Lake Natron, *Newbould 6,206* (K); 7 mi NE of Old Shinyanga, *Welch 62* (K). TIBET: Lhasa, *Richardson s.n.*, autumn 1946 (K). UGANDA: Jinja, *Hitchcock 24,954* (K, US); Karamoja, 16 mi W of Moroto, *Langdale-Brown 1,586* (K). UNION OF SOUTH AFRICA: Sunday River, N of Monkey Ford, *Burchell 2,862* (K); Zoutpansberg, Kruger National Park, *Codd 5,407* (K); 4 mi N of Kroonstad, 27°35'S, 27°5'E, *Scheepers 1,266* (K); 18 mi E of Pietersburg, *van Vieren 1,612* (K). UNITED ARAB REPUBLIC: Jebel Elba, Wadi Kasisrob, *Shabetai 6* (K). UNITED STATES: Alabama: Chambers Co., Langsdale, *Banks 306* (US); Arizona: Chiricahua Mts., Paradise, *Blumer 1,715* (K, MO, NY); Sulphur Spring Valley, *Forbes 1,634, 1,643* (NY, US); Toro Canyon, Baboquivari Mts., *Gilman 9* (NY); Pima Co., Wilmont Road, Tucson, *Ginter s.n.*, 22 Sept 1943 (UC); Santa Cruz Co., Patagonia, *Hitchcock 3,645, 3,664* (US); Ajo, *M.E. Jones 24,795* (MO, NY); California: Fresno Co., along Hwy 180, 5 mi W of Sanger, *Bacigalupi 2,487* (UC); Merced Co., S of Newman, *Mason and Smith 8,223* (UC); Riverside Co., Ford Dry Lake, 24 mi W of Blythe, *Grinnell 1,081a* (UC); Yolo Co., 3 mi N of Davis, along HWY 99 W, *Crampton 3,140* (UC). Colorado: Powers Co., roadside near Holly, *Harrington 740* (UC, US); Hawaii: Oahu, Honolulu, Kaimuki, *A. Chase*

12,677 (US); Kansas: Stevens Co., E of Hugoton, *McGregor 17,016* (KANU); Louisiana: beach, Lake Ponchartrain, *C.A. Brown 2,387* (US); Maine: North Berwick, wool waste, *Parlin 1,516* (US); Maryland: Canton, chrome ore piles, *Reed 32,714* (US); Massachusetts: Millbury, wool waste, *Gates 31,785* (US); Missouri: Courtney, *Bush 9,733* (MO); Nevada: Lincoln Co., between Crystal Springs and Ash Springs, *Train 2,415* (NY); New Mexico: Grant Co., Mangas Canyon, 16 mi WNW of Silver City, *Barkley 14,732* (NY); Sierra Co., Animas Creek, *Metcalf, s.n.* (MO, NY); New York: Yonkers wool mill, *Bicknell, s.n.*, 4 Sept 1898 (NY); North Carolina: Guilford Co., W of Greensboro, *Blomquist 1,962* (F); North Dakota: Norton Co., Mandan, *Stevens 2,649* (UC, US); Oklahoma: Payne Co., Stillwater, *Henson 343* (UC); South Carolina: Myrtle Beach, *Blomquist s.n.*, 22 Aug 1930 (US); Texas: Brewster Co., 9 mi S of Marathon, *Ferris and Duncan 2,841* (MO); Hemphill Co., 5 mi E of Canadian, *Rowell, Jr. 4,266* (TEX); Jeff Davis Co., 8 mi S of Ft. Davis, *W.V. Brown 3,269* (TEX); Utah: 0.5 mi N of south entrance, Zion National Park, *Harrison 11,092* (UC); Whipple Exped., Camp 60, Ft. Smith to Rio Grande, *Bigelow s.n.*, 1853-4 (NY); Wright Exped., western Texas to El Paso, *Wright 762* (MO, NY, US). VENEZUELA: vicinity of Caracas, *Bailey and Bailey 201* (NY, US). ZAMBIA: Zambra, Namuala-Pemb road, *Astle 2,107* (K); Abercorn, *Siame 608* (K), *Trapnell 1,735* (K); Monze, Lochinvar Ranch, *van Rensburg 1,238* (K); 10 mi NE of Serenje, *Vasey-Fitzgerald 2,956* (MO). ZANZIBAR: *Hitchcock 24,460* (US).

24. **CHLORIS GAYANA** Kunth, Rev. Gram. 1:89. 1829, in key; redescribed 2:293, pl. 58. 1830. (Holotype not seen, but Kunth's complete description and plate are of the species as commonly understood.) Fig. 37, 38.

Chloris abyssinica Hochstetter ex Achille Richard, Tentamen Florae Abyssinicae 2:406. 1850. (DUPLICATE OF SYNTYPE: "Sehimperi iter Abyssinicum, sectio tertia, 1800 . . . =nr. 79. Sect. 1, prope Djeladeranne in vallibus. V.i. 1844." BM! K!)

Chloris glabrata Andersson in Peters, Naturwiss. Reise Mossambique Bot. 2:557. 1864. (Holotype not seen, but description clear.)

Chloris gayana ssp. *Chl.* [sic] *oligostachys* Barratte and Murbeck in Murbeck, Acta

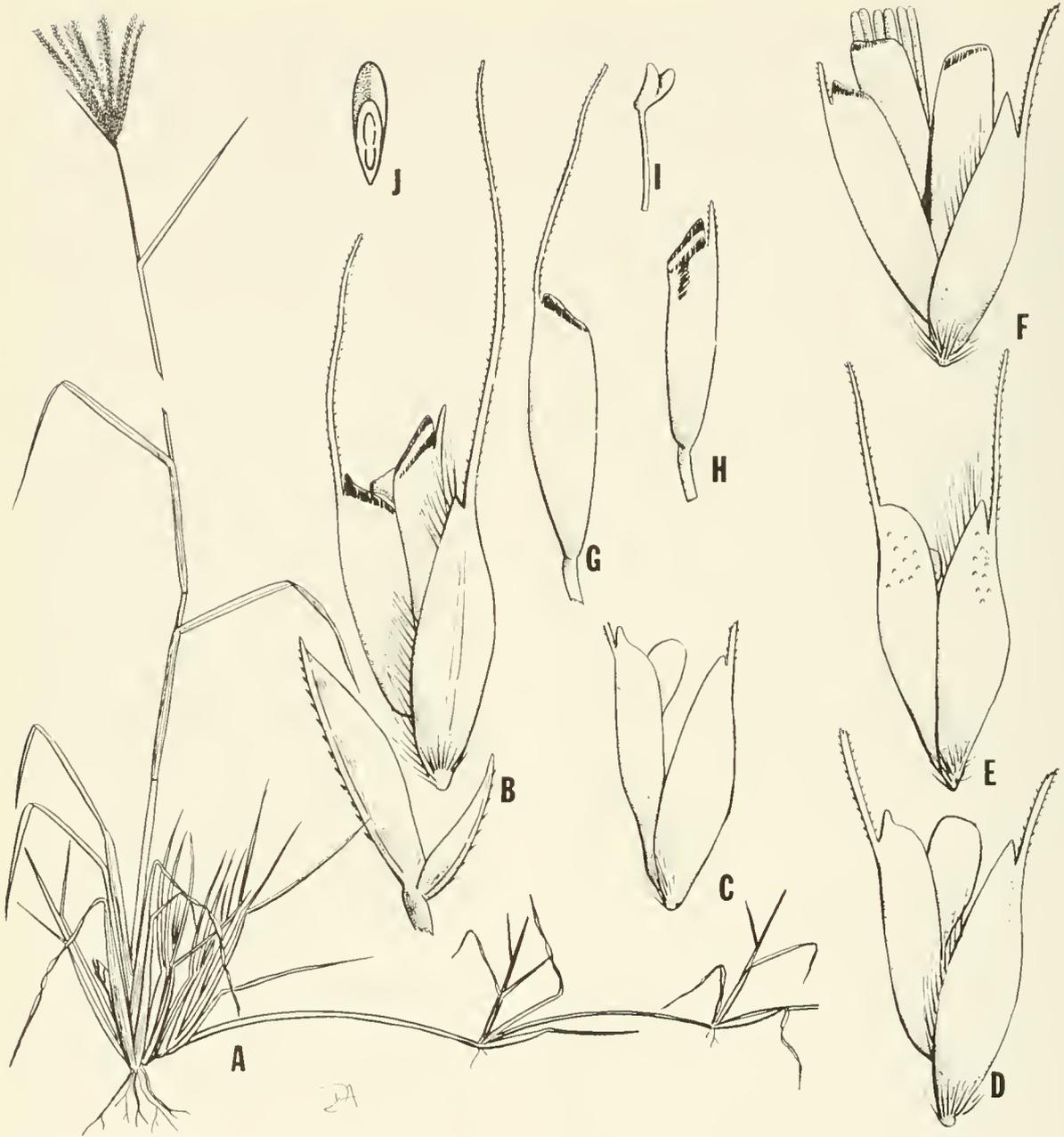


Fig. 37. *Chloris gayana* (A) habit, x 1/6; (B) spikelet, partly dissected; (C-F) florets, showing variation in size and shape of fertile lemma and size, shape, number, and sexual condition of sterile florets; (G) lowermost sterile floret; (H) middle sterile floret; (I) uppermost sterile floret; (J) caryopsis. (B-J) x 10.

Univ. Lund II. Sect. 2. 36:8. pl. 13. 1900. (The authors clearly refer to this as a new subspecies, yet they interjected an abbreviation of the generic name, thereby changing the relative order of taxa. The description and plate are of a variant with small spikelets.)

Eustachys gayana Mundy, Rhodesia Agric. Jour. 14:142. 1922. (Presumably based on

Chloris gayana Kunth, but basionym not cited.)

Chloris gayana f. *oligostachys* (Murbeck) Maire and Weiller, Flore Afrique Nord 2:204. 1953. (Based on *Chloris gayana* ssp. *oligostachys* Murbeck.)

Chloris gayana f. *genuina* Maire and Weiller, Flore Afrique Nord 2:204. 1953. (Based on *Chloris gayana* Kunth.)

Perennial up to 3 m tall, usually stoloniferous, sometimes tufted, erect; sheaths glabrous to scabrous, often ciliate apically; ligule ciliate; blades up to 30 cm long and 1.5 cm broad, scabrous; spikes nine to thirty, 8 to 15 cm long, usually somewhat divaricate; spikelets pale, rather densely imbricate, ca 10 per cm of the scabrous rachis; glumes lanceolate to narrowly ovate, scabrous, especially on the nerves; first glume 1.4 to 2.8 mm long, 0.3 to 0.4 mm wide, acute to awn-tipped; second glume 2.2 to 3.5 mm long, 0.3 to 0.6 mm wide, acute to awn-tipped; fertile lemma 2.5 to 4.2 mm long, 0.7 to 1.0 mm wide, ovate to obovate to elliptic, pubescence variable, margins usually with a prominent tuft of hairs near the apex, occasionally appressed-pilose for full length, internerves usually glabrous, sometimes scabrous or appressed-pilose, lateral nerves usually glabrous, occasionally appressed-pilose, somewhat gibbous, callus bearded, awn 1.5 to 6.5 mm long; sterile florets two to four (rarely one), the lowest 2.2 to 3.2 mm long, 0.5 to 0.8 mm wide, similar to the lemma, but more cylindrical, staminate or barren, awn 0.8 to 3.2 mm long; upper florets awnless or awn-tipped, progressively smaller with the terminal reduced to a turbinate cup; caryopsis 1.0 to 1.5 mm long, 0.5 mm wide, ellipsoidal; chromosome number $2n=20, 30, 40$.

This species is the most variable of the perennial species in the genus. Both stolonifer-

ous and nonstoloniferous plants are found, with the former much more common. Individuals vary greatly in size, though plants less than 0.5 m are uncommon. Spikelet morphology is inconstant. Lemma pubescence varies from glabrous to densely pilose. The number of sterile florets ranges from two (very rarely one) to four, with the lowest "sterile" floret usually staminate, occasionally sterile. The second lowest floret is usually sterile; upper florets are always so. Twenty-one spikelets randomly chosen from one collection (*Wickens 2,715*) showed five different combinations of floret number (two or three) and sexual condition (male or barren).

A number of variants have been named. Of these *Chloris abyssinica* Hochstetter ex Achille Richard has been mostly widely used, though generally not recently. Duplicates of a syntype were examined (BM, MO, K); these did not differ markedly from the variation spectrum exhibited by the remaining specimens that were examined. Stapf (1931) provided a short key to *Chloris abyssinica* and *C. gayana*, separating them on the presence or absence of stolons and the length, sexuality, and number of sterile florets. These characters were studied on a representative number of specimens collected throughout Africa, but neither discontinuities in measurements nor major patterns could be distinguished.

There is a possibility of a very casual cor-



Fig. 38. Distribution of *Chloris gayana*. Inset A: Hawaiian Islands.

relation with ecological conditions, for tufted plants were frequently, but not always, collected from salt pans.

Representative specimens examined: (A total of over 800 different specimens of this species were studied. The following list represents only a small portion of this group.) AN-GOLA: Huila Dtr.: Namaculungo, *Teixera 1,407* (BM). ARGENTINA: Prov. Córdoba: Cruz del Eje, *Villafarie 2,413* (US); Prov. Corrientes: Dep. Lavalle, Estancia "La Pastrol" *Pedersen 3,864* (NY, UC, US); Prov. Salta: Metán, *Cabrera 3,089* (NY); Prov. Tucuman: Trancas, *Venturi 6,480* (US). AUSTRALIA: New South Wales: Kenebri, 11 mi N of Baradine, *Constable 15,978* (UC); Northern Territory: near Darwin, *Allen 67* (K); Queensland: Conjuboy, *Blake and Lazarides s.n.*, 26 Feb 1954 (US); Kenmore, *Clemens s.n.*, 18 May 1943 (US); Western Australia: Latham, *Moore K197* (K). BOTSWANA: Koudoum Valley, 30 km E of Southwest Africa border, *Wild and Drummond 7,056* (BM). BRAZIL: Minas Geraes: Lavras, A. Chase *8,827* (F, MO, NY, US); Rio Grande do Sul: Morro Santa Ana, *Rambo 41,982* (US). COLOMBIA: Pasto, Medellín, *Rivera 131* (K); vicinity of Medellín, *Toro 299* (NY, US). COSTA RICA: Turrialba, Leon *286* (MO). CUBA: Prov. Herradura: Pinar del Río, *Ekman 14,108* (NY). EASTER ISLAND: Mataverí, waste land, *Chaplin 1,041* (NY). ECUADOR: Prov. Guayas: Milagro, *Acosta-Solis 70,693* (US); Prov. Pichincha: Valle del Guailabamba River, *Acosta-Solis 21,259* (US), *Asplund 7,036* (K). ETHIOPIA: Oeule Casai, *Pappi 2,081* (MO, NY, UC); 10 mi N of Assale, *Semple 2* (US); Metahara, *Semple 10* (US). GUATEMALA: near Chimaltenango, *Standley 80,483* (F, K). HAITI: plaine du Nord, *Ekman H.9,890* (K, US). HONDURAS: Dep. Morazán: Zamorano, *Rodriguez 103* (F), *3,217* (F, MO, US); *Standley 1,767a*, *13,035*, *21,041* (F), *18,979* (F, NY, US); *Williams and Molina 12,216* (F). INDIA: Mysore, Bangalore, *Koeltz 19,898* (UC); Salem Dtr.: Hosen Cattle Station, *Narayanawami 3,028* (K). JAMAICA: St. Andrew Parish, Richmond Park, *Harris 12,707* (F, K, MO, NY). KENYA: Kiboko, *Bogdan AB 2,239* (UC); Longonot, *Hitchcock 24,828* (K, US); Nakuru, *Hitchcock 25,075*, *25,082* (K, US); between Oljoro-o-Nyon River and Lake Naivasha, *Mearns 636* (US); between Narok River and Lake Naivasha, *Mearns 628* (NY, US). LORD HOWE ISLAND: *Bingley 25* (K, UC). MALI: El Oualadji, *Chevalier 43,927* (K); Tombouctou, *Olafsen 205* (US). MALAWI: Southern Nyasa Dtr.: Dambo, Namwera Road, *Ballard C.b.7* (K); Chikwawa Dtr.: *Brass 17,996* (MO, NY, US); Kasita River near Ekwendeni, *Jackson 366* (K); Port Herald Dtr.: *Phipps 2,606* (MO). MAURITIUS: Curepipe, *Vaughan 1,844* (K). MEXICO: Morelos: Cuernavaca, *Lyonnet 2,807* (US). MOÇAMBIQUE: Nyassa Dtr.: Amaramba, 22 km de Nova Freixo, *Torre and Paiva 10,624* (K). NEW ZEALAND: near Tauranga, *Hodgkins 70,536* (US). NIGERIA: Prov. Bornu: Lake Chad, *Daggash 24,970* (K); Ngala Dtr.: Wulgo, *Davey 2* (K); Rann Dtr., *Davey s.n.*, 17 Apr 1947 (K); River Kalkala, SW corner of Lake Chad, *Golding 76* (K). REPUBLIC OF THE CONGO: Kasenye, *Johnston 1,057* (US); Albertville, *Linder s.n.*, 23 Jan 1927 (K). RWANDA: Parc National Kagera, *Lebrun 9,482* (K); Biumba, Mutara, colline Nyaka Kanga, *Troupin 8,813* (K). SIKKIM: Gangtok, *Dr. Bor's collector s.n.*, 15 Jul 1945 (K). SOMALI REPUBLIC: *Farquaharson s.n.*, Sept 1931 (K). SOUTHERN RHODESIA: Katasi Reserve, Bikita, *Cleghorn 177* (BM). SOUTHWEST AFRICA: Omuramba Khaudum, ca 18½°S, 20½°E, *de Winter and Marais 4,667* (K); Okavango, at Bagani pontoon, Kaprivi, *de Winter and Wiss 4345* (K). SUDAN: Zalingei, *Robertson 10* (BM); Dafur Prov.: Nyertiti, *Robertson 22* (BM); Jebel Marra, Dariba Crater, *Robertson 140* (BM, K); Equatoria Prov.: Nimule, *Shantz 907* (US). SYRIA: Ali al Gharbi, *Graham 360* (BM). TANZANIA: Mbeye Dtr.: Rujewa, *Anderson 1,117* (K); Musoma, *Emson 232* (US); Ngari Rongi plain, western slopes of Mt. Kilimanjaro, *Greenway 6,741* (K); Arusha Region, Ol Doingo Sambu, *Greenway 4,413* (K); Moshi Dtr.: Sanya River, *Haarer 1,097* (K); Rukwa, *Lea LRS* (K); Banagi, Serengeti National Park, *Leippert S603* (K); 45-65 mi S of Dodoma, *Lynes 76a* (US); Selous Game Reserve, *Nicholson 48* (K); Ngorongoro Crater, *Paulo 317* (K), *Piemiesel and Kephart 506* (US); Kilwa, Rifiji, *Schlieben 2,541* (K); Lindi Dtr.: Lutamba, *Schlieben 5,880* (K); Monduli, near Arusha, *Semple s.n.*, May 1945 (US); Olduvai, *Williams 681* (K). THAILAND: Hua Hin, *Jones s.n.*, June 1931 (BM). TONGA-TAPU ISLAND GROUP: 'Eua, Houma, *Setchell and Parks 15,431* (UC, US). UNITED STATES: Arizona: Yuma Valley, *Fochtman 70* (NY); California: Merced Co., N of Los Banos, *Mason and Smith 8,226* (UC); Florida: Hernando Co., Brooksville, *McFarlin 6,072* (US); Hawaii: Kiholo, A. Chase *12,688* (US); Mississippi: Lumberton, *Beal s.n.*, 10 Jun 1920 (US); Texas: Port Lavaca, *Allen 17* (US); Kleberg Co., 5.5 mi S of Kingsville, *Cory 51,303* (NY, UC); Hidalgo Co., 0.5 mi N of Edinburg, *Ferris and Duncan 3,064* (MO, NY, US); Rock-

port, *Fisher 41,145* (US); Kleberg Co., King Ranch, *Lundell 14,877* (US); Cameron Co., Port Isabel Road, *Runyon 4,138* (MO, NY). UGANDA: Old Entebbe, *Darker 257* (UC); Luzinga, *Dummer 4,351* (US); Mbulamuti, *Hitchcock 24,975* (US); Tororo, Swamp, *Hitchcock 24,980* (US); vicinity of Kabula Muliro, *Mearns 2,532* (US); Mbale, near Mt. Elgon, *Snowden 1,098* (US); S of Namasagali to Kamuli Road, Bugabula City, *Wood 948* (MO). UNION OF SOUTH AFRICA: between Sellen-dam and Riversdale, *Godfrey SH 1,312* (UC, US); near Pietermaritzburg, thornveld, *Godfrey SH 1,912* (US); Mposa, *Godfrey and Bayer SH 1,463* (US). URUGUAY: Dep. Montevideo: *Osten 19,923* (US). VENEZUELA: Mérida, La Mesa, *Haubury-Tracy 16* (K). ZAMBIA: Mweru Wantipa swamp, 8°50'S x 29°40'E, *Tyrer 206* (BM).

25. **CHLORIS CASTILLONIANA** Lillo and Parodi ex Parodi, *Physis* 4:176. 1918. (TYPE: not seen. Originally collected by Castillon in the Calchaqui Valley, Argentina. The original description and accompanying illustration positively identify the plant.) Fig. 33, A-D.

Caespitose perennial up to 1 m tall; sheaths glabrous; ligule short-ciliate; blades 10-20 cm long, 4 to 5 mm wide, glabrous; spikes eight to fifteen, 9 to 11 cm long, appressed to strongly ascending; spikelets densely imbricate, appressed, about eight per cm of the scabrous rachis; glumes lanceolate, thin, membranous, glabrous except for the scabrous midnerve; first glume 1.6 to 2.0 mm long, 0.3 to 0.4 mm wide; second glume 2.9 to 3.9 mm long, 0.4 to 0.6 mm wide, sometimes delicately mucronate; fertile lemma 3.5 to 4.7 mm long, 1.0 to 1.3 mm wide, lanceolate-elliptic, rather prominently gibbous, callus flattened and elongate, densely bearded, lemma margins densely ciliate with hairs 1 to 2 mm long, keel glabrous, occasionally an appressed-pilose groove present along the lemma side, awn 2.2 to 2.5 mm long, arising from well below the acute apex; sterile floret one, 1.5 to 2.0 mm long, ca 0.4 mm wide, glabrous, narrowly obovoid, the apex somewhat truncate, awn arising subapically, curving upward, awn 1 to 2 mm long; earyopsis ca 2 mm long, 0.5 mm wide, ellipsoidal, somewhat trigonous.

Chloris castilloniana is most closely related to *C. virgata*, from which it may be separated by its perennial habit as well as in having prominent cilia along most of the lemma margin (Fig.

33, A-D; 35). *Chloris virgata* is an annual with the cilia restricted to the upper portion of the lemma margin.

The few specimens that have been collected are from sandy savannas in Argentina (Fig. 39, triangles).

Specimens examined: ARGENTINA: Formosa Territory: orillos del arroyo Ferreyra, *Asp 20* (US); Las Lomita, *Parodi 8,455* (NY, US); Prov. Catamarca: Mollecito, 20 km S of Andalgalá, *Bartlett 20,239* (US); Dep. Belen, Las Faldas, *Lillo 45,625* (NY, US); Prov. La Rioja: Patquia, *Lahitte y Castro 3* (US).

26. **CHLORIS ORTHONOTON** Doell in Martius, *Flora Brasiliensis* 23:64. 1878. (ISOTYPES: "Glaziou n. 3610" BR! K! US!) Fig. 39; 40, A-E.

Chloris guaranitica Parodi, *Revista Argentina Agron.* 28:106. Fig. 2. 1961. (ISOTYPE: Argentina: Corrientes, Dep. Mburucuya, Estancia Santa Maria . . . Pederson no. 3742." K!)

Stoloniferous, erect perennial to 70 cm tall; sheaths glabrous, occasionally pilose near the ligule; ligule prominently pilose; blades 0.5 to



Fig. 39. Distribution of *Chloris orthonoton* (dots) and *C. castilloniana* (triangles).

0.7 mm wide, up to 25 cm long, pilose near the base, otherwise glabrous to scabrous; spikes four to eleven, 4 to 10 cm long, in several verticils near the culm apex; spikelets eight to ten per cm of the scabrous rachis, densely imbricate, appressed; glumes lanceolate, acuminate, glabrous except for the scabrous midnerve; first glume 1.6 to 2.4 mm long, 0.2 to 0.3 mm wide; second glume 2.3 to 3.6 mm long, 0.3 to 0.5 mm wide; fertile lemma 3.0 to 4.5 mm long, 0.7 to 1.6 mm wide, narrowly lanceolate to elliptic, margins long-ciliate, especially near the apex, keel glabrous to appressed-pubescent, internerves with a longitudinal groove bearing one or more rows of dark glandular hairs, callus bearded, awn 7.5 to 20.0 cm long; sterile floret one, 1.5 to 2.2 mm long, 0.3 to 0.5 mm wide, cylindrical-turbinate, glabrous, awn 3.5 to 9.0 mm long; anthers ca 0.4 mm long; caryopsis ca 1.7 mm long, 0.4 mm wide, narrowly ellipsoid, trigonous.

Chloris orthonoton is closely related to *C. aristata*. Table 9 and Fig. 40 show the main differences between the two.

Occasional specimens of *Chloris orthonoton* may resemble *C. virgata*. The latter, however, is a fibrous-rooted annual, lacks glandular hairs in the lateral groove of the lemma, and has a prominent tuft of cilia only along the upper portion of the lemma margin.

A variant of this species, lacking pubescence on the midnerves of the lemmas and having somewhat coarser spikes, has been named *Chloris guaranitica* Parodi (1961). In all other respects the plant is identical with typical *C. orthonoton*, and I do not feel it worthy of nomenclatural recognition.

Representative specimens examined: ASCENSIÓN ISLAND: roadside near airfield, *Duffey 1/83* (US). ARGENTINA: Prov. Corrientes: Dep. Mburucuya, *Parodi 3,742* (BR). BRAZIL: Prov. Bahia: Bahia, *A. Chase 7,871, 8,033, 8,051* (US); Feira de Santana, *A. Chase 8,060* (US); Prov. Ceara: Acude, Municipio de Maranguape, *Drouet 2,180* (F, US); Camocim to Granja, *Swallen 4,634* (US); Martinopolis,

Swallen 4,641 (US); Minas Geraes: Lavras, *Black 887B* (US); Juiz de Fora, *A. Chase 8,625* (US); São Miguel, NW of Formiga, *A. Chase 10,544* (US); between Sueupira and Omega, *A. Chase 11,162* (US); Paraíba: Soledade, *Cesan 692* (US), *Pickel 3,827* (US); Pernambuco: Bello Jardim, *A. Chase 7,700* (F, US); vicinity of Recife, *A. Chase 7,720* (F, NY, US); Tapera, *Pickel 81* (F); Rio de Janeiro, NW of Cabo Frio, *A. Chase 10,122* (US); Niteroi, *A. Chase 10,037* (US); Rio Grande do Norte: Estremoz to Natal, *Swallen 4,773* (US); Nova Cruz to Montanhas, *Swallen 4,822* (US); Santa Cruz, *Swallen 4,861* (US); Rio de Janeiro, *Glaziou 17,363*, 1888 (NY, US).

27. **CHLORIS ARISTATA** (Cervantes) Swallen, North Amer. Flora 17:596. 1939. (Based on *Agrostomia aristata* Cervantes.) Fig. 40, F-J.

Agrostomia aristata Cervantes, Naturaleza (Mexico City) 1:345. 1870. (TYPE: "San Angel. San Agustin de las Cuevas." Not seen, but description is clear.)

Stoloniferous perennial with erect culms to 80 cm tall; sheaths glabrous; ligule a short-ciliate crown; blades up to 15 cm long, 5 mm wide, usually glabrous or scabrous, occasionally the upper surface pilose; spikes four to eight, 4.0 to 8.5 cm long, erect, somewhat appressed, radiate; spikelets appressed, densely imbricate, ca five to eleven per cm of scabrous rachis; glumes narrowly lanceolate, glabrous except for the scabrous midnerve; first glume 1.8 to 2.3 mm long, 0.2 to 0.4 mm wide; second glume 3.0 to 4.1 mm long, 0.2 to 0.5 mm wide; fertile lemma 3.4 to 4.5 mm long, 0.8 to 1.0 mm wide, lanceolate to elliptic, apex acute, margins appressed-pilose below, the hairs slightly spreading above, keel usually glabrous, occasionally with a few appressed hairs, midnerves glabrous, callus bearded, awn 6.0 to 12.0 mm long; sterile floret one, 1.6 to 2.4 mm long, 0.6 to 0.7 mm wide, awn 5 to 7 mm long; caryopsis 1.5 to 1.9 mm

Table 9. Comparison of characteristics of *Chloris orthonoton* and *C. aristata*.

Species	Ligule	Lemma margin pubescence	Lemma internerves
<i>C. orthonoton</i>	long-ciliate (ca 2 mm long)	cilia more than 1.5 mm long; appressed basally, becoming spreading apically	lateral groove glandular-pubescent; otherwise glabrous
<i>C. aristata</i>	short-ciliate (less than 1 mm long)	cilia less than 1 mm long; appressed most of length or only slightly spreading apically	lateral groove and internerves glabrous, occasionally appressed-pubescent, but not glandular



Fig. 40. *Chloris orthoton* and *C. aristata*. (A-E) *C. orthoton*. (A) habit, x 1/4; (B) spikelet, x 5; (C) florets, x 5; (D) sterile floret, x 5; (E) caryopsis, x 7.5. (F-J) *C. aristata*. (F) habit, x 1/4; (G) spikelet, x 5; (H) florets, x 5; (I) sterile floret, x 5; (J) caryopsis, x 7.5.

long, ca 0.5 mm wide, ellipsoid, trigonous; chromosome number $2n=100$.

Differences between *Chloris aristata* and *C. orthoton* have been discussed previously.

This species has occasionally been called *Chloris rufescens* Lagasca, a name which cannot be typified and the original description of which is not complete enough for positive iden-

tification. Accordingly, this name is rejected (see under excluded names.)

Chloris aristata has been widely collected from prairies and grasslands throughout much of Central America (Fig. 41).

Representative specimens examined: COSTA RICA: cerca de San Ramón, Brenes s.n., 3 Jan 1935 (F); San José, Cooper 5,997, Hitch-



Fig. 41. Distribution of *Chloris aristata*.

cock 8,469 (US), Valerio 104 (F, K); San Rafael de Cartago, Pittier 7,109 (US); between San Pedro de Montes de Oca and Curridibát, Standley 32,817 (US). GUATEMALA: mountains E of Quiché, Grant 640 (US); Guatemala City, Hitchcock 9,039 (US); La Aurora, Ruana 699 (US); Dep. Alta Verapaz, near San Juan Chamelco, Standley 92,435 (US); 3 km S of Huehuetenango, Williams et al. 22,109 (F, US). HAITI: W of Palmiste, Leonard and Leonard 12,538 (NY). HONDURAS: Dep. Choluteca: vicinity of San Marcos de Colon, Standley 15,765 (F); Dep. Morazan: vicinity of El Zamorano, Standley 1,501, 26,327 (F); Swallen 10,832 (US). MEXICO: Aguascalientes, Hitchcock 7,454 (US); Chiapas: Monserrate, Purpus 388 (F); Coahuila: Parras de la Fuentes, Palmer 450 (F, MO, NY); Saltillo, Hitchcock 5,620 (US); Durango: Durango, Hitchcock 7,657 (US); Guanajuato: 2.5 km N of San Francisco del Rincón, Sohns 355 (US); Irapuato, Hitchcock 7,412 (US); Acámbaro, Hitchcock 6,927 (US); Hidalgo: Jacala, V. H. Chase 7,098 (US); La Placita, 10 mi S of Jacala, Gould 10,389 (US); Jalisco: 15.5 mi E of Guadalajara, Leavenworth 1,852 (US); San Nicolás, Hitchcock 7,193 (US); Michoacán: vicinity of Morelia, Arsenè 3,134 (MO, NY, US); Uruapan, Hitchcock 6,965 (US); Nuevo León, Monterrey, Hitchcock 1,263 (MO, NY); Galeana, V. H. Chase 7,738 (US); Oaxaca: Cuicatlan, San Juan Bautista, Conzatti 4,024.5 (US); Cd. Oaxaca, Hitchcock 6,110, 6,129, 6,170 (US); Puebla: Tehuacan, Hitchcock 6,033 (US); Querétaro: Querétaro, Hitchcock 5,804 (US); San Luis Potosí: Cárdenas, Hitchcock 5,749 (US); Venado, Whiting 624, 711 (US); Veracruz: Jalapa, Hitchcock 6,692 (US); Orizaba, Hitchcock 6,336 (US).

28. **CHLORIS BRANDEGEI** (Vasey) Swallen, Amer. Jour. Bot. 22:41. 1935. (Based on

Diplachne brandegei Vasey ex Brandege.) Fig. 42.

Diplachne brandegei Vasey ex Brandege, Proc. California Acad. Sci. II, 2:213. 1889. (HOLOTYPE: "Magdalena Island. T. S. Brandege 18 January 1889." US!)

Leptochloa brandegei (Vasey ex Brandege) Hitchcock, U.S. Dept. Agric. Bur. Plant Industry Bull. 33:21. 1903. (Based on *Diplachne brandegei* Vasey ex Brandege.)

Gouinia brandegei (Vasey ex Brandege) Hitchcock, U.S. Dept. Agric. Bur. Plant Industry Bull. 33:21. 1903. (Based on *Diplachne brandegei* Vasey ex Brandege.)

Perennial to 1 m tall, densely tufted from a coarse, fibrous root system; lower sheaths floccose, becoming glabrous above; ligules pilose, the lower more so than the upper; blades scabrous; inflorescence with up to 20 spikes arranged in a series of somewhat distant subverticils, occasionally the spikes single at a node; spikes 5 to 10 cm long; spikelets distant, ca three or four per cm of the spike length, strongly appressed; glumes markedly unequal, narrowly lanceolate, thin, hyaline, glabrous except for the slightly scabrous midnerve; first glume 1.5 to 1.8 mm long, ca 0.3 mm wide; second glume 3.3 to 4.0 mm long, ca 0.5 mm wide; fertile lemma 4.7 to 5.5 mm long, 0.5 to 0.8 mm wide, strongly dorsally compressed, narrowly elliptic to linear in side view, more broadly elliptic in face view, apex acute to shortly acuminate, margins, keels, and internerves scabrous to hirsute, callus bearded, awn 1.0 to 4.5 mm long; sterile floret one, ca 1.5 mm long, 0.3 mm wide, very narrowly cylindrical to ellipsoid, scabrous to sparsely appressed-pilose, awn 0.7 to 1.9 mm long; caryopsis 2.5 to 3.0 mm long, ca 0.7 mm wide, ca 0.3 mm thick, strongly dorsally compressed, ellipsoid, slightly trigonous.

Chloris brandegei is similar to and probably closely related to *C. chloridea*, though distinguished from it by very short awns on the lemmas and a lack of underground spikelets.

Chloris brandegei is endemic to Baja California Sur, Mexico (Fig. 43, triangles), where it grows on rocky slopes and in arroyos.

Specimens examined: MEXICO: Baja California Sur: La Purísima, Brandege L91 (US); San José del Cabo, Brandege s.n., 6 Oct 1890 (NY); Sierra de la Giganta, 25°58'N, 111°32½'W, on road from Loreto to San Javier, Carter 5,014 (UC); Cerro Teombo, 25°51'N, 111°25'W, N of Fortezuelo de Gabilan, 1100 m,



Fig. 42. *Chloris brandegei* (A) habit, x 1/4; (B,C,E) spikelet, partly dissected; (D,F,G) florets, showing variation; (H) caryopsis. (B-H) x 5.



Fig. 43. Distribution of *Chloris brandegei* (triangles) and *Chloris submutica* (dots).

Carter 5,064 (UC); 37 km SE of San Ignacio, among lava rocks in gravelly arroyo, *Carter et al. 1,977* (UC, US); Sierra de la Giganta, Arroyo del Cajon de Tecomaja, SW of Puerto Escondido, 25°43'N, 111°20'W, *Carter and Kellogg 2,897* (UC, US); El Triunfo, *M. E. Jones 27,658* (UC); Carmen Island, *Palmer 8,621*, 1 to 7 Nov 1920 (US); Punta San Lorenzo, ca 25 mi E of La Paz, *Wiggins 15,638* (UC).

29. **CHLORIS CHLORIDEA** (Presl) Hitchcock, Proc. Biol. Soc. Washington 41:162. 1928. (Based on *Dineba chloridea* Presl.) Fig. 44.

Dineba chloridea Presl, Rel. Haenke 1:291. 1830. (TYPE: Not seen, but there is a fragment in US!, from Haenke Herbarium, PR, labeled: "Mexico . . . Presl." This and the description clearly identify the name.)

Eutriana chloridea (Presl) Kunth, Rev. Gram. Supplenda, p. 23. 1834. (Based on *Dineba chloridea* Presl.)

Gymnopogon virletii Fournier, Mex. Pl. 2:144. 1886. First published as *nomen nudem* in Hemsley, Biol. Centr. Amer. Bot. 3:560. 1855. (TYPE: "San Luis de Potosí. Virlet n. 1441." There is a fragment in US!, from P, labeled "Mexique. Prov. de San Luis . . . Virlet d'Aoust 1851," which is *C. chloridea*.)

Gymnopogon longifolius Fournier, Mex. Pl. 2:144. 1886. (FRAGMENT OF TYPE: US!, originally from P, labeled ". . . Mexique prov. Vera Cruz. Gouin. 1867. 52.")

Chloris longifolia (Fournier) Vasey, Contr. U.S. Nat. Herb. 1:284. pl. 19. 1893. *Non Steudel*, 1854. (Based on *Gymnopogon longifolia* Fournier.)

Chloris clandestina Scribner and Merrill, U.S. Dept. Agric. Div. Agrost. Bull. 24:25. 1901. (Based on *Gymnopogon longifolius* Fournier.)

Perennial to 1 m tall, tufted, erect, bearing cleistogamous spikelets at the tips of long, scaly, branched rhizomes; each cleistogamous spikelet consists of a series of three to five overlapping bracts enclosing a saclike structure, which in turn encloses a pistil and three stamens; mature cleistogamous fruit broadly ovoid-ellipsoid, up to 4 mm long and 2.5 mm wide, brown; sheaths mostly glabrous, occasionally becoming sparsely long-pilose near the ligule; lower ligules with a prominent tuft of hairs, upper ligules often reduced to a low crown; blades up to 30 cm long and 1 cm wide, scabrous, occasionally pilose, innovations often sparsely pilose; spikes three to fifteen (usually less than 10), usually 6 to 10 cm long, in several well-separated verticils, occasionally borne singly at a node; spikelets rather distant, ca four per cm of the scabrous rachis, appressed except for the divergent awns; glumes markedly unequal, glabrous except for the scabrous midnerve; first glume 1 to 2 mm long, ca 0.4 mm wide, lanceolate; second glume 2.0 to 3.5 mm long, ca 0.3 mm wide, narrowly lanceolate; fertile lemma 4.5 to 7.5 mm long, ca 1 mm wide, ca 0.5 mm thick, dorsally compressed, linear to narrowly lanceolate in side view, lanceolate in top view, apex acuminate, callus densely bearded, margin ciliate, lemma otherwise glabrous, awn 6.5 to 15.0 mm long, often arising from between two setae; sterile floret one, 1.4 to 3.0 mm long, less than 0.3 mm wide, often somewhat flattened, scabrous to short-pilose, awn 2 to 8 mm long; caryopsis ca 4.5 mm long, 0.8 mm wide, somewhat flattened, long-acuminate; chromosome number $2n = 40, 80$.

The underground cleistogamous spikelets of *Chloris chloridea* make it one of the most unusual grasses. These spikelets are borne on a rather intricately branched rhizome system (Fig. 44, A), the branches of which are brittle and often are not collected. The cleistogamous spikelets on the specimens studied set a high proportion of seed, while most of the above ground spikelets were sterile. Whether this is due to the immaturity of the specimens examined, environmental factors, or is an indication of a more complicated reproductive pattern, must await further field studies.

Chloris chloridea is quite variable in spikelet size, and some plants may approach *C. brandegei* in lemma length, but *C. chloridea* will al-

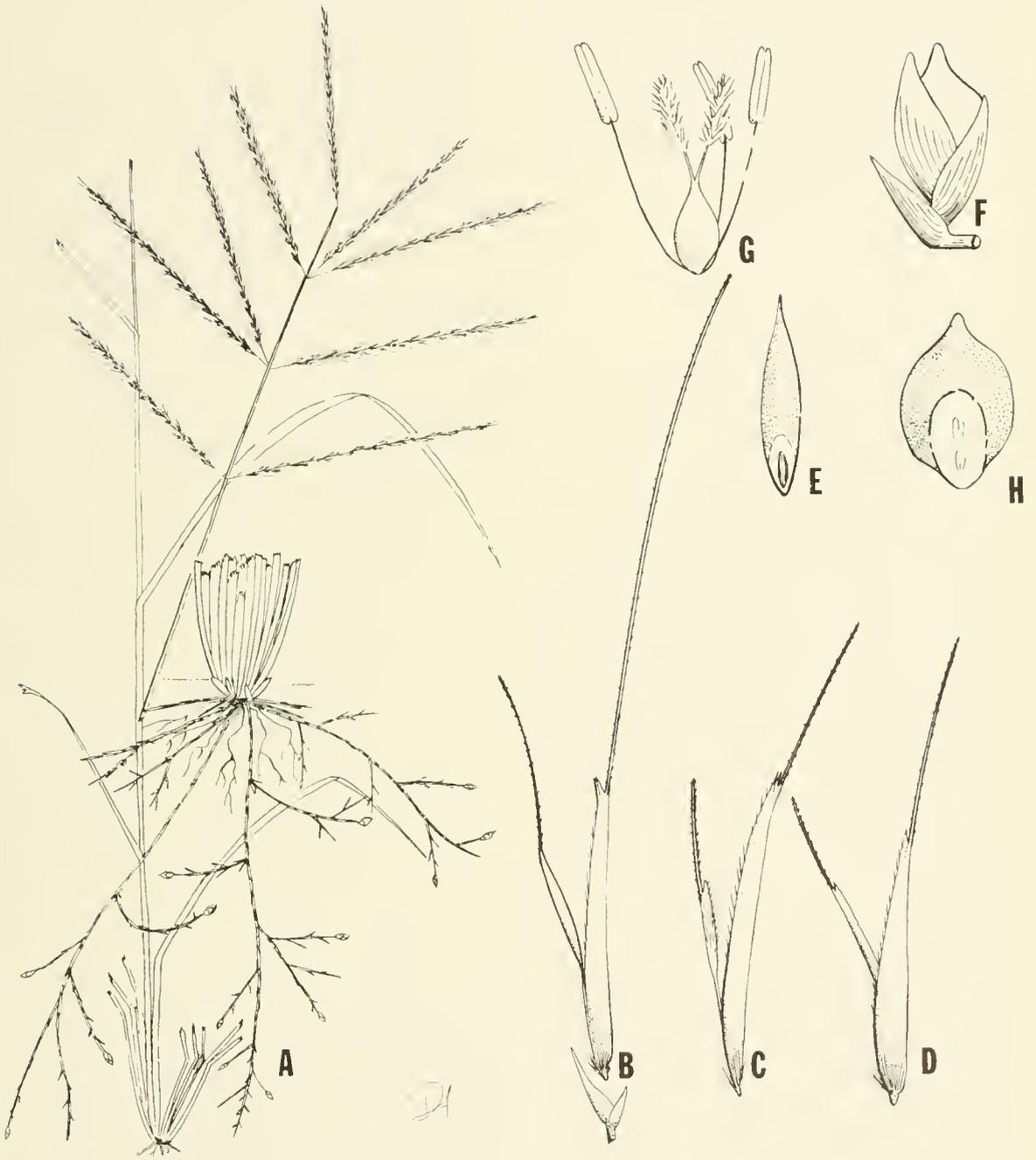


Fig. 44. *Chloris chloridea*. (A) habit, x 1/3; (B) spikelet, partly dissected, x 7.5; (C,D) florets, showing variation, x 7.5; (E) caryopsis from aboveground spikelet, x 5; (F) underground spikelet, x 5; (G) flower of underground spikelet, x 15; (H) caryopsis from underground spikelet, x 5.

ways have relatively long awns and, of course, the underground spikelets.

This species is widely distributed in the southwestern United States, Mexico, Honduras, and Venezuela and has been collected in grasslands, brushy areas, and old fields (Fig. 45).



Fig. 45. Distribution of *Chloris chloridea*.

Representative specimens examined: HONDURAS: Dep. Morazan: El Zamorano, *Rodriguez* 3,516 (F, US), *Standley* 13,076 (F, NY, US), 14,454 (F), 14,896 (F, UC, US), 16,073 (F), 3,936 (US), *Swallen* 11,156 (US). MEXICO: Baja California Sur: El Triunfo, *M. E. Jones* s.n., 6 Oct 1930 (US); Guanajuato: 6 km S of León, *Solms* 384 (MO, US); Jalisco: Tuxpan, *Mexia* 1,046 (F, MO, UC, US); Michoacán: Monte León, *Pringle* 3,994 (US); Morelos: near Cuernavaca, *Pringle* s.n., 23 Oct 1902 (F, NY); Nuevo León: Colonia del Valle, Monterrey, *F. F. Smith* M267 (TEX); Oaxaca: Tomellin, *Hitchcock* 6,226 (US); San Luis Potosí: Las Canoas, *Hitchcock* 5,766 (US); Sinaloa: Topolobampo, *Palmer* 238, Sept 1897 (K, US); Sonora: Hermosillo, *Hitchcock* 3,572 (US); Tamaulipas: 3 mi N of Santo la Marina on road to Jiménez, *Crutchfield* and *Johnston* 4,972 (TEX); Veracruz: 5 mi E of San Luis Potosí border, *M. C. Johnston* 6,106 (TEX, UC, US). UNITED STATES: Arizona: Pima Co., W of Topawa, *Goodling* 194-45 (NY, US); Texas: Cameron Co., Laguna Atascosa Refuge, *Fleetwood* 3,857 through 3,859, 3,861 (TEX); Brownsville Municipal Airport, *Runyon* 2,928 (US); Brownsville, *Silveus* 379 (K, US, TEX); 1 mi N of Combes, *Silveus* 1,583, 1,586 (MO); 0.5 mi N of Conches, *Silveus* 6,781 (TEX); 5 mi S of San Benito, *Silveus* 7,432 (TEX); Kleberg Co., Kingsville, *Diaz* 1,951 (US); 4 mi S of Kingsville, *Meyer* s.n., 24 Oct 1958 (US); Nueces Co., ca 5 mi S of Banquete, *M. C. Johnston* 542,273 (TEX); San Patricio Co., Odem, *Silveus* 2,408 (TEX). VENEZUELA: Estado Lara, La Rucza, cerca de Barquisimeto, *Tamayo* 4,230 (US).

30. **CHLORIS VENTRICOSA** Robert Brown, Prodr. Flora Nov. Holl. 186. 1810. (HOLOTYPE: "1. *Chloris ventricosa* Richmond" BM!) Fig. 46.

Chloris sclerantha Lindley in Mitchell, Jour. Exped. Interior Australia 31. 1848. (TYPE: "New South Wales; near Muddal banks of Bogan River, Mitchell" CGE. Not seen. Fragment of type at K!)

Chloris ventricosa var. *tenuis* Bentham, Flora Australiensis 7:613. 1878. (SYNTYPE: "Rockhampton, O'Shanesy. Herb. F. Mueller 1879 [?]" K!)

Perennial to 1 m tall, stoloniferous, erect; sheaths glabrous, scabrous or sparsely pilose; ligule area scabrous to prominently pilose; blades glabrous, scabrous, or sparsely pilose; spikes two to nine, 5 to 11 cm long; spikelets densely imbricate, averaging 10 per cm of the scabrous rachis; glumes scarious, narrowly lanceolate to ovate, acute to acuminate, glabrous except for the scabrous midnerves; first glume 1.2 to 2.3 mm long, ca 0.5 mm wide; second glume 2.5 to 4.1 mm long, ca 0.8 mm wide; fertile lemma 2.0 to 5.4 mm long, 0.6 to 1.2 mm wide, elliptic to obovate, sometimes ventricose, acute to obtuse, usually glabrous except for the scabrous midnerve, occasionally scabrous on the internerves and with a few scattered, appressed hairs along the scabrous inrolled margin, especially near the apex, callus bearded, awn 1 to 11 mm long; sterile floret one (very rarely two), 1.0 to 2.6 mm long, 0.3 to 1.0 mm wide, cylindric to narrowly turbinate, apex obtuse to truncate, awn 0.5 to 7.5 mm long; anthers 0.7 to 1.4 mm long; caryopsis 1.5 to 2.1 mm long, ca 0.4 mm wide, narrowly obovoid, \pm trigonous.

This species is quite variable, mostly with respect to the height and apparent vigor of the plant, the size of spikelet parts, and the shape of the sterile florets. Attempts at correlating various features of about 75 specimens were made, but no conspicuous patterns could be detected. This corroborates an earlier study by Everist (1935b), in which he found many intermediate plants between various extremes. Certain of these have received names. *Chloris ventricosa* var. *tenuis* Bentham is based on a small plant with relatively small spikelets, while a somewhat larger variant was called *C. sclerantha* Lindley.

Chloris ventricosa and *C. truncata* are closely allied. Most specimens can be differentiated by the length of the spikes, but some specimens of *C. truncata* have abnormally short spikes. The following key will separate most specimens:

1. Lemma margins appressed-pilose, rarely sparsely so; awn of sterile floret (the lower, if two are present) 3.1 to 16.0 mm long, usually 4 mm or more; spikes 5 to 23 cm, usually 10 cm or more in length; lemmas 0.7 mm wide or less, usually ca 0.5 mm wide; spikelets usually very dark, black or nearly so.

C. truncata, Fig. 48.

1. Lemma margins usually glabrous or scabrous, not appressed-pilose, rarely very sparsely pilose; awn of sterile floret (the lower, if two are present) 0.5 to 7.5 mm long, usually about 2 mm long; spikes generally short, 5 to 11 cm long, usually less

than 8 cm long; lemmas 0.6 mm wide or more, usually about 0.8 to 1.0 mm; spikelets tawny, rarely dark brown.

C. ventricosa, Fig. 46.

Chloris ventricosa is widespread in eastern Queensland and New South Wales (Fig. 47, B), where Everist (1935b) reported that it appears to prefer heavier and richer soils.

Representative specimens examined: AUSTRALIA: New South Wales: Gravesend, *Breakwell s.n.*, May, 1913 (F); Warialda, *Hadley s.n.*, Apr 1908 (F); Hunter Valley, 9 mi NW of Scone, *Story 6,932* (K); between Windsor and Kingswood, *Vickery and Constable 16,121* (K,

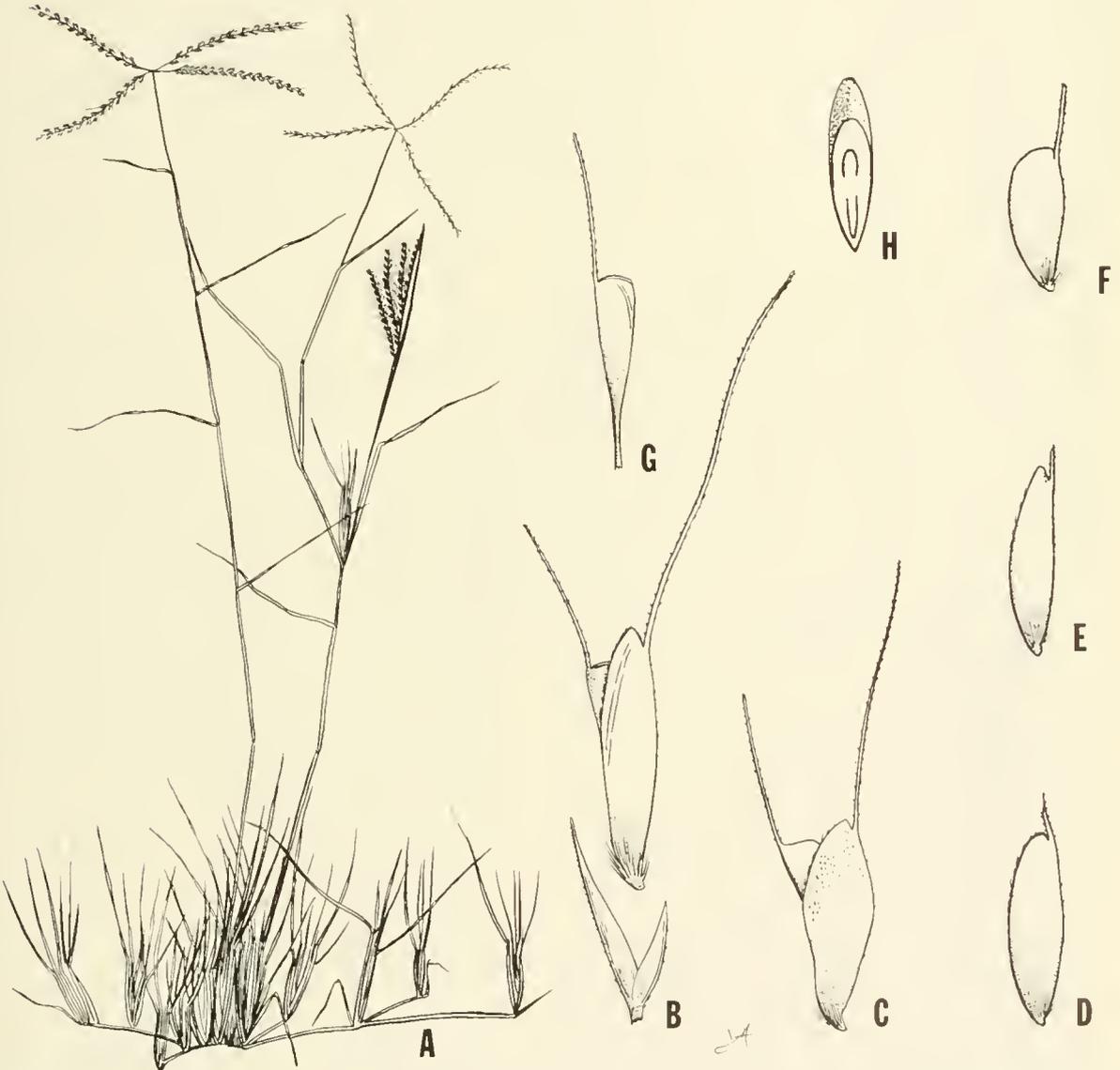


Fig. 46. *Chloris ventricosa*. (A) habit, x 1/6; (B) spikelet, partly dissected, x 15; (C-F) florets, showing variation, x 15; (G) sterile floret, x 15; (H) caryopsis, x 10.



Fig. 47. Distribution of *Chloris truncata* (A) and *C. ventricosa* (B).

MO, US); Sydney, *Wilkes Exped. s.n.*, 1832-42 (US); Queensland: Chinchilla, *Beasley 128A* (K); near Wandoan, *Belson s.n.*, 1930 (K); Miles, *Belson s.n.*, 1930 (K); Wallumbilla, *Belson s.n.*, 1930 (K); Downfall Creek, near Gilgulgil, *Belson s.n.*, 1930; near Petrie, *Blake 24* (K); Allora, Darling Downs, *Blake 294* (K); Drayton, *Blake 5,177* (K); Mundubbera, *Blonsome 19, 54* (K); Laidley, *Clemens s.n.*, 11 May 1943 (US); Kenmore, *Clemens s.n.*, 18 May 1943 (US); Crow's Nest, *Clemens s.n.*, 24 Feb 1944 (US); Yarraman Forest Reserve, *Clemens s.n.*, 2 Aug 1944 (NY, UC, US); Moreton Dtr., Mt. Coolon, *Clemens s.n.*, Mar 1945 (K); Jericho vicinity, *Clemens s.n.*, Mar-Apr 1946 (US); Calhde Cotton Research Station, Biloela, *Cowdry 55* (K); Maranoa Dtr., *Cumming 20* (NY); Rockhampton, *Davies s.n.*, 23 Apr 1932 (K); Gatton, *Davies s.n.*, May 1932 (K); Maranoa Dtr., Boatman Station, *Everist 2,779* (K, US); Darling Downs Dtr., Benandri, 35 mi SE of Texas, *Everist 7,137* (US); Mt. Gravatt, *Jackson s.n.*, Mar 1931 (K); near Mt. Sturgeon Station, *Lazarides 3,644* (K, US); Leichhardt Dtr., 2 mi NE of Moura Township, *Lazarides 6,910* (K); Moonie River, *Roe 822* (US); Burnett, Kingaroy, *Smith 3,042* (K); Toowoomba, *White 6,642*; Wondai, *White 7,214* (K); Dalby, *White s.n.*, Apr 1916 (K).

31. **CHLORIS TRUNCATA** Robert Brown, *Prodr. Flora Nov. Holl.* 186. 1810. (HOLOTYPE: "Port Jackson . . . R. Brown" BM! ISOTYPE: K!) Fig. 48.

Chloris elongata Poirlet in Lamarek, *Encycl. Suppl. Meth. Bot.* 2:236. 1811. (HOLOTYPE: Photograph and fragment, from Desfontaines Herbarium at FI, in US!)

Chloris megastachya Schrad. ex Schultes, *Mantissa* 2:340. 1824. (TYPE: "In Nova Hollandia." Not seen, but description is clear.)

Chloris truncata R. Br. f. *abbreviata* Thellung, *Vierteljahr. Naturforsch. Gesell. Zurich.* 64:706. 1919. (ISOTYPE: Switzerland: Derendingen, Probst 27 Sept 1917. K!)

Perennial, 30 to 50 cm tall, stoloniferous; sheaths glabrous, ligules short-ciliate; blades 9 to 17 cm long, 0.2 to 0.3 mm wide, glabrous to scabrous; spikes five to thirteen, 5 to 23 cm long, radiate; spikelets appressed, rather distant, ca six per cm of the scabrous rachis; glumes narrowly lanceolate, thin, hyaline, glabrous except for the scabrous midrib; first glume 1.4 to 2.3 mm long, 0.2 to 0.3 mm wide; second glume 2.8 to 4.2 mm long, 0.2 to 0.4 mm wide; fertile lemma 1.8 to 4.5 mm long, 0.2 to 0.7 mm wide,

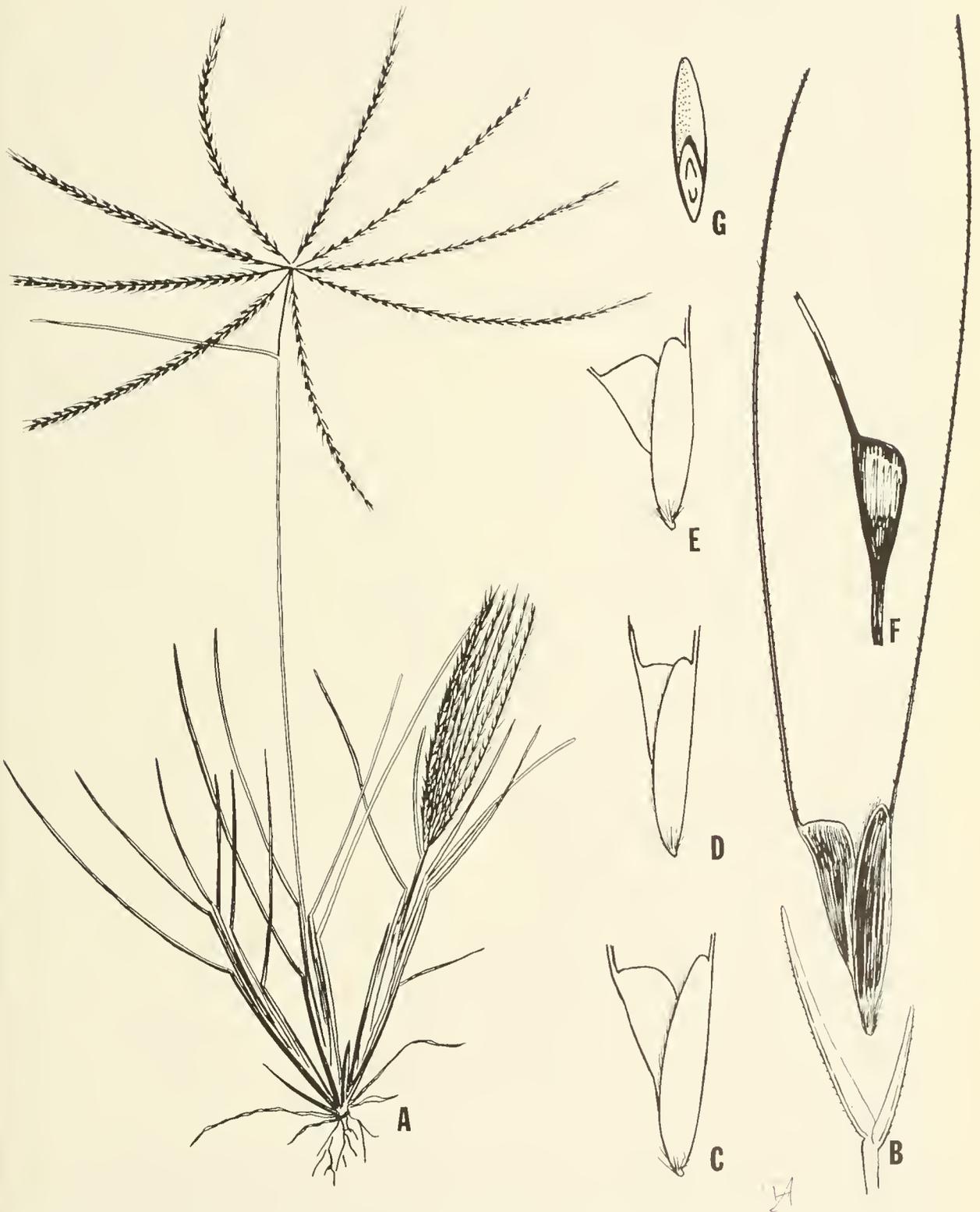


Fig. 48. *Chloris truncata*. (A) habit, x 1/3; (B) spikelet, partly dissected; (C-E) florets, showing variation; (F) sterile floret; (G) caryopsis. (B-G) x 10.

narrowly elliptic, glabrous except for the appressed-pilose margins, often becoming black at maturity, apex truncate, callus bearded, awn 3.1 to 16.0 mm long; sterile floret one, rarely two, 1.3 to 3.5 mm long, 0.5 to 0.9 mm wide, apex truncate, awn 3.1 to 12.5 mm long; anthers ca 0.6 mm long; caryopsis 1.7 to 2.2 mm long, 0.3 to 0.5 mm wide, ellipsoid to narrowly obovate, trigonous; chromosome number $2n=40$.

Chloris truncata is most closely related to *C. ventricosa*. Differences between the two have been discussed under *C. ventricosa*.

Everist (1935b) reported that this species seems to favor "black soil open downs, edge of red soil country, and the edges of brigalow and balah country." Fig. 47—A illustrates the distribution in Australia.

Representative specimens examined: AUSTRALIA: Capital Terr.: Canberra, *McKee* 7,712 (US), 8,931 (K), *Evans* 2,608 (K); New South Wales: Nyngan, *Baker s.n.*, Dec. 1899 (US); Hastings River, *Beckler s.n.* (K); Tocumwal, *Black* 173 (US); Ballina, *Black s.n.*, Feb 1894 (US); Singleton, *Boorman s.n.*, Nov 1914 (K); Menindee Dtr., Quondang Tank, *Constable* 4,716 (K, US); Warialda, *Hadley s.n.*, Apr 1908 (F); Narromine, *Helms* 31,321 (K, NY); Guym, *McKee* 646 (K); Stephen's Creek, *Morris* 489 (K); near Sydney, *Vickery* 88 (K); Warren to Collie Road, *Vickery* K26 (K); Coonamble, *Vickery* K27 (K); Windsor to Kingswood, *Vickery* and *Constable* 16,085 (K); Belltrees via Scone, *White* 8 (US); Queensland: Brisbane River, *Bick and White s.n.*, May 1916 (K); Petrie, near Young's Crossing, *Blake* 48 (K); Wallangarra, *Blake* 4,422 (K); Cambooya, *Cashmore* 808 (US); Dalveen, *Clark s.n.*, Mar 1916 (K); Darling Downs Dtr., Ballandean, *Clemens* 44,480 (K); Brisbane, Turbot Street pavement, *Clemens s.n.*, 18 Mar 1942 (US); Stanthorpe, *Clemens s.n.*, 13 Nov 1943 (US); Bald Mt., *Clemens s.n.*, 9 Nov 1944 (US); 35 mi SE of Texas, *Everist* 7,140 (K, US); Cunnamulla, Gilruth Plains, *Hartley* A185 (US); Roma, *White* 9,573 (K); Darling Downs, between Inglewood and Milmerran, *White* 9,778 (K); Dalby, *White s.n.*, Apr 1916 (K); Noondec Station near Warwick, *Young* 12 (K); South Australia: Koonamore Vegetation Reserve, *Paltridge* 22 (K); Victoria: 2 mi S of Bacehus Marsh, *Aston* 282 (US); Rochester, *Davies s.n.*, 28 Jan 1932 (K); Melbourne University ground, *Sonenberg s.n.*, Jan 1935 (K); Western Australia: Merredin, *Allbary* H.48 (US); Carnarvon, red muddy soil, *Gardner* G 3,003 (K); Yundamindera Run, 120 mi NW of Kalgoorlie, *Pearse* 1,931 (K). FIJI ISLANDS: Suva, *Tur-*

bet 42 (K). UNITED STATES: Hawaii, Ft. Shafter, *Hitchcock* 13,849 (F).

32. *CILORIS PUMILIO* Robert Brown, Prodr. Flora Nov. Holl. 186. 1810. (LECTO-TYPE: BM! Additional specimens K! BM! See discussion of nomenclature below.) Fig. 49, J-P; 50, B.

Chloris pallida Hackel, Bot. Jahrb. 6:244. 1885. (HOLOTYPE: "In Australia boreali-occidentali lg. Pemberton-Walcott." W, Fragment at K!)

Chloris pumilio (Robert Brown) Kuntze, Rev. Gen. Pl. 2:771. 1891. (Based on *C. pumilio* Robert Brown.)

Chloris ruderalis Domin, Biblioth. Bot. 85:365. 1915. (SYNTYPES: "Queensland: Prope opp. Atherton legi H. 1910." ". . . in xerodrymio prope opp. Marceba legi H. 1910." ". . . prope opp. Charters Towers legi H. 1910." All at K!, on extended loan from PR.)

Chloris ruderalis f. *biaristulata* Domin, Biblioth. Bot. 85:365. 1915. (HOLOTYPE: A specimen at K!, on extended loan from PR, labeled: ". . . Queensland apud Mungana prope opp Chillagoe legi H. 1910" consists of several plants, one of which fits the description in having two very short lateral teeth at the base of the sterile floret awn and is possibly the plant upon which this form is based.)

Chloris ruderalis f. *robusta* Domin, Biblioth. Bot. 85:365. 1915. (TYPE: Apparently one of the specimens on the sheet discussed above, but no particular plant can be assigned positively to this name.)

Annual 60 to 90 cm tall, tufted, or rooting at the lower nodes, from a fibrous root system; sheaths glabrous except pilose near the apex; ligule a short-ciliate crown with a few long hairs; blades 7 to 12 cm long, ca 3 mm wide, scabrous above with a few long hairs near the base, glabrous below except for the scabrous midrib; spikes four to twelve, 4 to 8 cm long, erect to slightly divergent; spikelets densely inserted, averaging 9 to 16 per cm of the scabrous rachis; glumes narrowly lanceolate, glabrous except for the scabrous midnerve, membranous; first glume 1.5 to 2.5 mm long, ca 0.3 to 0.4 mm wide; second glume 2.5 to 5.0 mm long, with a short hairlike awn; fertile lemma 3.7 to 10.0 mm long (including the lateral awns), 0.4 to 0.8 mm wide, narrowly lanceolate-elliptic, callus bearded, margins in-



Fig. 49. *Chloris lobata* and *C. pumilio*. (A-I) *C. lobata*. (A) habit, x 1/4; (B) spikelet, partly dissected, x 5; (C-E) florets, showing variation, x 5; (F) sterile floret, ventral view, x 5; (G) sterile floret, semilateral view, x 5; (H) group of sterile florets, showing variation, x 5; (I) caryopsis, x 10. (J-P) *Chloris pumilio*. (J) spikelet, partly dissected, x 5; (K) group of fertile florets, showing variation, x 5; (L) lower sterile floret, lateral view, x 5; (M) upper sterile floret (not always present), x 5; (N) sterile floret, ventral view, x 5; (O) group of sterile florets, showing variation, x 5; (P) caryopsis, x 5.

rolled, appressed short-pilose below, becoming spreading long-pilose above, otherwise minutely scabrous, apex bifid, the lobes gradually tapering into awns up to 7 mm long, midnerve extending as an awn 7 to 16 mm long, almost always at least twice the length of the lateral awns; sterile floret one (rarely two), 1.3 to 4.0 mm long (including the lateral awns), 0.3 to 0.7 mm wide, glabrous to slightly scabrous, apex minutely ciliate, divided to as much as halfway into two lobes, the lobes asymmetrical and with lateral awns 1.0 to 3.5 mm long, central awn 3 to 15 mm long, apex minutely ciliate; caryopsis 1.2 to 3.3 mm long, ca 0.5 mm wide, ellipsoid, trigonous.

Chloris pumilio and *C. lobata* are very similar. The best characters to use to distinguish *C. pumilio* are: lemma margins pilose for full length, sterile floret bilobed only halfway to the base, and the asymmetrically awned lobes of the sterile floret.

Robert Brown (1810) described *Chloris pumilio* on the basis of specimens collected on islands off the northern coast of Australia. The description is as follows:

"4. *C. pumilio*, spicis 2 - 4 erectiusculis, glumis bifloris: valvulis acuminato-aristatis, perianthiis ciliatis lanceolatis, triaristatus, aristis lateralibus valvula brevioribus: intermedia elongata. (T.) v.v."

This description was compared with the original Brown manuscript notes at the library of the British Museum (Natural History). While many of the words in this manuscript description are illegibly written, it seems to match Brown's published description in the important points.

The phrase ". . . arista lateralibus valvula brevioribus . . ." suggested something quite different from the taxon that has been called *C. pumilio* for many years—the plant treated under *C. lobata* in this paper. The latter species has lateral awns that are clearly equal or nearly equal to the central awn and much longer than the lemmas. As with many of Brown's specimens, typification is not straightforward, since many were distributed and confused after his death. In the case of this plant, however, there can be little doubt; for in the British Museum (and also at Kew), there are several sheets of Brown's specimens containing many plants—all fitting the above description. Most of these have the typical blue label of the Bennett distribution of Brown's specimens and, as such, are not necessarily strictly authentic. One sheet, however, has on the back the handwritten notation "Nova Hollandia Ora Septentrionalis. R.

Brown." The latter sheet is taken here to be the lectotype, for it is the particular sheet selected and annotated by Brown. All of the specimens of the Bennett distribution at the British Museum and Kew match the lectotype as well.

The totality of this evidence leads to only one conclusion: the plant (commonly called *Chloris ruderalis* for many years) must now be called *C. pumilio*, leaving the plant commonly called *C. pumilio* without a name. This was correctly recognized by Lazarides (1972), who provided the new name *C. lobata* for it.

Specimens examined: AUSTRALIA: Northern Territory: Katherine River levee, 14°20-21'S, E of 132°E, *Black 17,414* (K, US); Queensland: Stannary Hills, *Bancroft 1,908*; Forest Home Station, *Brass 1,821* (K); Gilbert River, Cumberland, *Brass 8,857* (K); Gilbert River, without precise location, *White 1,489* (K); Stanley, near Townsville, *Chisholm-Ellis 16* (K); Townsville, *White s.n.*, 11 Feb. 1918 (K); Thursday Island, *Hockings s.n.*, Apr 1931 (K); 2 mi S of Normanton Township, *Lazarides 4,272* (K); Hayman Island, *White 10,222* (K); Western Australia: De Grey River, Mulgee Station, *Anderson 1,898* (K); North Kimberley Dtr., May River, *Baselow 75* (K); Broome, *Bates 1,902* (K); *Holmes 1270.210* (US); Wandagee, Mouribandy, *Gooch s.n.*, 16 Jul 1937 (K); Kunmaya, *Holmes s.n.*, Apr 1942 (US); Whim Creek, *Mitchell*, without precise location or date (K); Mulyic, Roebourne, *Morrison s.n.*, Mar 1899 (K).

33. **CHLORIS LOBATA** Lazarides, Australian Jour. Bot. Supplement 5. 20. 1972. (HOLOTYPE: "Queensland: Burke District; 4 miles east of Normanton Township. 6. iii. 1954. *Lazarides 4,289*." CANB. ISOTYPES: K! US!) Fig. 49, A-I.

Chloris pumilio auct. non Robert Brown.

Annual 15 to 45 cm tall, erect or geniculate, often branching from the lower nodes; sheaths glabrous, often sparsely pilose toward the summit; ligule a densely ciliate crown with a few long hairs intermingled near the edges; blades up to 15 cm long, 0.2 to 0.6 mm wide, glabrous to scabrous above and below; spikes three to nine, erect to somewhat divergent, 2.5 to 6.0 cm long; spikelets appressed and imbricate, ca 8 to 15 per cm of the scabrous rachis; glumes narrowly lanceolate, acuminate, membranous, glabrous except for the scabrous midnerve; first glume 1.6 to 2.5 mm long, 0.2 to 0.4 mm wide; second glume 2.6 to 3.9 mm long, 0.2 to 0.3 mm

wide; fertile lemma narrowly elliptic, 5.5 to 11.0 mm long (including the lateral but not the middle awn), 0.3 to 0.6 mm wide, callus white bearded, margins glabrous to scabrous below, rather prominently long-ciliate near the apex, remainder of lemma prominently scabrous and punctate, lateral nerves of lemma prolonged into two awns 2 to 6 mm long, midnerve prolonged into an awn 3.0 to 10.5 mm long; sterile floret one, 3.3 to 7.5 mm long (including the lateral awns), 0.4 to 0.5 mm wide, divided nearly to the base into two flattened lanceolate lobes, each with an awn ca 2 to 4 mm long, middle awn 3 to 8 mm long; caryopsis 1.7 to 2.4 mm long, ca 0.4 mm wide, ellipsoid, trigonous.

As has been discussed under the previous species, this taxon has for many years been mistakenly called *Chloris pumilio*.

Collected on heavy soils on banks, water-holes, and alluvial flats, mostly in Queensland, Australia, but also occasionally found in Northern Territory and Western Australia. (Fig. 50, C).

Representative specimens examined: AUSTRALIA: Northern Territory, on levee of Roper

River, Eley Station, E of Mataranka, *Blake 17,517* (K, US); Katherine, *Tyack-Bake*, May 1943 (UC). Queensland: Forest Home Station, Gilbert River, *Brass 1,704, 1,787* (K); Gilbert River, without precise location, *White 1,492* (K); Norman River, *Gulliver*, without precise collection number and date (K, US); near Normanton, *Lazarides 4,243* (K, US); Mt. Molloy, *McKee 9,121* (K); 39 mi E of Lawn Hill Station, *Perry 1,115* (K, US); between Townsville and Rollingstone, *White 8,895* (K, US). Western Australia: 10 mi SE of Mt. House Station, *Lazarides 5,157* (K, US).

34. CHLORIS DIVARICATA Robert Brown, Prodr. Flora Nov. Holl. 1:186. 1810. (LECTOTYPE: "3. *Chloris divaricata*, Port I. Keppel Bay, Whorlwater Bay . . ." BM! See additional nomenclature note below.) Fig. 51, K-R.

Chloris cynodontoides Balansa, Bull. Soc. Bot. France 19:318. 1872. (HOLOTYPE: "Bords des Chemins, Nouvelle Calédonie . . . Pancher, 18-70" P!)

Perennial 20 to 50 cm tall, tufted to shortly stoloniferous, sometimes apparently mat-forming; sheaths glabrous; ligule a short-ciliate crown; blades up to 15 cm long, generally 5 to 9 cm, 1.0 to 1.5 mm wide, glabrous to scabrous; spikes three to nine, 4 to 17 cm long, divaricate, becoming horizontal; spikelets sparsely inserted, about three to seven per cm of the scabrous rachis, appressed, only the awns divergent; glumes very narrowly lanceolate, thin and membranous, glabrous except for the scabrous midnerve; first glume 0.9 to 1.8 mm long, ca 0.3 mm wide; second glume 2.0 to 2.9 mm long, ca 0.3 mm wide; fertile lemma linear to narrowly lanceolate, 2.9 to 4.0 mm long, including the teeth at the apex, callus bearded, margins glabrous, scabrous or with a few appressed short hairs near the apex, keel scabrous, internerves scabrous, awn 7.5 to 17.0 mm long, sterile floret one, 1.2 to 1.9 mm long, ca 0.3 mm wide, narrowly elliptic, glabrous, apex acute, bilobed $\frac{1}{3}$ to $\frac{1}{2}$ of its length; awn 4.5 to 9.5 mm long; caryopsis ca 2.2 mm long, 0.4 mm wide, narrowly ellipsoid.

Brown's original description listed the symbol "T.v.v." as the place of collection. According to studies of original expedition charts by Burbidge (1956), this is taken to be Cape Shield near Groot Eylandt in the Gulf of Carpentaria. I could not find specimens labeled as such at the British Museum, but there were five specimens labeled "*Chloris purpuram*, East Coast,"

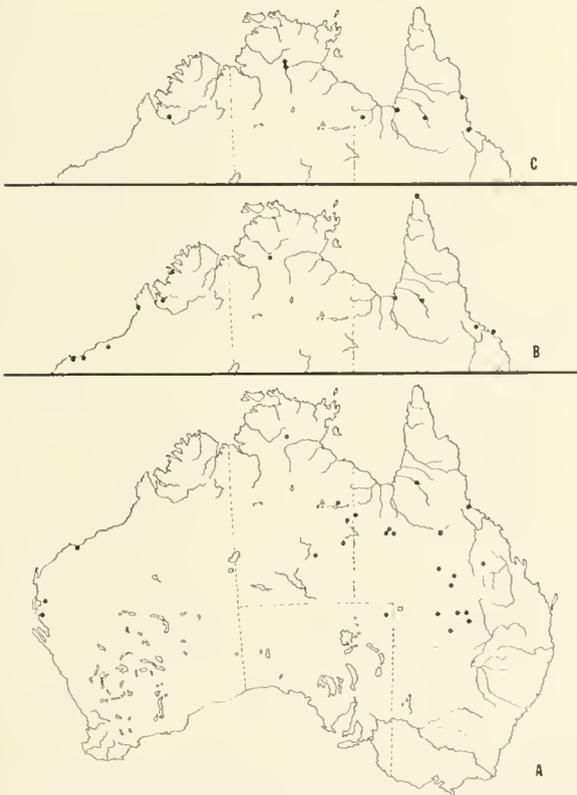


Fig. 50. Distribution of *Chloris pectinata* (A), *C. pumilio* (B), and *C. lobata* (C).

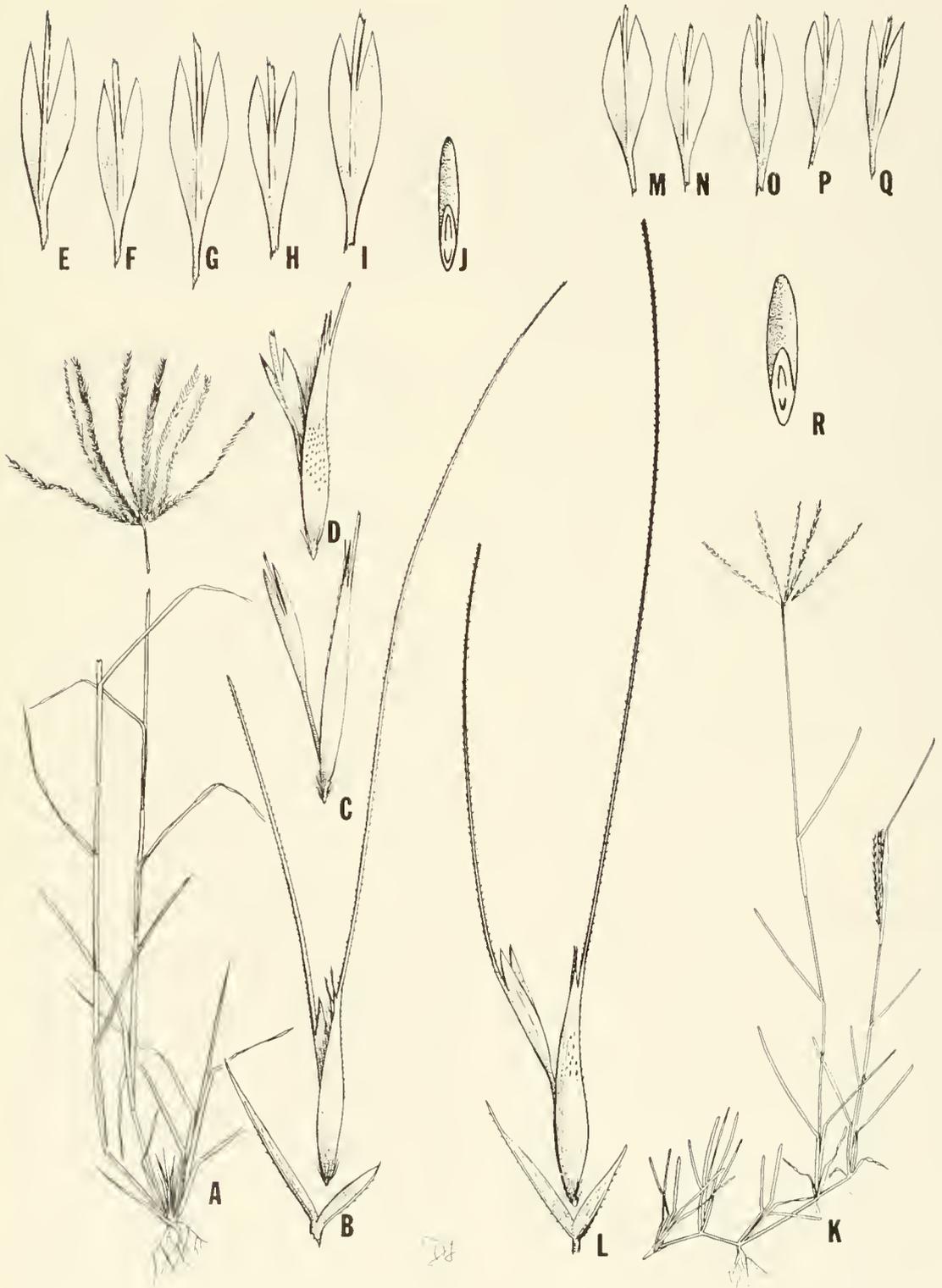


Fig. 51. *Chloris pectinata* and *C. divaricata*. (A-J) *C. pectinata*. (A) habit, x 1/4; (B) spikelet, partially dissected; (C,D) florets, showing variation; (E-I) sterile florets, dorsal view, partially flattened, showing variation; (J) caryopsis. (K-R) *C. divaricata*. (K) habit, x 1/4; (L) spikelet, partially dissected; (M-Q) sterile florets, dorsal view, partially flattened, showing variation; (R) caryopsis. (B-J) and (M-R) x 10.

a sixth of the Bennett distribution of Brown's specimens, with the usual blue label, and a seventh, labeled "3. *Chloris divaricata*, Port I. Keppel Bay. Whorlwater Bay, Broadsound . . ." The label of the last specimen is handwritten and has two slits cut in it—a feature thought to indicate that this is the specimen selected by Brown from the bulk of the collections and studied by him on his journey home from Australia. Fortunately, all specimens are of the same taxon.

The two collection sites mentioned, the one in the description and the second on the various Brown specimens at the British Museum, are widely separated—Cape Shield being on the west shore of the Gulf of Carpentaria and "Port I. Keppel Bay . . ." on the east coast of Queensland. The latter specimen was obviously seen and studied by Brown; and even though its collection site is at variance with that cited in the description, it seems best to designate it as the lectotype of the species.

Chloris divaricata from Australia and *C. cynodontoides* from Fiji, Tonga, and New Caledonia have commonly been treated as distinct species, though, more recently, Lazarides (1972) treated them as varieties of *C. divaricata*. The primary differences emphasized are that *C. divaricata* is not stoloniferous and has relatively long spikes, while *C. cynodontoides* is stoloniferous and has short spikes. Table 10 presents the results of measurements of 56 different specimens from all of the geographic areas represented.

As can be seen, only minor statistical differences exist between the two populations. While average spike number and length may differ, the ranges overlap greatly. Likewise, the presence or absence of stolons is not sufficiently exclusive to be used in separating the two groups.

Lazarides (1972) has mapped the two varieties, showing var. *cynodontoides* in inland areas of southern Queensland and coastal only in the north. Collections of var. *divaricata* may also be noted from these regions but are much

more commonly found eastward and southward, extending well into New South Wales.

The specimens I have seen do not support such a clear-cut separation, for stoloniferous plants with relatively large numbers of long spikes are intermingled with tufted plants with fewer, shorter spikes. Plants showing different combinations of these features or showing intermediate values may also be found. Until additional field studies are made, I feel that recognition of distinct varieties is not warranted.

Chloris divaricata most closely resembles *C. pectinata*, though it differs in having sterile florets 1.2 to 1.9 mm long (as opposed to 1.7 to 2.9) and only slightly imbricate spikelets. The spikelets of *C. pectinata* are strongly imbricate.

Everist (1935a) reported that this species occurs in "practically all types of soil, from heavy black soils to light sandy loams." It has been collected in eastern Queensland and New South Wales, Australia; Fiji Islands; and Tonga Islands (Fig. 52). Specimens from Hawaii, Texas, and France are adventives, as are probably those from New Caledonia.

Representative specimens examined. AUSTRALIA: New South Wales: 6 mi NW of Muswellbrook, *Story* 7,079 (K); Warialda, *Vickery* 18,028 (K). Queensland: Brisbane River, on ridges, *Bailey* without collection number or date (K); Brisbane, *Bailey* without collection number or date (US 879,412); Dalby, *Beiers* 47 (K); near Wallumbilla, *Belson s.n.*, 1930 (K); Petrie, near Young's Crossing, *Blake* 49 (K); Drayton, *Blake* 5,176 (K); Mundubbera, *Blonsome* 41 (K); Mt. Molloy, *Brass* 2,405 (K); South Brisbane Park, *Clemens s.n.*, 20 Feb 1943 (US); near Mt. Gravatt, *Clemens s.n.*, 11 Mar 1943 (US); Kenmore, *Clemens s.n.*, 18 May 1943 (US); Rosewood, *Clemens s.n.*, 18 Jan 1944 (US); Bunya Mts., *Clemens s.n.*, Mar 1944 (US); Bauple, Wide Bay Dtr., *Clemens s.n.*, 10-20 Jun 1945 (K); Charleville, Warrego Dtr., *Clemens s.n.*, 9 Nov. 1945 (K); Mt. Fox, *Clemens s.n.*, Sept-Dec 1949 (K); Callide Cotton Research Station, Biloela, *Cowdry* 1,930 (K);

Table 10. Comparison of spike length, spike number, and growth habit of plants called *C. divaricata* and *C. cynodontoides*.

Geographic origin of plant	Number of spikes		Length of spikes		Stolons	
	Range	Average	Range	Average	Number of plants having stolons	Number of plants lacking stolons
Australia	3-9	5.7	4.5-16	11.1	16	27
Fiji, Tonga, and New Caledonia	3-9	5.2	4-8	6.3	11	2

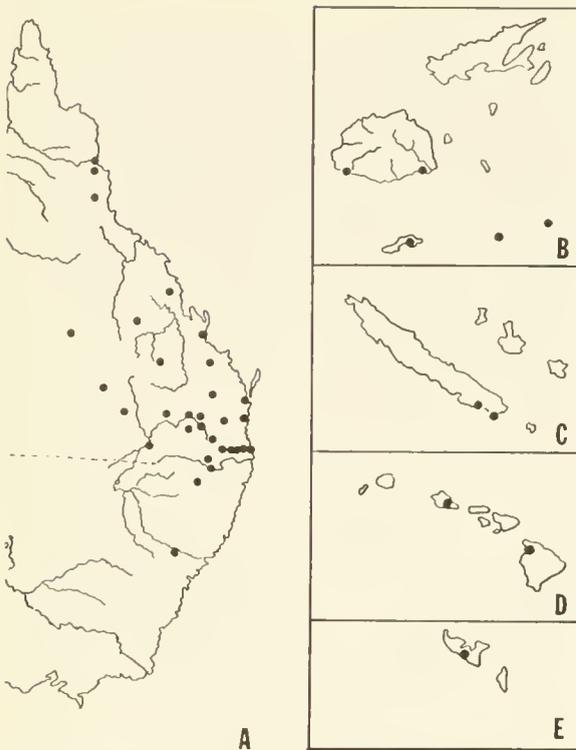


Fig. 52. Distribution of *Chloris divaricata*. (A) eastern Australia. (B) Fiji Islands. (C) New Caledonia. (D) Hawaiian Islands. (E) Tonga Islands.

Rosedale, *Dovey* 439 (K); Boatman Station, *Everist* 2,778 (K), 2,931 (K, US); Benandri, 35 mi SE of Texas, *Everist* 7,139 (K, US); Bishop Island, mouth of Brisbane River, *Everist and Blake* 367 (K); Macalister, *Harris* 5,505 (K); 10 mi S of Miles, *Johnson* 719 (K); Reedsdale, 5 mi NW of Bymount, *Johnson* 2,251 (K); Gympie, *Kenny* without collection number or date (US I,386,466); Conjuboy Station, *Lazarides* 4,137 (K); 1 mi NE of Niall Station, *Lazarides* 4,630 (K, US); Moreton Dtr., Waterford, *Meal* 7 (K); Jandowae, NE of Dalby, *Moore* 36 (K); King's Creek, E of Bowman, *Mueller s.n.*, 1870 (K); Mitchell Dtr., Brixton, *Rawson s.n.*, 13 Nov 1930 (K); Holcombe, via Tara, *Salter s.n.*, 21 Jun 1930 (K); near Lake Elphinstone, 28 mi WNW of Nebe Township, *Story and Yapp* 85 (K); St. George, *White* 789 (US); Rockhampton, *White* 3,375 (K, US); Clermont, *White* 3,416 (K, US); Murgon, *White* 7,230 (K); Rolleston, *White* 8,830 (K); Darling Downs, between Inglewood and Milmeran, *White* 9,790 (K); Wellington, *White s.n.*, 17 Mar 1916 (K); Mareeba, *White s.n.*, Jan 1918 (K); Laidley, *White s.n.*, 17 Mar 1921 (K). FIJI ISLAND: Suva, *Greenwood* 226A (K); Viti Levu, Nandronga, Singatoka, *Greenwood* 226C (K, NY, US); Viti Levu, Nafasiri,

near Nasinu, *Greenwood* 226D (US); Viti Levu, near Casey, Suva, *Tothill* 43 (K); Totoya Island, *Tothill* 201 (K); Matuka Island, *Tothill* 291 (K); Kondavu Island, *Turbet* 8 (K). FRANCE: Dunquerque, port area, anon. (K). NEW CALEDONIA: Noumea, *Bernier* 812 (K); foot of Ouen Toro, *McKee* 11,499 (K, US). TONGA ISLANDS: Tongatapu, Kolomotuia, *Sokai* 843 (K). UNITED STATES: Hawaii: Honolulu, near Bishop Museum, *Neal s.n.*, 7 Sept 1934 (K); Niuhau, *St. John* 23,623 (K); University of Hawaii campus, *St. John* 24,832 (K); *Wilder s.n.*, 19 Jan 1931 (K). Texas: Bexar Co., U.S. Experiment Station, San Antonio, *Silveus* 2,564 (TAES); Nueces Co., near Tuloso-Midway High School, Hwy. 9, between Corpus Christi and Calallen, W. V. *Brown* 755 (TAES); Refugio Co., 2 mi SE of Woodsboro, along Road 1360, *Waller et al.* 2,118 (TAES).

35. *CHLORIS PECTINATA* Bentham, *Flora Australiensis* 7:612. 1878. (SYNTYPE: "Charlotte Waters. Giles" K!) Fig. 51, A-J.

Chloris divaricata var. *muelleri* Domin, *Repert. Sp.* Nov 9:553. 1911. (ISOTYPE: "Sturts Creek. Feb 56 . . . Mueller." K!)

Chloris pectinata var. *typica* Domin, *Biblioth. Bot.* 85:366. 1915. (Based on *C. pectinata* Bentham.)

Chloris pectinata var. *fallax* Domin, *Biblioth. Bot.* 85:366. 1915. (HOLOTYPE: "Queensland . . . Rolling Downs . . . Domin II. 1910." K!, on extended loan from PR.)

Chloris divaricata var. *minor* Black, *Flora South Australia* Pt. 1. 83. pl. 4. 1922. (ISOTYPE: "Oodnatta . . . Miss Staer . . ." K!)

Annual 20 to 75 cm tall, erect, often branched above, especially on taller specimens; sheaths glabrous; ligule a dense short-ciliate crown, occasionally with a few longer hairs intermixed; blades up to 15 cm long, 2 to 5 mm wide, glabrous to seabrous; spikes four to thirteen, 5 to 11 cm long, erect at first, later becoming widely divaricate to horizontally spreading at maturity; spikelets densely inserted on the rachis, spreading, ea 10 to 14 per cm of the seabrous rachis; glumes narrowly lanceolate, membranous and glabrous except for the seabrous midnerve; first glume 1.4 to 2.5 mm long, 0.1 to 0.3 mm wide; second glume 2.9 to 4.3 mm long, 0.2 to 0.3 mm wide; fertile lemma 3.0 to 6.2 mm long (including lateral teeth), 0.4 to 0.6 mm wide, linear to narrowly lanceolate, becoming dark gray to black at maturity, callus bearded, margins

glabrous, scabrous, or appressed short-pilose (the hairs less than 0.2 mm long), sides of lemmas sparsely to densely glandular and scabrous, occasionally glabrous, lemma teeth 0.5 to 10.0 mm long, awn 6 to 37 mm long; sterile floret one, 1.7 to 2.9 mm long, 0.2 to 0.3 mm wide, flattened, bilobed no more than halfway to the base, glabrous, awn 4 to 10 mm long; anthers ca 0.6 mm long; caryopsis ca 2.3 mm long, 0.3 mm wide, narrowly ellipsoid, trigonous.

Chloris pectinata is most closely related to *C. divaricata*. Differences have been discussed under the latter taxon.

This species is widely distributed in central and western Queensland and also in Northern Territory and South Australia (Fig. 50, A). Everist (1938) reported that it occurs in a variety of habitats but develops best in low-lying clay soils.

Representative specimens examined: AUSTRALIA: Northern Territory: 26 mi NNW of Brunette Downs, *Blake 17,819* (K, US); Macdonald Downs, *Chalmers 32* (K); 22 mi NE of Argadargada Station, *Lazarides 5,258* (K, US); Barkly Highway, James River crossing, *Perry 710* (K); Queensland: Eulo, near Cunnamulla, *Allan 10,948* (US); Forest Home Station, Gilbert River, *Brass 1,822* (K); Charleville Dtr., Warrego, *Clemens s.n.*, 7 Nov 1945 (K); Jericho, *Clemens s.n.*, 6 Mar 1946 (US); Mitchell Dtr., Springvale, *Clemens s.n.*, 2 Apr 1946 (US); Maranoa Dtr., Boatman Station, Everist 2,778 (US); Cook Dtr., road from Tabacum to Springmount, *Goodall s.n.*, 2 Apr 1961 (US); Hughenden, *Hawthorn s.n.*, Jun 1919 (K); 27 mi NW of Cloncurry, *Lazarides 4,308* (K, US); 3 mi SW of Malbon Township, *Lazarides 4,401* (K, US); Toorak Experiment Station, *Lazarides 4,446* (K, US); Adovale, *MacGillivray 1,029* (K); Cunnamulla, *McKee s.n.*, 11 Apr 1963 (K); 25 mi NNE of Camooweal, *Perry 955* (K, US); Blackall, *Ranking 13* (K); Longreach Dtr., *Thomas s.n.*, Mar 1927 (K); Clermont, *White 3,422* (K); Antil Plains near Townsville, *White 8,893* (K, US); Warrego Dtr., Carbeen, near Cunnamulla, *White 11,556* (K); Mitchell Dtr., Tower Hill, *White s.n.*, Apr 1919 (K); Quilpie, *White s.n.*, 20 May 1928 (K); South Australia: Cordillo Downs, *Cleland s.n.*, May 1924 (K); Oodnadatta, *Staer s.n.*, Jan 1913 (K); Western Australia: Wandagee, Minilya River, *Gardner 3,236* (K); Wandagee Station, near Carnarvon, *Meadly M71* (K); Warrambie, Roebourne, *Meares 345* (K).

36. CHLORIS CRINITA Lagasca, Var. Cienc. Lit. Arts (Madrid) 4:143. 1805. *Nomen*

nudem; Nov. Gen. et Sp. 5. 1816. The first cited publication has not been located in any United States library, but Mrs. Agnes Chase found the series in the British Museum and placed copies of Lagasca's protologues on file at US! The name was apparently first used without a description; later Lagasca provided a description in the second work mentioned above. Parodi (1947) states that no specimen with the appropriate number could be found among the types at Madrid, but that a figure bearing Lagasca's handwritten annotation is of the species as commonly understood. Fig. 53, D-F.

Chloris mendocina Philippi, Anales Univ. Chile 36:208. 1870. The original description cites a collection by Mendoza. A specimen in P! labeled "Phillipe pl. chilense Mendocina. Chloris mendocina Phil. Ipse Mendoza" may be the type. It and the description are *Chloris crinita*.

Trichloris fasciculata Fournier ex Bentham, Jour. Linn. Soc. Bot. (London) 19:103. 1881. *Nomen nudem*; Fournier, Mex. Pl. 2:142. 1886. (HOLOTYPE: "San Luis de Potosí. Viri. n. 1440" P!)

Trichloris blanchardiana Fournier ex Scribner, Bull. Torrey Bot. Club 9:146. 1882. (HOLOTYPE: "Santa Cruz Valley near Tucson . . . Pringle, May 19" US!)

Chloropsis blanchardiana (Fournier) Kuntze, Rev. Gen. Pl. 2:771. 1891. (Based on *Trichloris blanchardiana* Fournier.)

Chloropsis crinita (Lagasca) Kuntze, Rev. Gen. Pl. 2:771. 1891. (Based on *Chloris crinita* Lagasca.)

Chloropsis fasciculata (Fournier ex Bentham) Kuntze, Rev. Gen. Pl. 2:771. 1891. (Based on *Trichloris fasciculata* Fournier ex Bentham.)

Leptochloris crinita (Lagasca) Munro ex Kuntze, Rev. Gen. Pl. 2:771. 1891. (Based on *Chloris crinita* Lagasca.)

Trichloris verticillata Fournier ex Vasey, U.S. Dept. Agric. Div. Bot. Bull. 12. Pt. II: pl. 25. 1890. "*Chloropsis blanchardiana* Gay in Herb." is cited; description and illustration are of *C. crinita*.

Chloropsis mendocina (Philippi) Kuntze, Rev. Gen. Pl. 3:348. 1898. (Based on *Chloris mendocina* Philippi.)

Trichloris mendocina f. *blanchardiana* (Fournier ex Scribner) Kurtz, Bol. Acad. Nac. Ciencias Córdoba (Rep. Argentina)



Fig. 53. *Chloris pluriflora* and *C. crinita*. (A-C) *C. pluriflora*. (A) habit, x 1/5; (B) spikelet, partly dissected, x 10; (C) caryopsis, x 10. (D-F) *C. crinita*. (D) habit, x 1/5; (E) spikelet, partly dissected, x 10; (F) caryopsis, x 10.

16:270. 1900. (Based on *Trichloris blanchariana* Fournier ex Scribner.)

Chloris trichodes Lagasca ex Parodi, Revista Argentina Agron. 14:62. 1947. Citation of an herbarium name.

Trichloris crinita (Lagasca) Parodi, Revista Argentina Agron. 63. 1947. (Based on *Chloris crinita* Lagasca.)

Stoloniferous or tufted perennial up to 1 m tall; sheaths glabrous to sparsely hirsute; ligule ciliate with cilia up to 3 mm long; blades up to 20 cm long, 5 to 10 mm wide, scabrous above and below; spikes six to twenty, up to 15 cm long, erect, arising in several close verticils, spikelets densely arranged on the rachis, averaging ca seven to nine per cm of the scabrous rachis; glumes lanceolate to ovate, acuminate to awned, glabrous except for the scabrous midrib; first glume 0.8 to 1.1 mm long, ca 0.3 mm wide, linear to narrowly lanceolate; second glume 2.0 to 2.5 mm long, ovate, with an awn up to 2 mm long; fertile lemma 2.4 to 3.8 mm long, ca 0.5 mm wide, dorsally flattened, narrowly lanceolate to elliptic, scabrous, especially above the middle, apex three-awned, central awn 8 to 12 mm long, the lateral usually somewhat shorter; sterile floret usually one (occasionally two), greatly reduced, cylindrical, the floret proper ca 1.0 to 1.5 mm long, gradually narrowing at the apex into three subequal awns, the awns ca 5 to 7 mm long; second sterile floret (when present) similar to the first but smaller; caryopsis 1.7 to 2.3 mm long, ca 0.6 mm wide, ca 0.3 mm thick, strongly dorsally flattened; chromosome number $2n=40$.

Only three species in *Chloris* have three long awns on the fertile and sterile florets—*C. crinita*, *C. lobata*, and *C. pumilio*. *Chloris crinita* is a New World tufted perennial with the lemma apex tapering abruptly to the lateral awns. Both *Chloris lobata* and *C. pumilio* are Australian annuals in which the upper lemma is split, the lobes gradually narrowing into the awns. There are many additional, subtle, qualitative differences; and I believe the resemblance is largely superficial.

Chloris crinita is widely distributed in the south central to southwestern United States, northern Mexico, and, rarely, has been collected in South America (Fig. 54).

Representative specimens examined: ARGENTINA: Prov. Buenos Aires: Dep. Villarino, 60 km E of Río Colorado, *Eyerdam et al.* 23,516 (US); Prov. Catamarca: Santa María, *Castillon* 3,290 (US); Prov. Chaco: Sierra Blanca, *Jorgensen* 2,878 (US); Prov. Córdoba: Remedias, *Niedfeld s.n.*, 17 Apr 1920 (US); Prov. Corrien-

tes: Dep. Mburucuyá, Estancia Santa Teresa, *Pedersen* 63 (US); Prov. Formosa: Guayculca, *Jorgensen* 3,330 (US); Prov. Jujuy: Laguna de la Brea, *Fries* 115 (US); Prov. Mendoza: Vallee de Río Atuel, St. Raphael, *Wilczek* 526 (US); Prov. Salta: Coronel Moldes, *Hunziker* 1,110 (US); Prov. San Juan: Colonia Fiscal, Sarmiento, *Bartlett* 20,522 (US); Prov. Santiago del Estero: Río Huayco Hondo, *Bartlett* 19,754 (US); Prov. Tucuman: Trancas, Tapia, *Venturi* 2,345 (US). BOLIVIA: Mataral, anon., 1804 (US). MEXICO: Chihuahua: 100 km W of Cuarto Cienegas, *Harvey* 1,255 (US); Durango: Torreón, *Hitchcock* 7,724 (US); San Luis Potosí: 20 km NE of Río Verde, *Rzedowski* 5,157 (US). PARAGUAY: Dep. Chaco: Loma Para, *Rojas* 2,751 (US). UNITED STATES: Arizona: Benson, *Griffiths* 1,969 (US); New Mexico: Organ Mts., W of Dona Ana, *Wootton and Standley s.n.*, Sept 1907 (US); Texas: vicinity of El Paso, *Chase* 5,899 (US); Fort Worth, *Tracy* 8,208 (US); Pecos, *Silveus* 309 (US).

37. **CHLORIS PLURIFLORA** (Fournier) Clayton, Kew Bull. 21:102. 1967. (Based on *Trichloris pluriflora*.) Fig. 53, A-C.

Trichloris pluriflora Fournier in Hemsley, Biol. Centr. Amer. Bot. 3:560. 1885.



Fig. 54. Distribution of *Chloris crinita*. Inset A: Southwestern United States and Mexico.

Nomen nudem; Fournier Mex. Pl. 2:142. 1886, with description. (HOLOTYPE: "Karw. in Herb. Petrop." Fragment of type in US!)

Chloropsis pluriflora (Fournier) Kuntze, Rev. Gen. Pl. 2:771. 1891. (Based on *Trichloris pluriflora* Fournier.)

Trichloris pluriflora f. *macra* Hackel in Stuck., Anales Mus. Nac. Hist. Nat. Buenos Aires 14:116. 1911. *Nomen nudem*. Though this name is without a description, a duplicate of a specimen in US! from the Hackel Herbarium is typical *Chloris pluriflora*.

Trichloris lilloi Parodi, Physis 9:256. 1928. (HOLOTYPE: "Argentina, Tucuman, Esquina Grande, Departamento de Chieligasta . . . Jorgensen, no. 1396." Not seen, but description and accompanying illustration clearly refer to *Trichloris pluriflora*.)

Stoloniferous or tufted perennial up to 1.5 m tall; sheaths glabrous to sparsely hirsute; ligule ciliate, cilia up to 3 mm long; blades up to 30 cm long, up to 1 cm wide, scabrous to sparsely hirsute above and below; spikes seven to twenty, up to 20 cm long, erect, in few, rather distant verticils; spikelets densely arranged on the rachis, averaging ea seven to nine per cm of the scabrous rachis; glumes lanceolate to narrowly lanceolate, glabrous except for the scabrous midnerve; first glume 2 to 3 mm long, ea 0.2 to 0.3 mm wide; second glume 3 to 5 mm long, ea 0.5 mm wide; fertile florets one or two, occasionally a third with rudimentary pistils and stamens, narrowly lanceolate, 3 to 5 mm long, margins short-ciliate near the middle, upper portions sparsely scabrous, otherwise glabrous, central awn 8 to 12 mm long, lateral awns 0.5 to 1.5 mm long; sterile florets two or three (very rarely only one), the lower often with rudimentary pistils and stamens, narrowly lanceolate; lowermost sterile floret 1.5 to 3.0 mm long, ea 0.3 mm wide; upper sterile florets progressively reduced, margins sometimes short-ciliate near the middle, otherwise glabrous, central awn up to 8 mm long, lateral awns ea 0.2 to 1.0 mm long; caryopsis 1.8 to 2.2 mm long, ea 0.5 mm wide, ea 0.2 mm thick, strongly dorsally flattened; chromosome number $2n=80$.

Chloris pluriflora is most similar to *C. mollis* (a Central and South American species) and to *C. pumilio* and *C. lobata* (both from Australia). It may be separated from all three in having usually two or more sterile florets. In addition, the presence of the lateral awns will differentiate it from *C. mollis*. Neither of the

Australian species has the sterile floret with a bearded callus.

The presence of the lateral awns in *Chloris pluriflora* and in some Australian species would suggest a close relationship, but there are many features that are not shared; and I believe the similarity is superficial.

Chloris mollis is very similar phenetically, lacking only the well-developed lateral awns; I believe that it and *C. pluriflora* are closely related.

For many years *Chloris pluriflora* has been placed in *Trichloris*, along with *C. crinita*. Arguments for the merger of the two genera were presented by Clayton (1967). Earlier in the present study, I discussed the difficulty of maintaining *Trichloris* as a separate genus.

Chloris pluriflora is found in the southwestern United States, northern Mexico, and South America (Fig. 55).

Representative specimens examined: ARGENTINA: Prov. Buenos Aires: Palermo, *Burkart* 4,658 (US); Prov. Catamarca: Andalgalá, *Jorgensen* 1,396 (US); Prov. Córdoba: without location, *Stuckert* 8,959 (US); Prov. Jujuy: Ceoro Moreno, *Venturi* 8,191 (US); Prov. Salta: Coronel Moldes, *Bartlett* 19,646 (US); Prov. Santiago del Estero: C. Pelligrini, *Venturi* 5,716 (US); Prov. Tucumán: Barranca Colorado, *Venturi* 810 (US). BOLIVIA: Villa-



Fig. 55. Distribution of *Chloris pluriflora*. Inset A: Southern United States, Mexico, Central America, and Caribbean Islands.

montes, anon., K. Pflanz no. 2,097 (US). CUBA: Prov. Habana: Casa Blanca, *Ekman* 16,879 (US). ECUADOR: Prov. Loja: between La Toma and Loja, *Hitchcock* 21,400 (US). GUATEMALA: Peten, Tikal National Park, *Lundell* 16,066 (US). MEXICO: Coahuila: Sabinas, *Nelson* 6,827 (US); Nuevo León: 12 mi S of Monterrey, *Mueller* 375 (US); Oaxaca: Cañon de Santa Catarina, *Conzatti* 3,985 (US); Tamaulipas: Podilla, *Swallen* 1,734 (US). PARAGUAY: Asunción, Puerto Casado, *Rojas* 2,307 (US). PERU: Cuzco, *Gunther* 66.5 (US). UNITED STATES: Texas: Cameron Co., Resaca del Rancho Viejo, 6 mi NE of Brownsville, *Cory* 51,411 (US); Duval Co., 2 mi SW of Benavides, *Harvey* 895 (US); Kleberg Co., W of Kingsville, *Swallen* 10,258 (US); Webb Co., Laredo, *Griffiths* 6,542 (US); Wil-lacy Co., E of Raymondville, *Swallen* 10,100 (US).

38. **CHLORIS CUCULLATA** Bischoff, Ann. Sci. Nat. Bot. (Paris) III. 19:357. 1853. (TYPE: "Provincia Tamaulipas prope Matamoros . . . Engelman, 1849". Not seen, but description clearly refers to this taxon.) Fig. 56, A-K.

Perennial, tufted, erect, 15 to 60 cm tall; sheaths glabrous; ligule a crown of very short hairs; blades 2 to 4 mm wide, up to 20 cm long, often greatly reduced in size upward on the culm, glabrous to scabrous; spikes ten to twenty, 2 to 5 cm long, borne in several close, radiating verticils at the apex of the culm, flexuous or curved; spikelets densely inserted on the scabrous rachis, averaging 14 to 18 per cm of rachis, spreading at nearly right angles, straw-colored at first, later becoming fuscous; glumes lanceolate to obovate, glabrous except for the scabrous midnerve, membranous; first glume 0.5 to 0.7 mm long, 0.4 to 0.5 mm wide, ovate to broadly lanceolate; second glume 1.0 to 1.5 mm long, 0.4 to 0.6 mm wide, obovate; fertile lemma 1.5 to 2.0 mm long, 0.7 to 1.0 mm wide, broadly elliptic, apex obtuse, callus short-bearded, keel and marginal nerves appressed-pilose, otherwise glabrous, awn 0.3 to 1.5 mm long; sterile floret one, 1.0 to 1.5 mm long, 1.0 to 1.5 mm wide, markedly inflated with the upper margins inrolled, unawned or with a short awn up to 1.5 mm long; earyopsis 0.9 to 1.2 mm long, ca 0.5 mm wide, obovoid, rounded to trigonous; chromosome number $2n=40$.

Chloris cucullata is quite distinct from most other species in the genus. It hybridizes readily with *C. andropogonoides* and *C. verticillata*, but,

in pure form, it differs markedly from these two species (see Table 11 and Fig. 56, A-K, L-U; 5S, D-K). A complete discussion of the hybridization and introgression between these species follows the description and discussion of *C. andropogonoides* (p. 95).

Chloris cucullata is widely distributed throughout much of Texas and is also found in adjacent areas of New Mexico and Mexico (Fig. 57, shaded circles). It is a common roadside or waste area weed in many areas.

Representative specimens examined: NOTE: Additional citations may be found in the list of hybrid populations studied following the discussion of introgression and hybridization of *C. cucullata*, *C. verticillata*, and *C. andropogonoides*.) MEXICO: Nuevo León: below La Boea Canyon, R. F. Smith M596 (TEX). Tamaulipas: 34 mi S of Matamoros, *Crutchfield and Johnston* 5,475 (TEX); 5 km S of Nuevo Laredo, *Dominguez* 53 (TEX); 24 km S of Nuevo Laredo, *Dominguez and McCart* 8,208 (TEX). UNITED STATES: New Mexico: Chaves Co., 21 m E of Roswell along Hwy. 380, *Anderson* 4,740 (HSC); Dona Ana Co., Las Cruces, *Plank s.n.*, July 1894 (NY); Eddy Co., 21 mi NW of Carlsbad, *Gould and Kapadia* 9,543 (TEX). Texas: Andrews Co., 8 mi NW of Andrews, *Rowell* 5,879 (TEX); Armstrong Co., Palo Duro Canyon, *Goodman* 5,178 (TEX); Atascosa Co., 1 mi N of Pleasanton, *Tharp and Johnston* 541,745 (TEX); Bastrop Co., 2 mi NE of Cedar Creek, *McCart* 5,725 (TEX); Baylor Co., Seymour, *Reverchon* 3,440 (US); Bexar Co., San Antonio, near Lake Mitchell, *Hitchcock* 1,269 (UC); Brooks Co., 2.5 mi E of Falfurrias, *Gould, Reeves, and Morrow* 6,603 (TEX, UC); 4 mi SE of Encino Division, King Ranch, *Gould and Morrow* 6,720 (TEX, UC); Burnet Co., 3 mi E of Buehanan Dam, *Gould, Brown, and Celarier* 5,476 (UC); Caldwell Co., 8 mi E of Luling, M. C. *Johnston* 6,215 (TEX); Cameron Co., Laguna Atascosa Wildlife Refuge, *Fleetwood* 3,472 (TEX); Colorado Co., Columbus, *Anderson* 3,282a (HSC); Comal Co., E of New Braunfels, near Mission Valley Mills, *Anderson* 3,888 (HSC); Duval Co., E of Crestonia, *Barkley* 13,003 (TEX); Ector Co., 18 mi W of Odessa, *Warnock* 7,902 (TEX); Frio Co., 4 mi E of Zavala Co. line on Hwy. 76, M. C. *Johnston* 6,192a (TEX); Garza Co., E of Post, *Tharp and Gimbrede* 51-1,562 (TEX); Gonzales Co., Athens, *Tharp and Higdon s.n.*, 23 Apr 1938 (TEX); Hall Co., near Estelline, *Gould* 7,721 (UC); Hidalgo Co.: McAllen, vacant lot, *Anderson* 3,876 (HSC); Santa Ana National Wildlife Refuge, M. C. *Johnston*

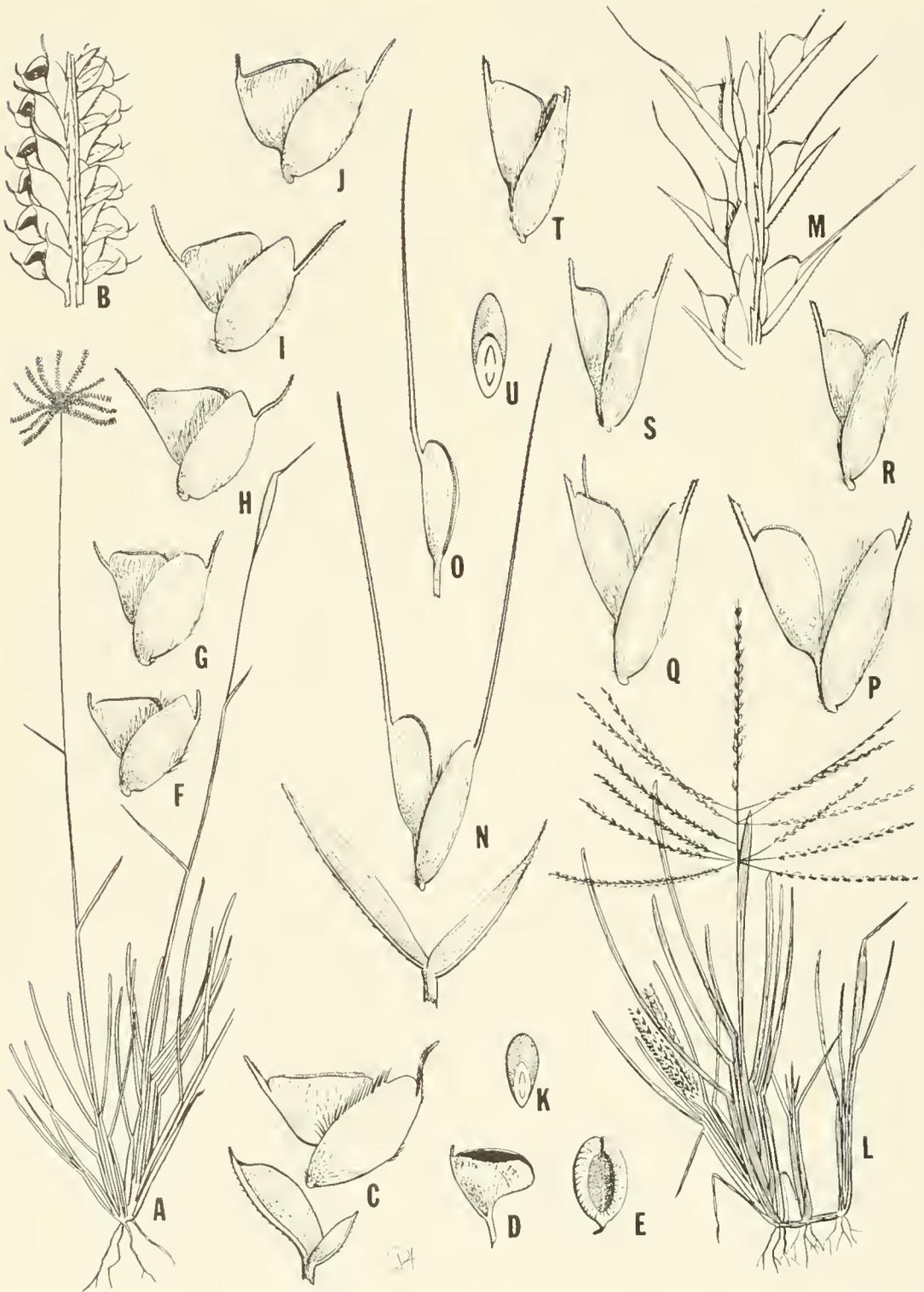


Fig. 56. *Chloris cucullata* and *C. verticillata*. (A-K) *C. cucullata*. (A) habit, $\times 1/4$; (B) portion of spike, upper (left) and lower side (right), $\times 4$; (C) spikelet, partly dissected, $\times 10$; (D-E) sterile floret, viewed from above, $\times 10$; (F-J) florets, showing variation, $\times 10$; (K) caryopsis, $\times 10$. (L-U) *C. verticillata*. (L) habit, $\times 1/4$; (M) portion of spike, upper side (left) and lower side (right), $\times 4$; (N) spikelet, partly dissected, $\times 10$; (O) sterile floret, $\times 10$; (P-T) florets, showing variation, $\times 10$; (U) caryopsis, $\times 10$.

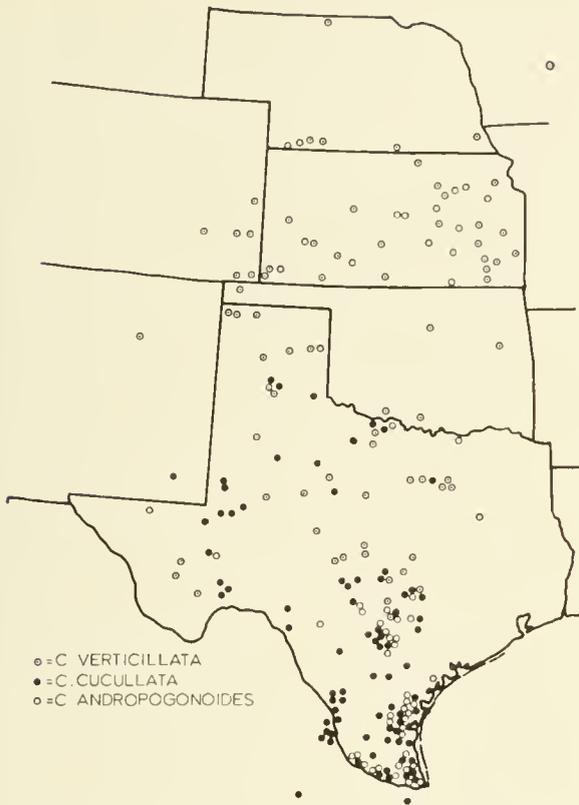


Fig. 57. Distribution of *Chloris cucullata* (shaded circles), *C. verticillata* (dotted circles), and *C. andropogonoides* (open circles).

53-674 (TEX); Jim Hogg Co., 30 mi S of Hebronville, *Tharp* 5,912 (TEX); Jim Wells Co., Romarsid Ranch, *Freeborn and Freeborn* 524 (TEX); Karnes Co., Karnes City, *J. C. Johnson* 813 (TEX); Kenedy Co., 2 mi S of Sarita, *Anderson* 3,305 (HSC); King Ranch, Norias Division, *M. C. Johnston* 5,319.77 (TEX); Kleberg Co., King Ranch, Santa Gertrudis Division, *M. C. Johnston* 5,319.76 (TEX); King Ranch, Laureles Division, *M. C. Johnston* 5,319.81 (TEX); 2 mi N of Kingsville, *Swallen* 10,085 (US); La Salle Co., 3 mi S of Dilley, *Painter and Barkley* 14,310 (TEX); Live Oak Co., *Tharp and Gimbrede* 52-552 (TEX); Llano Co., Enchanted Rock, *Webster* 47,261 (TEX); McMullen Co., 10 mi S of Tilden, *Alvarez et al.* 7,714 (TEX); Mason Co., 18 mi N of Fredricksburg, *Emery* 814 (TEX); Midland Co., Midland, *Tracy* 7,962 (TEX); Nolan Co., 10 mi S of jct. of Hwys. 126 and 53, *Anderson* 4,651 (HSC); Nueces Co., ca 1 mi N of Kingsville, *Anderson* 3,302 (HSC); Corpus Christi, *Heller s.n.*, 14-21 Mar 1894 (UC, US); Mustang Island, ¼ mi S of Port Aransas, *Anderson* 3,293 (HSC); Pecos Co., 6 mi N of Ft. Stockton, *Warnock* T464 (TEX); Randall Co., Palo Duro

Canyon, *Reed* 3,984 (TEX); San Patricio Co., Welder Wildlife Refuge, near Sinton, *Gould and Hycka* 8,020 (UC); Starr Co., 6 mi NW of La Gloria, *Sanchez et al.* 8,333 (TEX); Stonewall Co., Double Mt., *Tharp and Gimbrede* 51-1,551 (KANU, TEX); Tarrant Co., Ft. Worth, *McMullen s.n.*, Aug-Oct 1927 (TEX); Taylor Co., Abilene State Park, *Henderson* 63-899 (TEX); Terrell Co., 25 mi S of Sheffield, *Gould* 9,699 (TEX, UC); Travis Co.: Camp Mabry, Austin, *Tharp s.n.*, 21 Apr 1938 (TEX); near Bee Caves, jct. of Hwys. 620 and 71, *Anderson* 3,273 (HSC); east end of Mansfield Dam, *Anderson* 3,274 (HSC); Val Verde Co.: 9 mi S of Del Rio, along Hwy. 277, *Anderson* 4,466 (HSC); 35 mi N of Del Rio, near Loma Alta, *Warnock and McBryde* 15,154 (TEX); Ward Co., 1 mi NE of Sand Hills, *Rose-Innes and Moon* 183 (TEX); Webb Co.: Laredo, *Martinez and Trevino* 3 (TEX); 40 mi NW of Laredo, *Emery* 668 (TEX); Wichita Co.: Wichita Falls, *McKee s.n.*, Sept 1927 (TEX); Red River, above Burkburnett, *Tharp s.n.*, 20 July 1921 (TEX); Willacy Co.: 2.5 mi S of Ytturia, *Anderson* 3,311 (HSC); Redfish Bay, *Tharp s.n.*, 5 Mar 1934 (TEX); 7 mi N of Raymondville, *Tharp and Brown* 3,232 (TEX); Wilson Co., *Parks s.n.*, 25 Dec 1946 (TEX); Zapata Co., 19 mi S of Laredo, *Martinez and Trevino* 37 (TEX).

39. CHLORIS VERTICILLATA Nuttall, Trans. Amer. Philos. Soc., n.s. 5:150. 1837. (HOLOTYPE: "... Arkansas. Wm. Nuttall" Photograph of type, from PH, in US! ISO-TYPE: K!) Fig. 56, L-U.

Perennial 14 to 40 cm tall, tufted, erect or decumbent, sometimes rooting at the lower nodes; sheaths glabrous; ligule a ciliate crown with some hairs up to 2 mm long; blades to 15 cm long, 2 to 3 mm wide, glabrous to scabrous; spikes ten to sixteen, 5 to 15 cm long, usually in several verticils, these separated by 5 mm or more, inflorescence terminating in a vertical spike; spikelets sparsely inserted, averaging ca four to seven per cm of the scabrous rachis, appressed; glumes lanceolate, membranous, glabrous except for the scabrous midnerve; first glume 2 to 3 mm long, ca 0.3 mm wide; second glume 2.8 to 3.5 mm long, 0.3 to 0.4 mm wide; fertile lemma 2.0 to 3.5 mm long, 1.5 to 1.9 mm wide, elliptic to lanceolate, callus bearded, keel glabrous to appressed-pilose, margins appressed-pubescent, apex acute to somewhat obtuse, awn 4.8 to 9.0 mm long; sterile floret one, 1.1 to 2.3 mm long, 0.5 to 1.0 mm wide, oblong, somewhat inflated, trun-

cate, glabrous, awn 3.2 to 7.0 mm long; caryopsis 1.3 to 1.5 mm long, ca 0.5 mm wide, ellipsoid, rounded to trigonous; chromosome number $2n = ca\ 28, 40, 63$.

Chloris verticillata resembles the Australian *C. truncata*; it differs in having a single sterile floret (rarely two). *Chloris verticillata* also has several somewhat remote verticils of spikes terminated by a single erect spike, while *C. truncata* has a single verticil and lacks a terminal spike.

Chloris verticillata, *C. andropogonoides*, and *C. cucullata* introgress in Texas. A discussion of this follows the treatment of *C. andropogonoides*.

Chloris verticillata (commonly called "windmill grass") is widely distributed in the central United States, where it is commonly found as a weed of roadside, lawn, or waste areas (Fig. 57, dotted circles). Disturbance, cultivation, and overgrazing have largely eliminated much of the native vegetation in this area, but early records (Barkley, 1965) indicated that windmill grass was found in generally low areas of the native prairie.

Representative specimens examined: UNITED STATES: Arizona: Gila Co., 7 mi W of Young, anon. (UC). Colorado: Baca Co., Sand Canyon, 25 mi S of Pritchett, *C. L. Porter* 4,272 (TEX); Cheyenne Co., near Cheyenne Wells, *Harrington and Smith* 384 (UC); Crowley Co., Rocky Ford, *Harrington* 685 (UC); Powers Co., 10 mi W of Lamar, *Harrington* 724 (UC). Iowa: Story Co., Ames, *J. P. Smith* 2,597 (HSC). Kansas: Anderson Co., 3 mi S of Garnett, *Horr and McGregor* 3,591 (KANU, TEX); Barber Co., 1 mi W of Medicine Lodge, *McGregor* 14,029 (KANU); Bourbon Co., 1 mi S of Uniontown, *Ungar III* (KANU); Chase Co., 4 mi E of Marion, *Horr* 3,497 (KANU, TEX); Chautauqua Co., roadside grassland, *Horr* 1,540 (KANU); Clay Co., waste ground, *Imler s.n.*, 14 Jun 1929 (KANU); Coffee Co., Burlington, *Anderson* 2,765 (HSC); Dickinson Co., without precise location, *Imler s.n.*, 15 Jun 1929 (KANU); Ellis Co., 6 to 7 mi SW of Hays, *Rydberg and Imler* 1,248 (KANU); Ellsworth Co., 1 mi E of Terra Cotta, *McGregor* 9,212 (KANU); Finney Co., Garden City, *Kellerman s.n.*, 20 Aug 1882 (KANU); Ford Co., 1 mi NW of Ford, *Hulbert* 3,207 (KANU); Geary Co., waste land, *Imler s.n.*, 15 Jun 1929 (KANU); Grant Co., *Thompson* 55 (UC); Greenwood Co., 3.5 mi W or Woodson Co. line on Hwy. 54, *Lathrop* 3,186 (KANU); Harvey Co., 8.7 mi E of Newton, *Harms* 2,192 (KANU, UC); Kiowa Co., 7 mi SE of Haviland, *Horr*

and *McGregor* 3,785 (KANU, UC); Meade Co., County Park, *Horr* 3,272 (KANU); Montgomery Co., 1 mi N of Independence, along Hwy. 75, *Anderson* 2,761 (HSC); Morris Co., 4 mi SE of Council Grove, *Richards* 1,788 (KANU); Morton Co., 7.3 mi N of Elkhart, *Richards* 2,492 (KANU); Neosho Co., 5 mi E of Erie, *Holland* 488 (KANU); Osage Co., Lyndon, *Anderson* 2,766, 2,767 (HSC); Pottawatomie Co., without precise locality, *Imler s.n.*, 13 Jun 1929 (KANU); Republic Co., T4S, R2W, sec. 22, *Morley* 1,227 (KANU); Riley Co., without precise location, *Gates* 12,801 (UC); Shawnee Co., near Wakarusa, *Anderson* 2,768, 2,769 (HSC); Stafford Co., 8 mi NE of Hudson, *McGregor* 10,515 (KANU); Wichita Co., grassland, *Agrelius s.n.*, 12 Aug 1912 (KANU); Wilson Co., 8 mi N of Neodesha, along Hwy. 75, *Anderson* 2,762, 2,763 (HSC); Woodson Co., T24S, R14E, sec 21, *Lathrop* 471 (KANU). Missouri: Atherton, *Bush* 7,352B (TEX). Nebraska: Cherry Co., Valentine, *Tolstead* 4-463 (NEB); Dundy Co., 3 mi S of Benkelman, *Anderson* 2,774, 2,776 (HSC); Hitchcock Co., Swanson Reservoir, *Anderson* 2,772 (HSC); Nemaha Co., Auburn, *Anderson* 2,770 (HSC); Nickolls Co., Superior, *Bates* 6,635 (NEB); Redwillow Co., Indianola, *Anderson* 2,771 (HSC). New Mexico: Curry Co., 14 mi W of Melrose, along Hwy. 60, *Anderson* 4,663 (HSC); San Miguel Co., Las Vegas, *Whitehouse s.n.*, 3 Sept 1929 (UC). Oklahoma: Cimarron Co., 6 mi E of Kenton, *Rogers* 5,933 (TEX); Cotton Co., 5 mi N of Burkburnett, *Rose-Innes and Moon* 973 (TEX); Muskogee Co., rocky soil, *Bebb s.n.*, 8 Sept 1940 (TEX); Payne Co., W of Stillwater, *Estes* 57 (TEX). Texas: Anderson Co., Engeling Wildlife Management area, *Calley and Marsh* 13 (TEX); Archer Co., 7 mi S of Windthorst, *Anderson* 3,921 (HSC); Bell Co., old Tennessee Valley community site, *York and York* 54,447 (TEX); Brewster Co., 24 mi E of Alpine, along Hwy. 90, *Anderson* 4,447 (HSC); Altuda Pass, Glass Mts., *Warnock* W362 (TEX); Burnet Co., Longhorn Caverns State Park, near Marble Falls, *Silveus* 7,642, 7,643 (TEX); Clay Co., Prospect Hill, *Silveus* 117 (TEX); Comanche Co., DeLeon, *Anderson* 3,919 (HSC); Culberson Co., McKittrick Canyon, Guadalupe Mts., *Fischer s.n.*, 20 Jul 1950 (KANU); Dallam Co., 21 mi NW of Dalhart, *Rowell* 5,385a (TEX); Dallas Co., Dallas, common on prairie, *Bush* 1,164 (US); Garza Co., 3 mi E of Post, *Tharp and Gimbrede* 51-1,558 (TEX); Gray Co., 5 mi W of Pampa, *Brown* 3,382 and *Tharp* GR 239 (TEX); Hays Co., W of Wimberly, *J. C. Johnson* 258 (TEX); Hemp-

hill Co., 5 mi E of Canadian, *Rowell* 4,078, 4,174 (TEX); Howard Co., Big Spring, *Hitchcock* 13,366 (US); Hudspeth Co., 4 mi NW of Sierra Blanca, *Anderson* 4,420 (HSC); Jones Co., eastern part of county, *Tharp and Gimbrede* 51-1,556 (TEX); Lampasas Co., N of Lampasas, *Silveus* 7,540 (TEX); Menard Co., Ft. McCavett, *Tharp* 5,224 (TEX); Mills Co., Priddy, *Anderson* 3,918 (HSC); Nolan Co., 10 mi S of jet. Hwys. 126 and 53, along 53, *Anderson* 4,650 (HSC); Palo Pinto Co., 0.5 mi N of Strawn, *Anderson* 3,920 (HSC); Parker Co., SW of Weatherford, *Silveus* 7,543 (TEX); Pecos Co., 5 mi E of Brewster-Pecos Co. line, along Hwy. 90, *Anderson* 4,460 (HSC); Potter Co., N of Amarillo, *Brenckle* 48,302 (US); Randall Co., near Palo Duro Canyon, *Young s.n.*, Sept 1917 (TEX); Runnels Co., 0.5 mi N of Ballinger, *Anderson* 4,641 (HSC); San Saba Co., Richland Springs, *Anderson* 3,333 (HSC); 2.1 mi SE of San Saba, *Cory* 58,249 (UC); Sherman Co., 18 mi S of Stratford, *Weaver and McLaughlin*, without number or date (TEX); Sterling Co., Sterling City, park, *Anderson* 3,002 (HSC); Tarrant Co., near Ft. Worth, *Ruth* 302 (NY, UC); Taylor Co., Camp Berkeley, *Tolstead* 7,445 (UC); Travis Co., Bee Caves, *Anderson* 3,272 (HSC); Wichita Co., Burkburnett, *Anderson* 3,923 (HSC); Wichita Falls, *McKee s.n.*, June 1927 (TEX); Williamson Co., N of Leander, *Johnston and McCart* 5,279 (TEX).

40. **CHLORIS ANDROPOGONOIDES** Fournier, *Mex. Pl.* 2:143. 1886. (HOLOTYPE: "Mexique: Prov. de San Luis. Virlet d'Aoust. 1851. 1462." P! The specimen is depauperate, probably from overgrazing, but the spikelets are those of the species as commonly understood.) Fig. 58, D-K.

Chloris tenuispica Nash, *Bull. Torrey Bot. Club* 25:436. 1898. (HOLOTYPE: "... Nealley ... 1889." US!)

Perennial 10 to 40 cm tall, tufted to shortly stoloniferous; sheaths glabrous; ligule a short, naked crown; blades ca 1 mm wide, to 15 cm long, glabrous to scabrous except basally sparsely pilose; spikes six to thirteen, 4 to 15 cm long, usually radiate in a single series, occasionally a second poorly developed verticil produced above; spikelets distant, ca four to seven per cm of the scabrous rachis, appressed; glumes narrowly lanceolate, acute, thin, glabrous except for the scabrous midnerve; first glume 2.0 to 2.3 mm long, ca 0.2 mm wide; second glume 3.0 to 3.3 mm long, ca 0.3 mm wide; fertile

lemma 1.9 to 2.7 mm long, 0.5 to 0.6 mm wide, narrowly lanceolate to elliptic, apex acute, callus bearded, margins and keel appressed-pilose, otherwise glabrous, awn 1.9 to 5.2 mm long; sterile floret one, 0.9 to 1.7 mm long, 0.25 to 0.5 mm wide, narrowly cylindrical, apex obtuse, glabrous, awn 2.5 to 3.5 mm long; caryopsis 1.3 to 1.4 mm long, ca 0.4 mm wide, ellipsoid, rounded to trigonous; chromosome number $2n=40$.

Chloris andropogonoides is similar to *C. verticillata* and *C. texensis*. It may be separated from the former by its single verticil of spikes, generally shorter awns, and narrower sterile florets (Figs. 56, L-U; 58, A-C, D-K). Additional differences are given in Table 11.

Chloris andropogonoides is generally smaller in spikelet dimensions than *C. texensis* but differs more obviously in having spikes that are floriferous to near the base, while the spikes of *C. texensis* are naked for several cm above the base.

As discussed in the following section, *Chloris andropogonoides*, *C. cucullata*, and *C. verticillata* are involved in extensive hybridization and introgression in Texas.

Chloris andropogonoides is restricted primarily to grassy roadsides and prairie relicts of the coastal plain of southern Texas and northeastern Mexico (Fig. 57, open circles). Occasional very widely separated populations may be found farther inland, as at Rock Springs, Texas (Fig. 64).

Representative specimens examined: MEXICO: Coahuila, Musquiz Palm Canyon, *Marsh* 984 (TEX); Tamaulipas: 1 mi E of Ejido de San Lazaro, 24°35'N, 99°13'W, *Graham and Johnston* 4,291 (TEX); El Canelo Ranch, 24 mi N of San Fernando, *M. C. Johnston* 4,880 (TEX). UNITED STATES: Texas: Aransas Co., Rockport, *A. Chase* 6,067 (US); Atascosa Co., 3 mi S of Hindes, *M. C. Johnston* 6,197 (TEX); Bee Co., 2.6 mi N of Skidmore, *Anderson* 2,699 (HSC); Bexar Co., 7 mi N of San Antonio, *M. C. Johnston* 2,409 (TEX); Caldwell Co., near Luling, *Silveus* 4,170-A (TEX); Cameron Co.: 10 mi E of Brownsville on Hwy. 4, *Anderson* 3,318 (HSC); Laguna Atascosa National Wildlife Refuge, *Fleetwood* 3,374 (TEX); levee of Resaca de la Gringa, *M. C. Johnston* 542,186 (TEX); Comal Co., E of New Braunsfels, near Mission Valley Mills, *Anderson* 3,889 (HSC); Edwards Co., substation no. 14, *Cory* 52,467 (US); Hays Co., 2 mi W of San Marcos, *Emery* 835 (TEX); Hidalgo Co., Santa Ana National Wildlife Refuge, *Fleetwood* 3,161, 3,373 (TEX); Jim Wells Co., King Ranch, Santa Gertrudis Division, *M. C. Johnston* 542,104

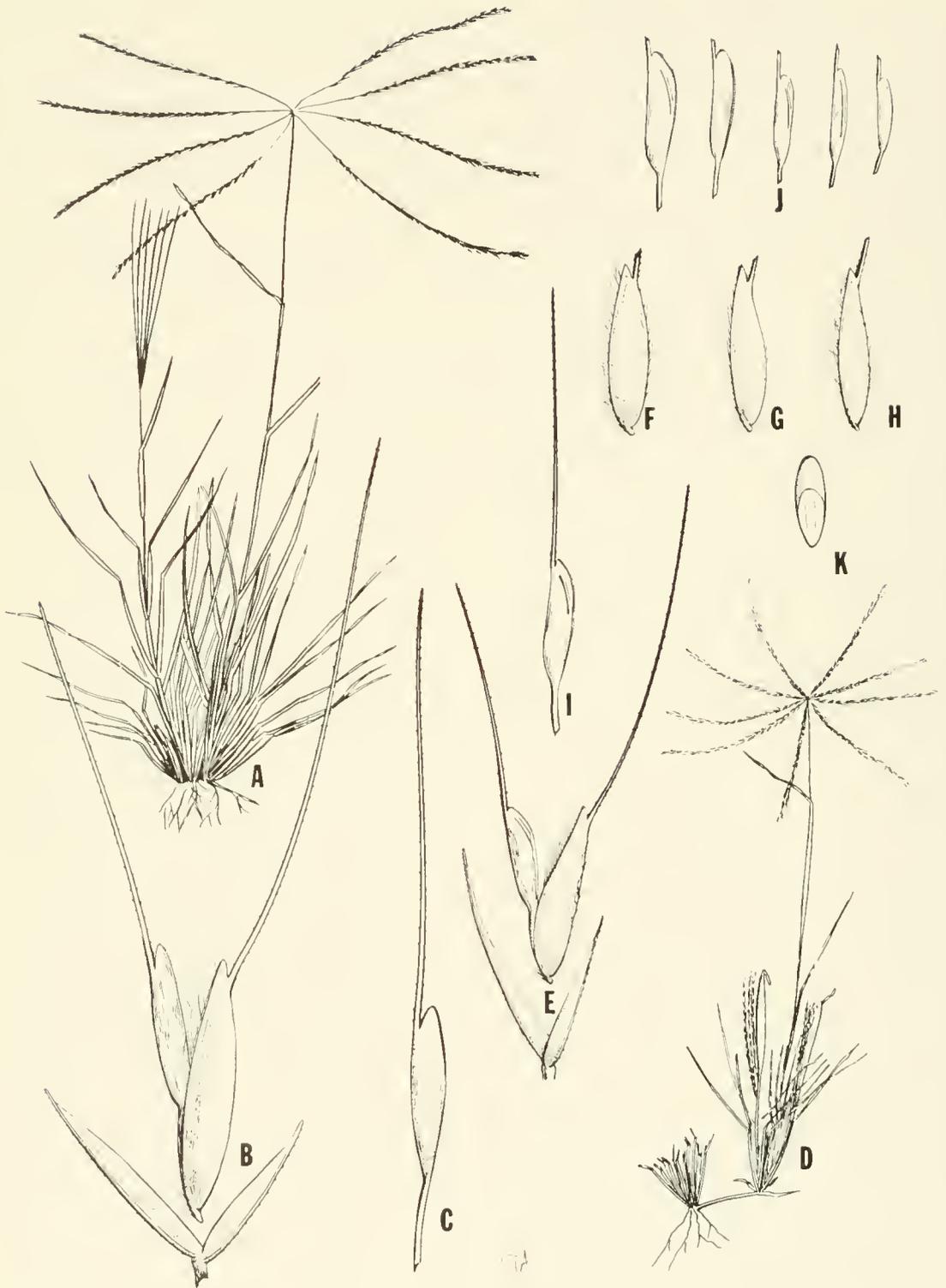


Fig. 58. *Chloris texensis* and *C. andropogonoides*. (A-C) *C. texensis*. (A) habit, x 1/4; (B) spikelet, partly dissected; (C) sterile floret. (D-K) *C. andropogonoides*. (D) habit, x 1/3; (E) spikelet, partly dissected; (F-H) fertile lemmas, showing variation; (I) sterile floret; (J) group of sterile florets, showing variation; (K) caryopsis. (B, C, E-K) x 10.

Table 11. Characteristics differentiating *Chloris cucullata*, *C. verticillata*, and *C. andropogonoides*.

Characteristic	<i>C. cucullata</i>	<i>C. verticillata</i>	<i>C. andropogonoides</i>
Height	15-60 cm	14-40 cm	10-40 cm
Length of spikes	2-5 cm	5-15 cm	4-15 cm
Number of verticils	2 or 3	2-5 cm	usually 1
Relative distance between verticils	very close together, appearing to arise from same point	usually well separated, 5 mm or more apart	
Number of spikelets per cm length of spike	14-18	4-7	4-7
Lemma length	1.5-2.0 mm	2.0-3.5 mm	1.9-2.7 mm
Lemma awn length	0.3-1.5 mm	4.8-9.0 mm	1.9-5.2 mm
Sterile floret			
Length	1.0-1.5 mm	1.1-2.3 mm	0.9-1.7 mm
Width	1.0-1.5 mm	0.5-1.0 mm	0.25-0.5 mm
Length/Width	0.6-1.5	1.6-3.0	2.7-4.8
Length of awn	0-1.5 mm	3.2-7.0 mm	2.5-3.5 mm
Method of seed dispersal	spikelets falling from spike at maturity	tumbleweed, culm dehisces at uppermost node, allowing inflorescence to break from plant at maturity and roll	tumbleweed, culm dehisces at uppermost node, allowing inflorescence to break from plant at maturity and roll

(TEX); Alice, *J. G. Smith s.n.*, 7 June 1897 (US); Kenedy Co., King Ranch, Norias Division, *Swallen 10,211* (US); Kerr Co., Kerrville, *Hitchcock 5,265* (UC); Lacey's Ranch, *Palmer II,230* (UC); Kleberg Co., King Ranch, Laureles Division, *M. C. Johnston 541,147* (TEX); between Kingsville and Ricardo, *Swallen 10,091* (US); Nueces Co., near Agua Dulce Creek, 10 mi W of Chapman Ranch, *Anderson 3,297* (HSC); San Patricio Co., Portland, *Silveus 50* (US); Starr Co., 1 mi S of Rio Grande City, *Anderson 4,524* (HSC); N of Roma, *Tharp 47,438* (TEX); Travis Co., Barton Springs, *Higdon 5* (TEX); Willacy Co., E of Raymondville, *Silveus 7,313* (TEX); Lyford, *Tharp 7,644* (TEX, US).

Hybridization and Introgression
Involving *Chloris cucullata*, *C. verticillata*,
and *C. andropogonoides*

The identification of specimens of *Chloris* from central and southern Texas often presents a difficult problem as characteristics of *C. cucullata*, *C. verticillata*, and *C. andropogonoides* seem to blend and recombine in various ways. "Pure" populations are well defined and may be keyed with few problems. The characteristics of such populations are presented in Table 11 and Figure 59.

Of these characters, the length of the lemma awn and the width of the sterile floret gave the best separation of all three species; these features were chosen as the main axes of the

scatter diagrams to follow. Of the remaining characters, the best for distinguishing all three species are the length of the spikes, the number of spikelets per unit length of the spike, the distance between successive verticils, and lemma shape. These are indicated on the scatter diagrams by radiating lines attached to the glyph.

Fig. 59 shows the disposition of selected specimens of *Chloris cucullata*, *C. verticillata*, and *C. andropogonoides* plotted by using the characters described above. Each sample entered into Fig. 59 is a single specimen chosen

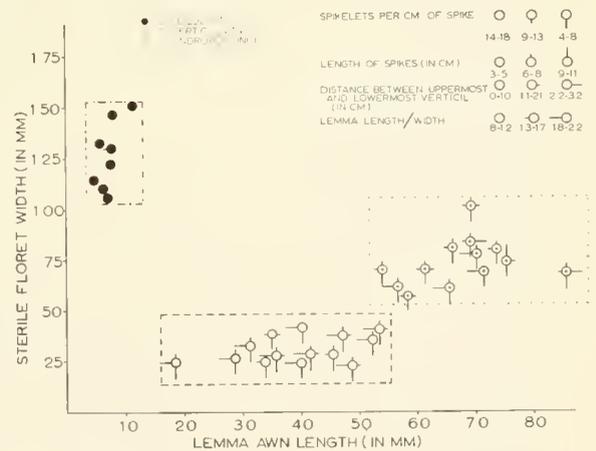


Fig. 59. Scatter diagram of selected specimens representing pure populations of *C. cucullata* (upper left), *C. verticillata* (right middle), and *C. andropogonoides* (lower middle).

from populations containing only one of the three species. In the case of *C. verticillata*, this presented little problem as the natural range of this species extends far to the north of the ranges of the other two (Fig. 57). Thus, the samples of *C. verticillata* used in Fig. 59 are representative of populations from Oklahoma, Kansas, Nebraska, and Colorado. The examples of *C. cucullata* and *C. andropogonoides* chosen for Fig. 59 were selected from those populations in Texas that had plants of only one species present and in which the other species were not present nearby.

From Fig. 59 it may be seen that the three species are well defined. *Chloris cucullata* stands well apart from the other two taxa on the basis of all six characters used. *Chloris verticillata* and *C. andropogonoides* are somewhat closer but are easily separated by the simultaneous use of sterile floret width and lemma awn length (see Fig. 56, L-U, 58, D-K). In addition, *C. andropogonoides* usually has longer and narrower lemmas than *C. verticillata*. The dashed lines drawn around each of the three species groupings in Fig. 59 represent the approximate range of variation of lemma awn length and sterile floret width on the specimens studied; these will be reproduced as frames of reference in the scatter diagrams to follow.

Chromosome numbers of $2n=40$ have been reported several times for all three taxa. A chromosome number of $2n=ca\ 28$ has been reported once by Gould (1960).

The collection sites sampled for cytological and mass collections of hybrid populations are shown on the map in Fig. 60 and listed in Table 12. For convenience of discussion, these areas are given the names of nearby landmarks or population centers.

In the illustrations of individual populations following, unshaded squares (\square) represent

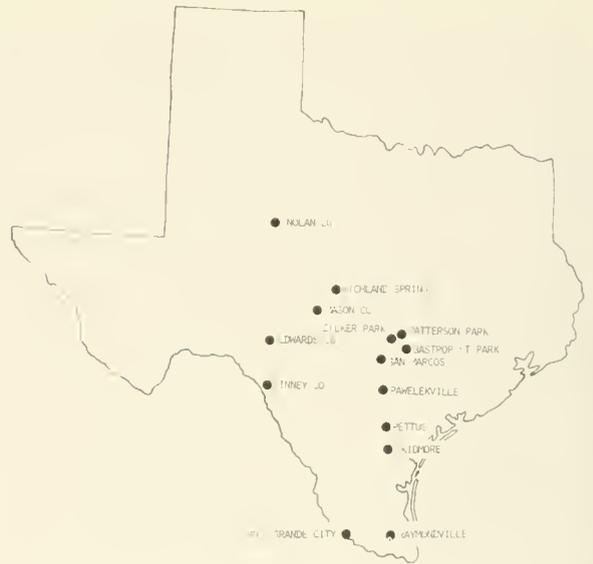


Fig. 60. Location of collecting areas sampled for introgression studies.

those plants in which virtually all of the pollen mother cells examined showed normal meiotic figures. Fully shaded squares (\blacksquare) depict those plants in which nearly all of the pollen mother cells or their products showed meiotic irregularity, including lagging chromosomes or chromosome fragments, micronuclei, multivalents, or excluded chromosomes. Half-shaded squares (\blacksquare) exemplify those plants in which less than 20 percent of the PMC's or their products showed meiotic aberrations. At least 25 PMC's were examined in determining the relative amount of meiotic regularity or irregularity of each plant plotted in the diagrams.

The following discussion of populations represents the different combinations of the three species involved: the three possible pairs of species and the combination involving all three species.

Table 12. Populations utilized in introgression studies (all from Texas)

Name of population	Species involved	Fig.
Bastrop State Park	anomalous	66
Edwards Co. (Rock Springs)	<i>C. andropogonoides</i> x <i>C. verticillata</i>	64
Kinney Co.	anomalous	68
Mason Co.	<i>C. cucullata</i> x <i>C. verticillata</i>	—
Nolan Co.	<i>C. cucullata</i> x <i>C. verticillata</i>	—
Patterson Park	<i>C. cucullata</i> x <i>C. verticillata</i>	61
Pawelekville	<i>C. cucullata</i> x <i>C. andropogonoides</i>	—
Pettus	<i>C. cucullata</i> x <i>C. andropogonoides</i>	—
Raymondville	<i>C. cucullata</i> x <i>C. andropogonoides</i>	63
Richland Springs	<i>C. cucullata</i> x <i>C. verticillata</i>	—
Rio Grande City	<i>C. cucullata</i> x <i>C. andropogonoides</i>	—
San Marcos	anomalous	69
Skidmore	anomalous	67
Zilker Park	<i>C. cucullata</i> x <i>C. andropogonoides</i> x <i>C. verticillata</i>	65

Chloris cucullata x *C. verticillata*

This hybrid type is well represented in Patterson Park, a city park in the northeast section of Austin, Texas (Fig. 60). In this area *Chloris cucullata* and *C. verticillata* and their introgressants form extensive colonies in disturbed areas, along roadways, paths, and in neglected sections of the park. This population is illustrated diagrammatically in the scatter diagram shown in Fig. 61 and in the photograph in Fig. 62.

The scatter diagram of the Patterson Park population shows a number of plants corresponding in all major characters with the "pure" populations of *C. cucullata* and *C. verticillata*. In addition, there are many intermediate forms that variously recombine the characters of these two species. In those specimens studied cytologically, the plants lying within the range of expected variation of the pure species have normal meiotic behavior, while those studied from the intermediate group show, for the most part, high percentages of irregular meiotic figures.

The Patterson Park population is just one of several showing this pattern of introgression. Others with similar characteristics, when represented in a graph, include Mason Co., Nolan Co., and Richland Springs (Fig. 60).

Chloris cucullata x *C. andropogonoides*

This population, represented graphically in Fig. 63, is found in a relatively stable grassland community along a railroad right-of-way near Raymondville, in southern Texas (Fig. 60). Many individuals of *Chloris andropogonoides* and *C. cucullata*, as well as intermediate plants, are found in this area. Two other species of *Chloris*, *C. gayana* and *C. ciliata*, are also com-

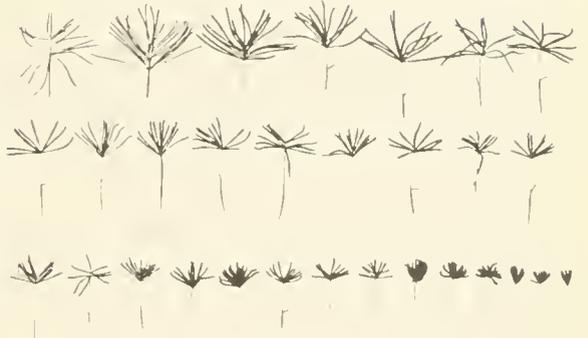


Fig. 62. Silhouette photograph of representative inflorescences of *Chloris* populations from Patterson Park, Travis Co., Texas.

mon in this area but are not involved in the percentage of any of the hybrids.

Again, the intermediate plants show a high frequency of meiotic irregularity. Unfortunately, preserved anthers of the parental species were too young for meiotic study. Several of the intermediate plants studied, however, showed higher chromosome numbers than the $2n=40$ reported for the parental species. Diploid counts of $2n=ca\ 60$ were most frequent, though the high degree of irregularity made exact counts impossible. Plants with $2n=ca\ 60$ could have resulted from the combination of reduced and unreduced gametes.

In this population the intermediates are well represented in the lower left quadrant of the graph. By comparison, the Patterson Park diagram (Fig. 61) shows a poor representation of intermediates in this section. This shift is largely influenced by variation in awn length and is to be expected in view of the differences

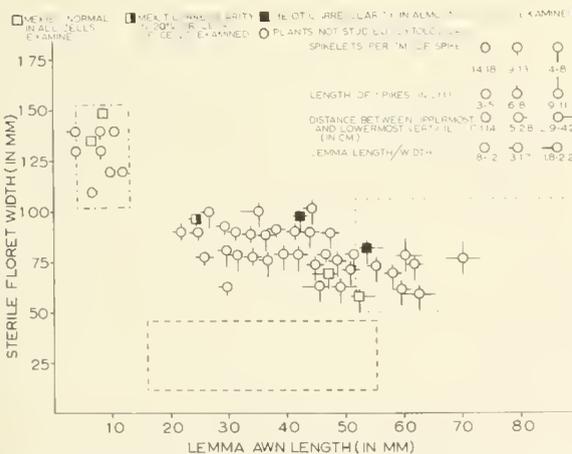


Fig. 61. Scatter diagram of population of *Chloris cucullata* x *C. verticillata* from Patterson Park, Austin, Texas.

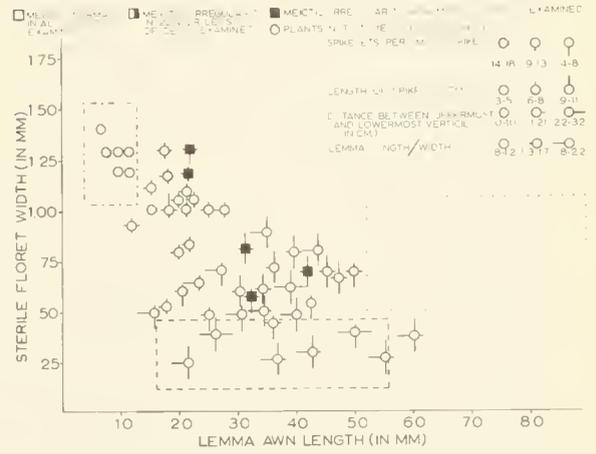


Fig. 63. Scatter diagram of populations of *Chloris cucullata* x *C. andropogonoides* from near Raymondville, Texas.

in awn length of the putative parents (see Table 12).

Several additional collection sites had populations with introgression patterns similar to that of Raymondville, including Pawelekville, Pettus, and Rio Grande City (Fig. 60).

Chloris andropogonoides x *C. verticillata*

The collection site for this population is in Edwards County, Texas, on the grounds of the Texas A and M Experimental Station about 25 miles northwest of Rock Springs (Fig. 60). While "good" *Chloris andropogonoides* and *C. verticillata* are present in abundance, *C. cucullata* was not observed in the area. The mass collection of plants made in this area is represented in Fig. 64.

Unlike previous scatter diagrams, the intermediate populations shown in Fig. 64 are not of obvious parentage. On the basis of the species present, it would be expected that the recombinants would fill the areas between *C. verticillata* and *C. andropogonoides* in the graph, though certainly more long-awned intermediates similar to *C. andropogonoides* are present than in either of the previous two populations discussed. The unexpected position of the remaining intermediate plants might be the result of the presence at some time in the past of *C. cucullata* in the area, still showing its influence on the remaining population. A more likely possibility, however, is that the intermediates merely represent recombinants of some of the more extreme morphological variants of *C. andropogonoides* and *C. verticillata*.

This population was collected when the plants were in seed and cytological studies were not possible.

I have been unable to find additional populations that I feel are representative of this species combination. *Chloris cucullata* is nearly ubiquitous in areas in which *C. andropogonoides* and *C. verticillata* are sympatric and usually enters into the introgression pattern when present.

Chloris cucullata x *C. andropogonoides* x *C. verticillata*

The population represented in Fig. 65 is from a grassy field utilized intensively as a recreation area in Zilker Park, a city park in the southwest part of Austin, Texas. Plants that can be referred without hesitation to *C. cucullata* are common in the area. Others are clearly close to *C. verticillata* and *C. andropogonoides* but are somewhat taller than expected. An abundant population of intermediates is also present.

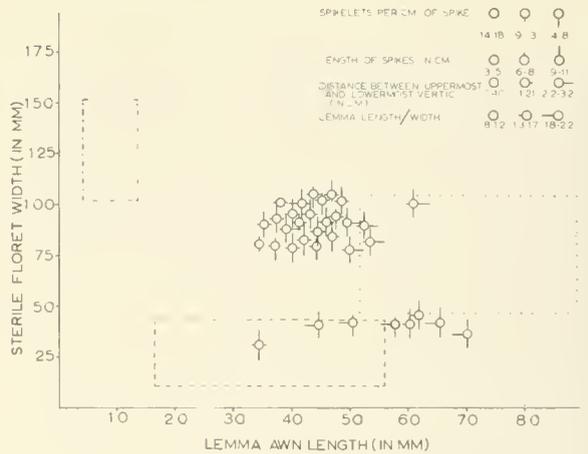


Fig. 64. Scatter diagram of population of *Chloris andropogonoides* x *C. verticillata* from the Texas A and M Experiment Station near Rock Springs, Texas.

In comparing Fig. 65 with the diagrams of Patterson Park and Raymondville (Fig. 61 and 63), one can plainly see a number of mutual features. The Zilker Park population shows many plants in the lower left and left center portions of the diagram, in this respect similar to the Raymondville population, and indicates a strong influence of *C. andropogonoides*. It is also strongly expressed in the upper right-hand portion of the recombinant cluster, a feature it shares with the Patterson Park population. By contrast, the Raymondville population is not well expressed in the upper right-hand portion of the diagram, nor is the Patterson Park population well represented in the lower left. Thus, the Zilker Park plants seem to represent various recombinations of all three species.

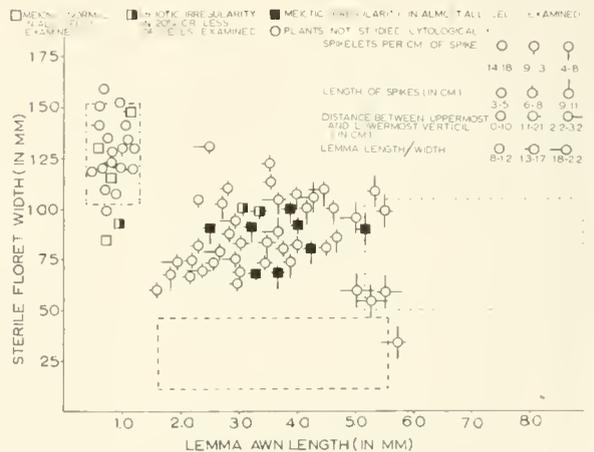


Fig. 65. Scatter diagram of population of *Chloris cucullata* x *C. andropogonoides* x *C. verticillata* from Zilker Park, Austin, Texas.

As with the other species combinations examined cytologically, the intermediate populations in Zilker Park show a high degree of meiotic irregularity. Only those plants assigned to *C. cucullata* show little or no meiotic aberrancy.

Anomalous populations

Not all populations in the areas of sympatry are as clearly understood as those just discussed, for many colonies of heterogeneous intermediate plants in southern Texas coexist with only one of the putative parents, the other probable parent having been completely swamped by introgression and existing only in a much diluted form. In these collections it is, most frequently, *Chloris andropogonoides* and *C. verticillata* that are missing; *C. cucullata* often persists in pure form. I have chosen four examples from among many studied as representative of these anomalous populations. These are: Bastrop State Park, Skidmore, Kinney Co., and San Marcos.

The Bastrop State Park population (Fig. 66) is found along a grassy roadside just outside the west entrance of the park (near Bastrop, in Bastrop Co.). On the basis of other mass collections examined, this appears to be the remains of a three-way cross involving *C. cucullata*, *C. andropogonoides*, and *C. verticillata*, with the latter two species swamped. *Chloris cucullata*, while still present, is no longer well defined, for a number of plants are similar to "pure" *C. cucullata* but lack certain character combinations.

The Skidmore population (Fig. 67) was collected in a low roadside ditch in Bee Co., Texas (Fig. 60). It is similar to the one at

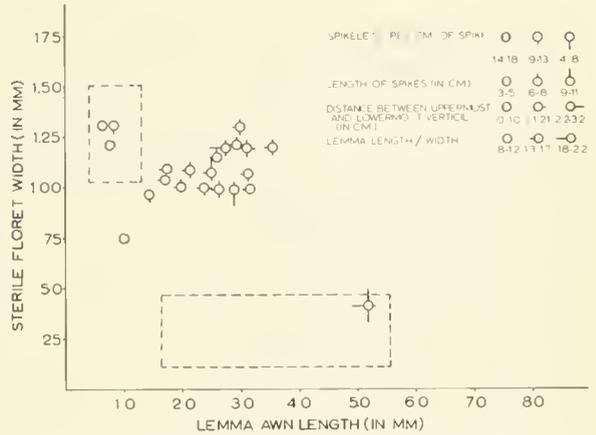


Fig. 67. Scatter diagram of anomalous *Chloris* population from near Skidmore, Bee Co., Texas.

Bastrop State Park except that only one plant typical of *C. andropogonoides* was found. The Skidmore site is out of the natural range of *C. verticillata*, and the presence of this species is not to be expected. *Chloris cucullata* is well represented, as is a series of intermediates. In this instance the intermediate plants do not closely approach *C. cucullata* morphologically.

The Kinney Co. collection (Fig. 68) is from open brushland, associated with such shrubs as *Prosopis* and *Leucophyllum*. In this population the intermediates are still more isolated from *C. cucullata*, and no plants even approaching *C. andropogonoides* or *C. verticillata* were found.

The San Marcos collection (Fig. 69) is from a dry, grassy roadside ditch near the Blanco River bridge northeast of San Marcos, Texas, and about two miles east of the eastern edge of the Edwards Plateau. This population shows well-defined *Chloris cucullata* and *C. andro-*

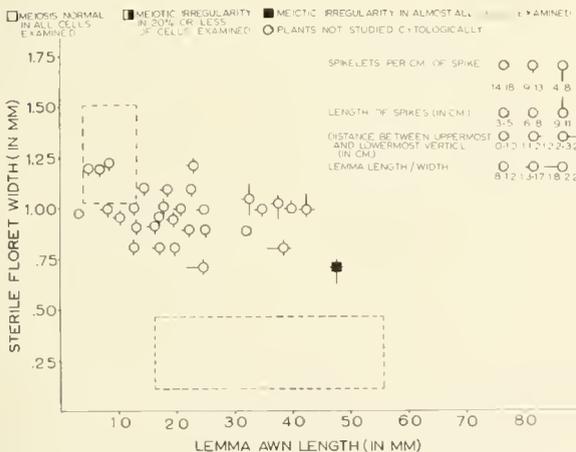


Fig. 66. Scatter diagram of anomalous *Chloris* population from near Bastrop State Park, Texas.

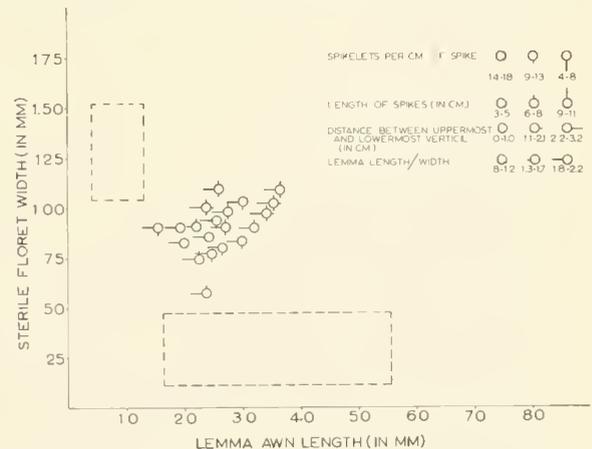


Fig. 68. Scatter diagram of anomalous *Chloris* population from Kinney Co., Texas.

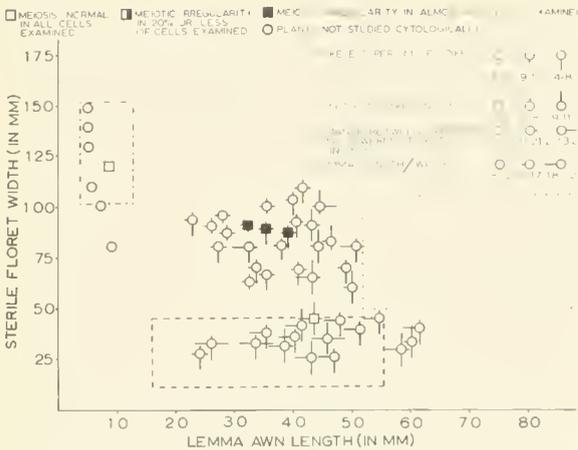


Fig. 69. Scatter diagram of anomalous *Chloris* population from near San Marcos, Texas.

pogonoides, as well as many heterogeneous, cytologically aberrant intermediates. The position of the intermediate plants is similar to the Zilker Park population (Fig. 65), suggesting that all three putative parents were present at one time. I searched the area many times over a period of several seasons and could not find well-defined *C. verticillata*, although plants similar to that species were found about a mile north of the site. Since this collection area is close to the limestone-rich Edwards Plateau, the seemingly preferred habitat of *C. verticillata*, one would expect the latter species nearby.

Discussion.

Ecologically, populations with large numbers of intermediate plants are most frequently associated with highly disturbed areas. The best collecting sites, therefore, are roadside ditches, waste places, and city parks. None of the species involved will persist in cultivated or grazed areas, nor will they compete well with an established native flora or such aggressive weeds as Johnson grass. Before the excessive disturbance caused by man, it is likely that the three species involved were only occasionally found, and then only in such areas as blowouts, slipouts, and banks and alluvial areas along creeks and streams. There is little information about the ecology of these species before the rampant habitat destruction by man; however, a report of a grass-collecting trip through the Kansas prairies by J. B. Norton in 1898 (Barkley, 1965) indicates that *Chloris verticillata* grew along the sides of sloughs and on low ground but did not compete well with upland grasses.

Cytological examination of the intermediate plants shows them to be highly aberrant in

meiosis, producing few stainable pollen grains. It would be expected on this evidence that the rate of seedset would be relatively low. This, however, is not always the case. Plants from the intermediate populations may actually have good seedset—in some cases, a high percentage. Such plants are frequently associated with stands that are quite uniform morphologically. The combination of highly aberrant meiotic behavior, good seedset, and extreme uniformity suggests that an apomictic mechanism may be in operation.

Nomenclature

The wide array of variable intermediate plants in this complex would thus seem to be the product of extensive hybridization and introgression, possibly still further complicated by apomixis. The intermediate plants will key to *Chloris subdolichostachya* and *C. latisquamica* in many standard grass floras but frequently will not fit the descriptions of these taxa precisely. It seems likely that these names, in reality, have been applied to segments of the much larger hybrid populations and do not represent biological species in the usual sense.

The extreme variability of the intermediate populations presents a difficult nomenclatural problem. The wide variety of morphological types represented certainly cannot be individually named, for this would saturate the literature with names that carry little biological meaning and might apply to plants of low genetic stability. The problems become additionally compounded in that there is no way of telling parts of the hybrid population of *C. cucullata* x *C. andropogonoides* from parts of the *C. cucullata* x *C. verticillata* populations (compare Fig. 61 and 63) and from the populations involving all three species (Fig. 65). To use the existing names *C. latisquamica* and *C. subdolichostachya* for the intermediates is unsatisfactory, for there is no way of determining which, or how many, of the three species are involved in the ancestry of their types. In short, these names cannot be precisely defined. Likewise, the usage of a single name for a complex of morphological forms obscures their biological nature.

I feel that the only solution is to designate the intermediate plants by a formula based upon their probable parentage. Thus, a population suspected to be the result of *C. cucullata* introgressing with *C. andropogonoides* should have its intermediate plants designated by the formula name *C. cucullata* x *C. andropogonoides*. While this will not satisfy those who want a particular name for a particular plant, it does

satisfy what is, to me, a more important aspect of taxonomy that is seldom reflected in existing nomenclature: it helps to define the reasons for the existence of a taxonomic problem.

The original descriptions of the following names seem to fit the characteristics of hybrid plants.

Chloris verticillata var. *aristulata* Torrey and Gray in Whipple, U.S. Rept. Expl. Pacific 2:176. 1857.

Chloris subdolichostachya C. Mueller, Bot. Zeitung (Berlin) 19:341. 1861.

Chloris verticillata var. *intermedia* Vasey in Coulter, Contr. U.S. Nat. Herb. 2:528. 1894.

Chloris brevispica Nash, Bull. Torrey Bot. Club 25:438. 1898.

Chloris latisqueamea Nash, Bull. Torrey Bot. Club 25:439. 1898.

Specimens and populations examined (all at HSC): *C. cucullata* x *C. verticillata*. TRAVIS CO.: Austin, Patterson Park, along Airport Blvd., 0.5 mi SE of its junction with Hwy. 35, *Anderson* 3,336, 12 July 1964 (mass collection), 3,338-3,361, 12 July 1964 (cytovouchers). MASON CO.: along Hwy. 29, 2.5 mi E of the junction of Hwys. 29 and 377, 3 mi E of Grit, *Anderson* 4,633, 2 July 1968 (mass collections). NOLAN CO.: along Hwy. 53, 9 mi S of the junction of Hwys. 126 and 53, *Anderson* 4,653, 2 July 1968 (mass collections). SAN SABA CO.: Richland Springs, along Hwy. 190, roadside ditch near city water tower, *Anderson* 3,333, 9 July 1964 (mass collections).

C. cucullata x *C. andropogonoides*. WIL-LACY CO.: grassy roadside, 1 mi N of Raymondville, along Hwy. 77, *Anderson* 3,308, 3,316, 1 July 1964 (mass collections), 3,309-3,315, 1 July 1964, 4,564-4,572, 28 June 1968 (cytovouchers). KARNES CO.: 6 mi S of the junction of Hwys. 123 and 889 and the village of Pawelekville, *Anderson* 4,611, 30 June 1968 (mass collection), 4,595-4,610, 30 June 1968 (cytovouchers). BEE CO.: 3.3 mi N of Pettus, 1.6 mi N of the junction of Hwys. 181 and 798, *Anderson* 2,781-2,789, 13 July 1964 (mass collections). STARR CO.: 8 mi W of Rio Grande City, along Hwy. 83, *Anderson* 3,330, 2 July 1964 (mass collection), 3,323-3,329 (cytovouchers); 1 mi S of Rio Grande City, *Anderson* 4,524, 27 June 1968 (mass collection); ca 1 mi SE of Arroyo Los Olomos bridge, ca 3 mi SE of Rio Grande City, *Anderson* 4,542, 27 June 1968 (mass collection), 4,525-4,541 (cytovouchers).

C. andropogonoides x *C. verticillata*. EDWARDS CO.: Texas A and M Field Station, 25 mi NW of Rock Springs, *Anderson* 3,903, 12 July 1965 (mass collection).

C. cucullata x *C. andropogonoides* x *C. verticillata*. TRAVIS CO.: Austin, Zilker Park playing field, *Anderson* 3,011-3,090, 6 June 1964 (mass collection); 2,603-2,628, 28 June 1963; 2,650-2,664, 3 July 1963; 3,262-3,268, 25 June 1964 (all cytovouchers).

Anomalous populations. BASTROP CO.: just outside W entrance of Bastrop State Park, *Anderson* 3,128-3,138, 10 June 1964 (mass collections), 3,116-3,127, 10 June 1964 (cytovouchers). KINNEY CO.: along Hwy. 693, 1-3 mi E of its junction with Hwy. 277, *Anderson* 4,479, 26 June 1968 (mass collection), 4,470-4,478, 26 June 1968 (cytovouchers). HAYS CO.: near bridge over Blanco River, 1 mi NE of San Marcos on Hwy. 21-80, *Anderson* 3,276, 28 June 1964 (mass collection), 3,278-3,282, 28 June 1964, 4,617-4,619, 30 June 1968 (all cytovouchers). BEE CO.: 2.6 mi N of Skidmore, *Anderson* 2,698-2,699, 13 July 1963 (mass collections), 2,691-2,697, 13 July 1963 (cytovouchers).

41. **CHLORIS TEXENSIS** Nash, Bull. Torrey Bot. Club 23:151. 1896. (HOLOTYPE: "Texas. G. C. Nealley." US!) Fig. 58, A-C. *Chloris nealleyi* Nash, Bull. Torrey Bot. Club. 25:435. 1898. (Based on *Chloris texensis* Nash.)

Perennial 30 to 45 cm tall, cespitose; sheaths glabrous to sparsely pilose; ligule a low membranous crown; blades narrow, ca 4 mm wide, up to 15 cm long, scabrous; spikes eight to ten, up to 20 cm long, radiate, occasionally in two verticils, bearing loosely imbricate spikelets only on distal half, naked at base; spikelets ca three or four per cm of the scabrous rachis; glumes lanceolate, glabrous except for the scabrous mid-nerve; first glume 2.7 to 3.0 mm long, 0.4 mm wide; second glume 3.5 to 3.8 mm long, 0.5 mm wide; fertile floret 3.7 to 4.3 mm long, 0.7 to 0.8 mm wide, lanceolate to narrowly ovate, callus bearded, upper margins sparsely appressed-ciliate, otherwise glabrous, apex acute, awn 7 to 11 mm long; sterile floret 2.0 to 2.5 mm long, 0.5 mm wide, narrowly elliptic, apex acute, glabrous, awn 4.5 to 6.5 mm long; caryopsis ca 2.3 mm long, 0.5 mm wide, ellipsoid, trigonous.

Chloris texensis is most closely allied to *C. verticillata* and *C. andropogonoides* (Fig 56, L-U; 58, D-K). It differs from *C. verticillata* in usually having a single verticil of spikes and relatively narrow sterile florets. It may be separated from *C. andropogonoides* by the relatively larger spikelets and longer spikes. *Chloris*

texensis lacks spikelets on the lower portion of the spikes, whereas both *C. verticillata* and *C. andropogonoides* are floriferous to the base.

Chloris divaricata, a similar Australian species, is separable in having deeply lobed sterile florets, scabrous fertile lemmas, and spikes that are floriferous to the base (Fig. 51, K-R). *Chloris texensis* has sterile florets that are merely acute, not deeply lobed, glabrous fertile lemmas, and spikes that are naked at the base (Fig. 58, A-C). *Chloris divaricata* is apparently an escape in Texas and has been confused with *C. texensis*.

Only six specimens of the species, including the type, have been found in herbaria consulted. All are from Brazoria, Brazos, or Harris County, Texas, except the type, for which a precise collection locality was not provided.

On two separate occasions I searched the area of two collections, *Silveus* 423 and 427, from the A and M Field Station near Angleton. Most of the land in the area is either cultivated, heavily grazed, or in stages of old-field succession; and I could not locate either *C. texensis* or any native vegetation that might support it. Because neither the plant nor native vegetation could be found, and because few specimens have been collected since 1931, I feel that it is quite likely that the species is in danger of becoming extinct.

Specimens examined: UNITED STATES: Texas: Brazoria Co., Columbia, *Bush* 1,361 (MO, NY); experimental farm near Angleton, *Silveus* 423 (TEX); open sandy woods and swamps, Angleton, *Silveus* 427 (TEX); Brazos Co., without precise location, *Malone s.n.*, October 1938 (TAES); Harris Co., exposed clay lowland, 3 mi S of Alvin, *Parks* 117 (TAES).

42. **CHLORIS SESQUIFLORA** Burkart, Bol. Soc. Argentina Bot. 12:287. 1968. (TYPE: "Dep. Concep. del Urug., bajos cerca del rio Gualeguaychu, vecindades del Parque Unzue, A. Burkart. 25,676 . . ." SI, not seen. ISOTYPE: HSC!) Fig. 70, A-C; 71, triangles.

Stoloniferous perennial up to 45 cm tall; sheaths glabrous; ligule a short-ciliate crown; blades up to 20 cm long, 4 to 5 mm wide, glabrous to scabrous; spikes four or five, 6.0 to 6.5 cm long, ascending, somewhat arcuate; spikelets rather densely inserted, appressed, imbricate, averaging about 11 per cm of the scabrous rachis; glumes lanceolate to narrowly ovate, acute to acuminate, glabrous except for the scabrous midnerve; first glume 2.1 to 2.2

mm long, 0.3 to 0.5 mm wide; second glume 2.7 to 2.9 mm long, 0.4 to 0.5 mm wide; fertile lemma 2.1 to 2.9 mm long, 0.9 to 1.1 mm wide, ovate to elliptic, apex acute, callus short-bearded, keel and margins densely appressed-pilose, awn 0.7 to 1.0 mm long; sterile floret one, ca 1 mm long, 0.3 mm wide, strongly flattened, membranous, elliptic, awn 0.3 to 0.5 mm long; anthers ca 0.7 mm long.

Only two specimens of *Chloris sesquiflora*, including the type, were seen. While it resembles outwardly some of the species with ciliate lemmas (especially *C. ciliata*), the flattened, poorly developed single sterile floret and the appressed pubescence of lemma margins and keels separate it easily. It is probably not closely related to *C. ciliata*.

Specimens examined: PARAGUAY: Plaine de Paraguari, plaques dessecles, dans les argiles imperméables, *Balansa* 264 (BR).

43. **CHLORIS HUBERTIANA** A. Camus, Bull. Soc. Bot. France 91:63. 1944. (HOLOTYPE: "Madagascar . . . Mananara . . . pentes orientales du Volipaly . . . Humbert, no. 14150." P! ISOTYPE: K!) Fig. 70, D-F.

Pterochloris humbertiana (A. Camus) A. Camus, Bull. Mus. Hist. Nat. (Paris) Ser. 2. 29:349. (Based on *Chloris humbertiana* A. Camus.)

Perennial 20 to 30 cm tall, stoloniferous, with erect culms arising at intervals from strong stolons; leaves basal; sheaths flattened, equitant, glabrous; ligule a very short-ciliate crown; blades 1.5 to 2.0 cm long, 3 to 5 mm wide, glabrous, folded, slightly arcuate, apex obtuse; spikes two or three, 3 to 4 cm long, partially enclosed in upper sheaths when young, becoming exerted at maturity; spikelets imbricate, ca five to seven per cm of the glabrous rachis; glumes lanceolate-ovate, thin and membranous, glabrous except for the scabrous midnerve; first glume 1.0 to 1.5 mm long, ca 0.3 mm wide; second glume ca 1.5 mm long, 0.2 to 0.3 mm wide; fertile lemma 2.3 to 2.5 mm long, 0.7 to 1.2 mm wide, body of lemma elliptic, with a prominent wing at the apex, making the lemma appear narrowly truncate, callus bearded, margins scabrous below, glabrous above, internerves densely pubescent with prominent, inflated hairs, awn 2.4 to 3.5 mm long; sterile floret ca 1 mm long, ca 0.5 mm wide, elliptic, flattened, apex acute, awn 3.0 to 3.8 mm long, arising below the apex.



Fig. 70. *Chloris sesquiflora* and *C. humbertiana*. (A-C) *C. sesquiflora*. (A) habit, x 1/3; (B) spikelet, partly dissected, x 10; (C) sterile floret, x 10. (D-F) *C. humbertiana*. (D) habit, x 1/3; (E) spikelet, partly dissected, x 10; (F) sterile floret, x 10.

Chloris humbertiana is a very distinct species; its strongly winged lemmas, with inflated hairs on the internerves, are unique in the genus.

Emphasizing these characters, Camus (1950) proposed the subgenus *Pterochloris* to include *Chloris humbertiana*. Later (1957), Camus elevated *Pterochloris* to generic rank, retaining *C. humbertiana* as its single species.

While *Chloris humbertiana* is unusual in *Chloris*, it is no more so than a number of other species and I am maintaining it in *Chloris*.

Only four specimens of this species were seen in the herbaria consulted and all are from xerophytic bushland in the Malagasy Republic (Madagascar).

Specimens examined: MALAGASY REPUBLIC: Pateau Mahafetz, *Bosser 15,698* (P); Cap Sainte-Marie, *Humbert and Capuron 29,264* (P); d'Amparihy à l'embouchure de la Menarandra, *Humbert and Capuron 26,347* (P); environs d'Ampanrandava, *Seyrig 809* (P).

44. **CHLORIS AMETHYSTEA** Hochstetter, *Flora* 38:205. 1855. (ISOTYPE: "... Abyssinia leg. Schimper recu 1855. 1267 . . ." G!) Fig. 72, A-K.



Fig. 71. Distribution of *Chloris halophila* (dots) and *C. sesquiflora* (triangles).

Stoloniferous perennial up to 80 cm tall; sheaths glabrous below, becoming loosely pilose toward the ligule, especially on the margins; ligule a short-ciliate crown, often with longer hairs near the edges; blades up to 10 cm long, ca 5 to 6 mm wide, glabrous with scabrous margins and midnerves; spikes four to six, 5 to 9 cm long, ascending when young, becoming more loosely spreading at maturity, usually radiate, sometimes in two verticils; spikelets appressed, ca 7 per cm of the scabrous rachis; glumes unequal, glabrous except for the scabrous midnerve; first glume 1.5 to 2.5 mm long, 0.2 to 0.5 mm wide, lanceolate, apex acute; second glume 2.5 to 3.8 mm long, ca 0.4 mm wide, linear, apex acute to mucronate, sometimes somewhat lacerate, glabrous except for the scabrous midnerve; fertile lemma 3.5 to 4.5 mm long, 0.7 to 1.2 mm wide, elliptic to obovate, often purplish tinted, callus densely bearded, margins densely appressed-pilose, keel sparsely to densely appressed-pilose, apex acute to obtuse, usually awnless, occasionally with a short awn less than 1.7 mm long; sterile floret one, 1.4 to 2.5 mm long, 0.6 to 1.2 mm wide, narrowly turbinate, apex truncate, somewhat inflated, awnless; caryopsis ca 2.2 mm long, 0.6 mm wide, trigonous, ellipsoidal.

Chloris amethystea seems most closely related to *C. gayana* and *C. mossambicensis*, differing from both in having short awns. While relatively few specimens are available, *C. amethystea* appears to be restricted to Ethiopia and Kenya (Fig. 73, triangles), occurring in montane scrub and grasslands at the forest edge on white or yellowish sandy loams and at elevations of 3,000-6,000 feet. Associated plants include *Ficus*, *Acacia*, *Combretum*, and *Commiphora*.

Specimens examined: ETHIOPIA: Territory Agow, Dschascha, *Hohenacker 2,247* (K, US); between Assala and Awash Rivers, *Semple 19* (US). KENYA: Mt. Marsabit, *Adamson E. A. H. 11,666* (K, US), *Bogdan A. B. 4,774* (K); Stony Athi River, 20 mi SE of Nairobi, *Bogdan AB 3,152* (K); Moyale, 3°32'N, 39°03'E, *Gillet 12,852, 14,065* (K).

45. **CHLORIS SUBMUTICA** Humboldt, *Bonpland, Kunth, Nov. Gen. Sp. 1:167. pl. 50.* 1816. (There is a fragment, in US!, from P, that may be from the type. It is labeled "Chloris submutica HBK mihi n. 4182. Mexique." The original description gives "Tezucucensi" as the collection site, but no other pertinent information is given. The detailed original description and accom-

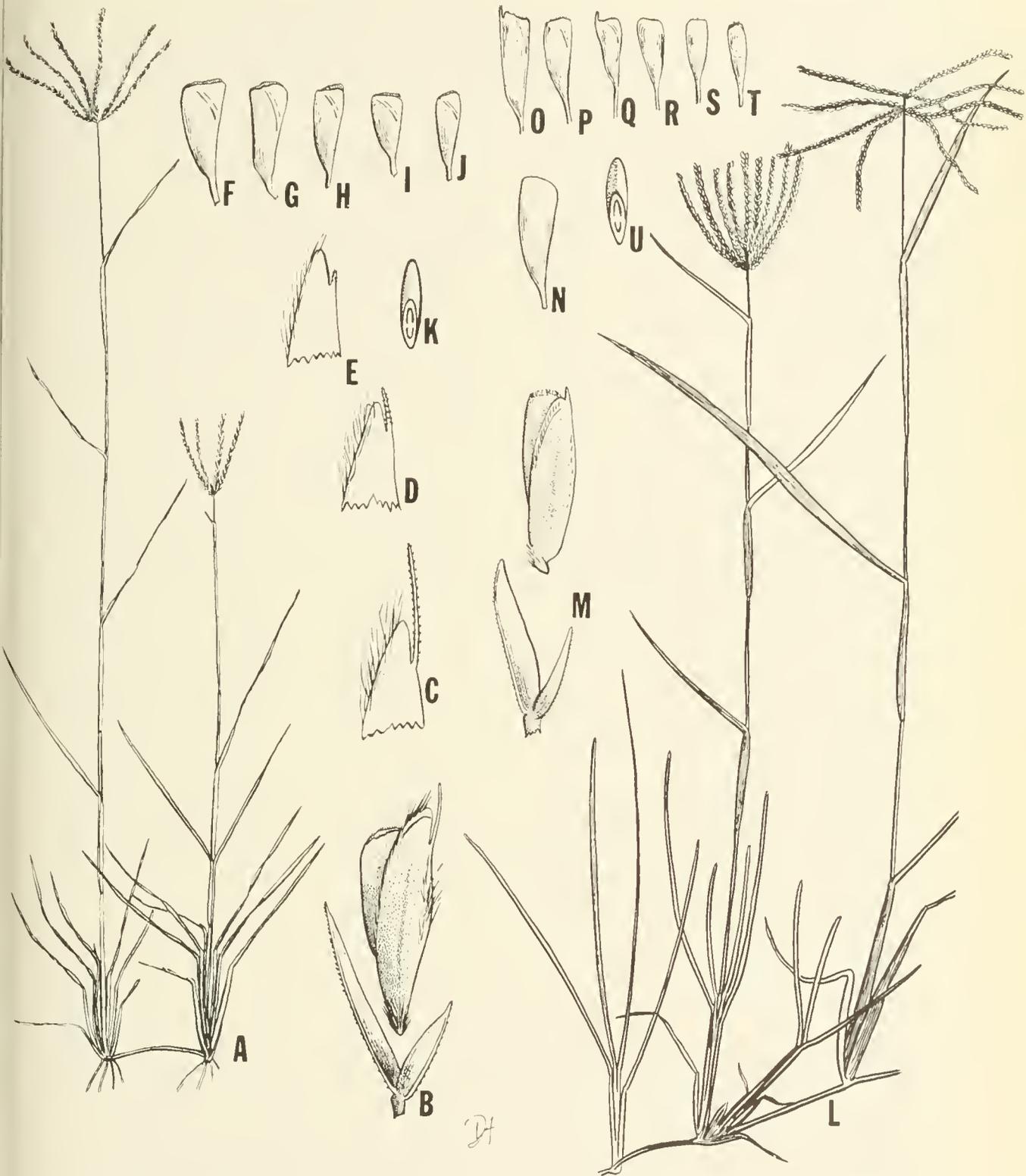


Fig. 72. *Chloris amethystea* and *C. submutica*. (A-K) *C. amethystea*. (A) habit, x 1/6; (B) spikelet, partly dissected, x 7.5; (C-E) lemma apices, showing variation in awn length, x 10; (F-J) sterile florets, showing variation, x 7.5; (K) caryopsis, x 5. (L-V) *C. submutica*. (L) habit, x 1/4; (M) spikelet, partly dissected, x 7.5; (N-T) sterile florets, showing variation, x 7.5; (U) caryopsis, x 5.



Fig. 73. Distribution of *Chloris amethystea* (triangles) and *C. somalensis* (circles).

panying illustration leave no doubt as to the taxon described.) Fig. 72, L-V.

Chloris polystachya Lagasca, *Elenchus Plantarum* 59. 1816. (A fragment of a specimen, in US! from "Hb. Madrid" labeled "*Chloris polystachya* Lag. Nee' iter Hb Madrid" may be from the type. The original description is inconclusive.)

Eustachys submutica (Humboldt, Bonpland, Kunth) Roemer and Schultes, *Syst.* 2:614. 1817. (Based on *Chloris submutica* Humboldt, Bonpland, Kunth.)

Chloris inermis Trinius, *Gram. Uniflorus* 232. 1824. (Based on *Chloris polystachya* Lagasca.)

Eustachys polystachya (Lagasca) Kunth, *Rev. Gram.* 1:88. 1829. (Based on *Chloris polystachya* Lagasca.)

Phacellaria panicea Willdenow ex Steudel, *Nom. Bot. ed. 2.* 1:353. 1840, *pro syn.*

Chloris subbiflora Steudel, *Syn. Pl. Glum.* 1:206. 1854. (HOLOTYPE: P! A fragment of an additional Steudel specimen, labeled by him as *C. subbiflora*, is in US!, originally from CN.)

Chloris pratensis Lesible ex Steudel, *Syn. Pl. Glum.* 207. 1854. *Pro syn.*, *C. subbiflora*.

Perennial 30 to 75 cm tall, erect, usually tufted, occasionally short-stoloniferous; sheaths glabrous below, becoming ciliate at the ligule with hairs up to 2 mm long; blades up to 20 cm long, ca 5 mm wide, the surfaces and margins scabrous, occasionally long-pilose at base of blade; spikes 5 to 17, up to 7 cm long, usually erect when young, becoming somewhat reflexed at maturity; spikelets rather densely imbricate, averaging about twelve per cm of the scabrous rachis; glumes lanceolate, acute, pale,

glabrous with scabrous midnerves; first glume 1.5 to 3.2 mm long, 0.2 to 0.9 mm wide; second glume 2.5 to 3.4 mm long, 0.3 to 0.7 mm wide; fertile lemma 2.8 to 3.7 mm long, 0.6 to 1.1 mm wide, pale, broadly linear to elliptic, callus bearded, rest of lemma glabrous except for the appressed-pilose margin, apex obtuse, unawned or with a very short mucro; sterile floret one, 1.4 to 2.2 mm long, 0.3 to 0.9 mm wide, truncate, awnless or occasionally with a very short mucro; anthers ca 0.5 to 0.9 mm long; caryopsis 1.7 to 2.3 mm long, 0.5 to 0.6 mm wide and thick, ellipsoid, trigonous; chromosome number $2n = ca\ 65, 80$.

Chloris submutica outwardly resembles species in *Eustachys*, primarily because of the appressed, awnless spikelets. The second glume, however, lacks the rounded apical lobes subtending the short awn, a characteristic of *Eustachys*. Also, *C. submutica* lacks the conspicuous equitant leaf sheaths of *Eustachys*.

Chloris submutica Humboldt, Bonpland, Kunth and *C. polystachya* Lagasca were both published in 1816. According to Stafleu (1967), the particular section of the *Nova Genera et Species Plantarum*, containing the original description of *C. submutica*, was published in May 1816; while *C. polystachya* Lagasca, published in *Elenchus Plantarum*, was probably published in June or July 1816. In addition to the slightly earlier date of publication, *C. submutica* is clearly identifiable and has been widely accepted, far more so than *C. polystachya*. For these reasons *C. submutica* is maintained here.

Chloris submutica has been extensively collected in Mexico, occasionally in Columbia, Guatemala, New Mexico, and Venezuela (Fig. 43, circles). Most specimens are from elevations of 3,000 to 6,000 feet and on a variety of soil types.

Representative specimens examined: COLOMBIA: Dep. Cundinamarca: Sabana de Bogota, cerca de Madrid, Tarragon et al. 18 Cu 104 (US). GUATEMALA: Quezaltenango, Chiquilaga, de Koninck II (US). MEXICO: Aguascalientes: Aguascalientes, Hitchcock 7,453 (US); Chiapas: N of San Cristóbal de Las Casas, Breedlove 6,759 (F); Chihuahua: Majalca, Pílares, 2,080 m, Harvey 1,483 (US); San Juanito, Knobloch 5,425 (F); Coahuila: Saltillo, 5,300 ft, Fisher 57 (US), Hitchcock 1,261 (NY, UC) 5,585 (US); Durango: Tepehuanes, Fisher 44,221 (MO), Palmer 262, 4-25 June 1906 (MO, NY, UC, US); Otinapa, Palmer 341, 25 June-5 Aug 1906 (MO, NY, UC, US); Distrito Federal: Lomas de Mixcoac, Lyonnet 2,701

(US); pyramid of Cuicuilco Tlalpan, *McDaniels* 47 (F); Guanajuato: 6 km S of San Felipe, *Sohns* 405 (US). Hidalgo: Pachuca, 8,000 ft, *Hitchcock* 6,748 (US). Jalisco: Zapotlan, *Hitchcock* 7,129 (US); Michoacán: 5 mi N of Patzeuaro, *Webster* 2,700 (US); Nayarit: Tepic, Santa Teresa, *Rose* 2,143 (US); Nuevo León: Galeana, Hacienda Pablillo, *Taylor* 127 (F, MO); Puebla: vicinity of Puebla, *Arsène* 330 (MO, NY, US); Queretaro: Cd. Queretaro, *Hitchcock* 5,818 (US); Sonora: Río de Bavispe, El Picaco de Pilar, *Santos* 2,168 (US); San Luis Potosí: Cd. San Luis Potosí, *Schaffner* 130 (NY, US); Tamaulipas: 6 km W of Miquihuana, 2,940 m, *Stanford et al.* 737 (MO, US); Tlaxcala: between San Cristóbal and Calpulalpan, *Sohns* 580 (US); Zacatecas: 15 km W of Concepción del Oro, near Zacatecas-Coahuila border, *Stanford et al.* 558 (MO, NY, UC, US). UNITED STATES: New Mexico: Dona Ana Co., State College, *Norris* 1,026 (US), *Parker* 459 (US). VENEZUELA: Estado de Mérida: between Mucaruba and Muehachies, *Rudd* 541 (US).

46. **CHLORIS SOMALENSIS** Rendle, *Jour. Bot. (London)* 37:66. 1899. (HOLOTYPE: "Wagga Mountain, Somaliland. Mrs. E. Lort Phillips. 1897." BM!) Fig. 74, F-L.

Perennial to 70 cm tall, caespitose, erect; sheaths glabrous, overlapping; ligule a short-pilose crown; blades 15 to 30 cm long, to 7 mm wide, glabrous; spikes three or four, ca 8.5 cm long, erect when young, later spreading; spikelets appressed, dense, ca ten per cm of the scabrous rachis; glumes unequal, linear-lanceolate, thin and glabrous to slightly scabrous, especially on the midnerve; first glume 1.4 to 3.0 mm long, 0.2 to 0.4 mm wide; second glume 3.2 to 5.0 mm long, ca 1.0 mm wide; fertile lemmas 3.5 to 5.2 mm long, 0.8 to 1.0 mm wide, lanceolate, olive-green, callus bearded, margins glabrous below, becoming sparingly appressed-pilose near the apex, otherwise glabrous, awn 7 to 12 mm long; sterile floret one, 0.5 to 2.0 mm long, 0.1 to 0.5 mm wide, usually greatly flattened and reduced, sometimes slightly inflated, scabrous, awn 1.5 to 3.5 mm long; anthers 1.0 to 1.5 mm long; caryopsis 2.0 to 2.2 mm long, 0.5 to 0.6 mm wide, ellipsoid, trigonous.

In general the olive-colored spikelets and greatly reduced sterile florets readily separate *Chloris somalensis* from related species. Occasional specimens have exceptionally large rudiments and may eventually prove distinct as better series of specimens become available.

Included here would be *Glover and Gilliland* 755 (BM!).

Only six specimens were available in all herbaria consulted. These were collected in Ethiopia and the Somali Republic (Fig. 73, circles) in open, grassy savannahs with *Juniperus* and *Dodonaea*. Soils were partly lava with black clay and partly sandstone with red, sandy soil in areas with moisture derived largely from low clouds.

Specimens examined: ETHIOPIA: Hamasen, Nefarit, *Baldrati s.n.*, 7 Mar 1916 (K); Sidamo, Mega, 4°5'N, 38°20'E, ca 2,200 m, *Gillett* 14,296 (K, US), *Mooney* 5,565 (K). SOMALI REPUBLIC: Golis Range, Baldostie Godie, *Drake-Brockman* 480 (K); Iya Makarai, 9°56'N, 45°E, *Drake-Brockman* 481 (K).

47. **CHLORIS CLEMENTIS** Merrill, *Philippine Jour. Sci.* 40:181. 1929. (HOLOTYPE: "Luzon: Pangasinan Province, Calasiao . . . Clemens 17,267." UC! ISOTYPES: BR! F! NY! US!) Fig. 74, A-E.

Perennial 20 to 30 cm tall, with delicate, erect culms arising from the prominent stolons; sheaths very short, glabrous below, becoming somewhat ciliate along upper margins; ligule a short membranous ring; blades 1.0 to 2.5 cm long, 2 to 4 mm wide, obtuse, slightly apiculate, glabrous; spikes two to five, 2 to 3 cm long, radiate; spikelets appressed, imbricate, ca five per cm of the scabrous rachis; glumes lanceolate to ovate, membranous, glabrous except for the scabrous midnerve; first glume 0.5 to 0.6 mm long, ca 0.2 mm wide; second glume 0.7 to 0.8 mm long, ca 0.2 mm wide; fertile lemma 1.5 to 1.8 mm long, 0.4 to 0.5 mm wide, lanceolate to elliptic, callus bearded, margins sparsely ciliate apically, scabrous below, keel sparsely scabrous, otherwise glabrous, awn 5.5 to 6.5 mm long; sterile floret one, ca 0.3 mm long, 0.1 mm wide, much reduced, flattened, often concealed within the lemma, awn ca 1 mm long; caryopsis ca 1.2 mm long, 0.3 mm wide, narrowly ellipsoid.

Chloris clementis resembles several other species in gross appearance, but differs markedly in detail. Its strongly stoloniferous habit is similar to that of *C. divaricata* as well as to *Eustachys tenera* and to various species of *Cynodon*. It differs from *Chloris divaricata* in having much smaller sterile florets (Figs. 73, A-E; 51, K-R). Sterile florets in *Cynodon* are either greatly reduced or absent. *Eustachys* is characterized by having bilobed second glumes.

Other species (such as *Chloris ekmanii*, *C. pycnothrix*, *C. radiata*, and *C. sagraeana*) may



Fig. 74. *Chloris clementis* and *C. somalensis*. (A-E) *C. clementis*. (A) habit, x 1/3; (B) spikelet, partly dissected, x 10; (C,D) sterile florets, showing variation, x 30; (E) caryopsis, x 10. (F-L) *C. somalensis*. (F) habit, x 1/3; (G) spikelet, partly dissected, x 10; (H-K) sterile florets, showing variation, x 10; (L) caryopsis, x 7.5.

have similar spikelets but are tufted rather than stoloniferous.

No specimens were seen other than the holotype and its isotypes.

48. **CHLORIS RADIATA** (Linnaeus) Swartz, Prodr. Veg. Indiam Oec. 26. 1788. (Based on *Agrostis radiata* Linnaeus.) Fig. 75, F-J.

Agrostis radiata Linnaeus, Syst. Nat. ed. 10. 2:873. 1759. (See nomenclatural note below.)

Cynosurus scoparius Lamarek, Encycl. Meth. 2:188. 1786. (HOLOTYPE: Not positively identified, but there is a fragment from P, in US!, labeled "*Cynosurus scoparius* de St. Dominique Lam.")

Chloris scoparius (Lamarek) Desfontaines, Tabl. École Bot. Mus. Hist. Nat. 14. 1804. (Based on *Cynosurus scoparius* Lamarek.)

Chloris glaucescens Steudel, Syn. Pl. Glum. 1:206. 1854. (HOLOTYPE: "Guadeloupe, Duchassaing" P! Fragment in US!)

Chloris tacnensis Steudel in Lechler Berberides Amer. Australis 56. 1857. *Nomen nudum*, but a specimen "St. 1569" is cited. This specimen, in P!, labeled *C. tacnensis* in Steudel's script is *C. radiata* (Linnaeus) Swartz.

Chloris biflora Regel, Annotationes Bot. Index Seminum 28. 1863. *Pro syn.*, *C. radiata*.

Chloris scoparius Regel, Annotationes Bot. Index Seminum 28. 1863. *Pro syn.*, *C. radiata*.

Chloris pallescens Regel, Annotationes Bot. Index Seminum 28. 1863. *Pro syn.*, *C. radiata*.

Chloris crinita Salzman ex Doell in Martins Flora Brasiliensis 23:64. 1878. *Pro syn.*, *C. radiata*. Non Lagasca, 1805.

Gymnopogon radiata (Linnaeus) Parodi, Physis 4:180. 1918. (Based on *Agrostis radiata* Linnaeus.)

Annual usually with dense fibrous roots, occasionally rooting at lower nodes, 30 to 60 cm tall; sheaths glabrous, occasionally pilose; ligule a short-ciliate crown, sometimes with a few longer hairs intermixed; blades 10 to 30 cm long, up to 10 mm wide, usually pilose, occasionally glabrous or scabrous, apex usually acute; spikes five to fifteen, 5 to 8 cm long in one, two, or sometimes three ascending verticils; spikelets densely imbricate, ca 11 to 15 per cm of the scabrous rachis; glumes very narrowly lanceolate, glabrous except for the scabrous midnerve; first glume 0.7 to 1.6 mm long, 0.1 to 0.2 mm wide; second glume 2.0 to 2.7 mm long, 0.1 to 0.2 mm wide; fertile lemma 2.8 to 3.3 mm long, 0.4 to 0.6 mm wide, lanceolate to elliptic, glabrous, except upper margins short-ciliate, callus bearded, awn 6 to 13 mm long; sterile floret one, 0.4 to 0.7 mm long, ca 0.1 mm wide, greatly reduced, borne on a long rachilla joint, awn 3 to 5 mm long; caryopsis 1.4 to 1.5 mm long, 0.3 to 0.4 mm wide, trigonous; chromosome number $2n=40$.

The correct name of this plant cannot be established conclusively. Linnaeus' original description refers to a plate and description in Sloane ("Sloane jam. t. 68. f. 3"). Neither the text nor the plate are clear enough for positive identification; both could fit the species

described above or possibly another Caribbean species, for example, *C. sagracana*. In the Linnaean herbarium there is a specimen of Patrick Browne's which Linnaeus might have seen; it is fragmented but seems to be more similar to *C. sagracana*. No other information can be obtained either to substantiate or refute the name. While most of the evidence in this problem is either nonsubstantive, or even somewhat negative, I do not wish to reject circumstantially a name that has been used commonly for this species for nearly two centuries. Until additional information can be found, I propose continued acceptance of *Chloris radiata* (Linnaeus) Swartz for the plant described above.

Chloris radiata most closely resembles *C. pycnothrix*. Differences have been discussed under the latter species. Other Caribbean species are similar in spikelet and inflorescence features but have larger sterile florets (see Table 13 for a further comparison.)

Chloris radiata is widely distributed throughout the eastern Caribbean, northern South Africa, and Central America, where it is a common weed in waste areas, along paths, and roadways, etc. (Fig. 76).

Representative specimens examined: BAHAMA ISLANDS: Nassau, *Hitchcock s.n.*, Nov 1890 (F, MO). BOLIVIA: Coripati, Yungas, *Bang 2,173* (F, MO, NY, US). CAROLINE ISLANDS: Palau group, Koror Island, *Fosberg 32,327* (NY, US). COLOMBIA: Div. Antioquia: Fradonia, *Archer 503* (US); Div. Cauca: El Valle, *Triana 345* (US); Div. Nariño, between Dos Ríos and La Union, *Archer 3,394* (US); Div. Santander: Boca de Rosario, Río Magdalena, *Pennell 3,904* (MO, NY, US). COSTA RICA: Port Limón, *Hitchcock 8,417, 8,428* (US); Prov. San José: between San Pedros Montes de Oca and Curridabat, *Standley 41,283* (US). CUBA: Prov. Pinar del Río: Mariel, *Ekman 12,939* (F, NY, US); Prov. Habana: Guatao, *Leon s.n.*, Oct. 1923 (US). DOMINICAN REPUBLIC: Prov. Pacificador: Pimentel, *Abbott 691* (US); Prov. Seibo: vicinity of Hato Mayor, *Allard 13,643* (US); Prov. Santiago: vicinity of Santiago, *Allard 14,553* (US); Prov. Duarte: Valle de Cibao, *Ekman 13,259* (US); Prov. Puerto Plata: Puerto Plata, *Ekman 14,448* (US). ECUADOR: Prov. Chimborazo: Alausi, *Hitchcock 20,695* (US); Prov. Esmeraldas: Río Santiago, *Acosta-Solis 19,710* (US); Prov. Manabi: Bahía, *Acosta-Solis 12,002* (F); Prov. Pichincha: between Santo Domingo and Quinindé, *Acosta-Solis 13,289* (US). FRENCH GUIANA: vicinity of Cayenne, *Broadway 44* (NY, US). GALÁPAGOS IS-

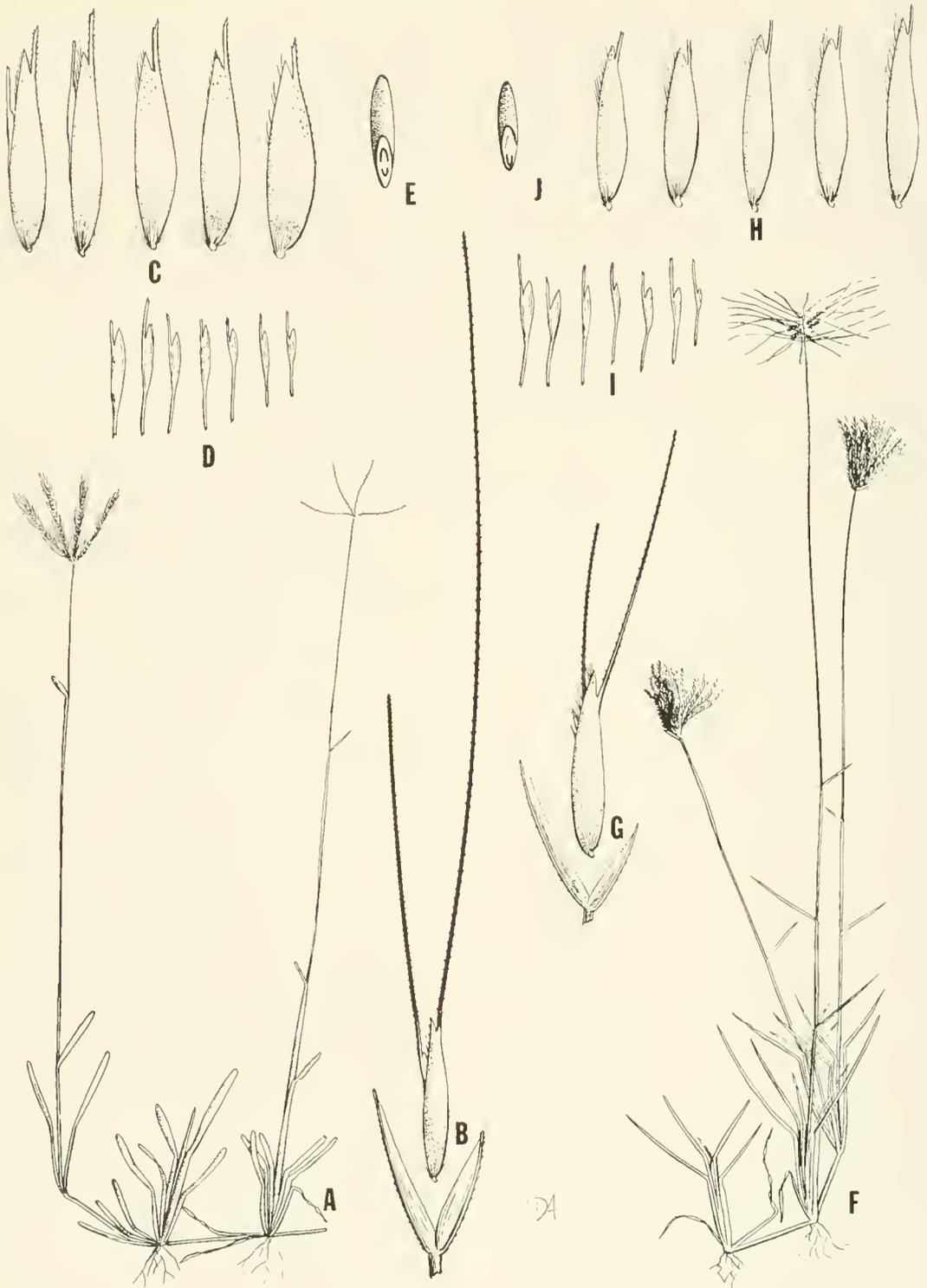


Fig. 75. *Chloris pycnothrix* and *C. radiata*. (A-E) *C. pycnothrix*. (A) habit, x 1/5; (B) spikelet, partly dissected, x 7.5; (C) group of fertile florets, showing variation, x 10; (D) group of sterile florets, showing variation, x 10; (E) caryopsis, x 10. (F-J) *C. radiata*. (F) habit, x 1/5; (G) spikelet, partly dissected, x 7.5; (H) group of fertile spikelets, showing variation, x 7.5; (I) group of sterile florets, showing variation, x 10; (J) caryopsis, x 10.

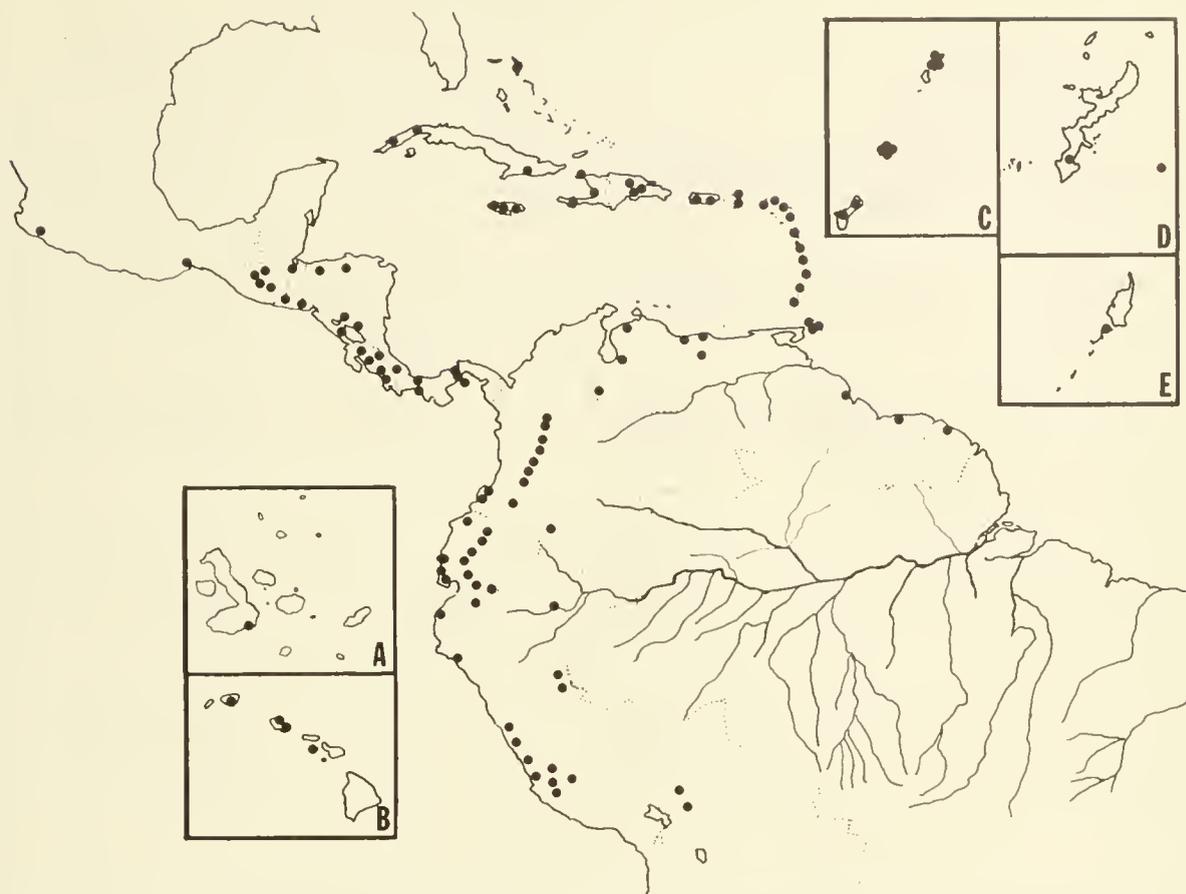


Fig. 76. Distribution of *Chloris radiata*. Insets: (A) Galápagos Islands. (B) Hawaiian Islands. (C) Marianas Islands. (D) Okinawa and adjacent islets. (E) Palau Islands.

LANDS: Albemarle Island, Villamil, *Howell* 8,954 (US). GUATEMALA: Dep. Izabel: vicinity of Puerto Barrios, *Standley* 24,761 (US); Dep. Jutiapa: between Jutiapa and La Celera, *Standley* 76,021 (US). GUYANA: New Amsterdam, *Hitchcock* 16,833 (F, MO, NY, UC, US). HAITI: Tortue Island, La Vallee, *Leonard and Leonard* 11,585 (NY, UC, US); vicinity of Jean Rabel, *Leonard and Leonard* 13,752 (US). HONDURAS: Dep. Morazan: vicinity of El Zamorano, *Standley* 24,665 (F). JAMAICA: Cornwall Co., Ipswich, *Hitchcock* 9,600 (US); Middlesex Co., Ewarton to Linstead, *Hitchcock* 9,437 (US); Surrey Co., Blue Mtns., Robertsfield, *Harris* 11,942 (F, MO, NY, US). LEEWARD ISLANDS: Antigua: Bendals Road, Box 4 (US); Guadeloupe: Point a Pitre, *F. W. Johnson* 1,093 (NY); St. Kitts, *Hitchcock* 16,538 (US). MARIANAS ISLANDS: Rota Island, *Fosberg* 3,027 (US); Saipan, Mt. Tapotchau, *Fosberg* 25,181 (NY, US). MEXICO: Oaxaca: vicinity of Cafetal Concordia, *Morton and Makrinus* 2,598 (F, US). NICARAGUA: San Juan del Sur, *Hitchcock*

8,592 (US); vicinity of Jinotepe, *Standley* 8,535 (F). PANAMA: Bocas de Toro, Laguna de Chiriqui, *Hart* 66 (US); Taboga Island, *Hitchcock* 8,073 (US); Barro Colorado Island, *Standley* 41,125 (US). PERU: Dep. Cajamarca: Chilete, *Anderson* 744 (US); Dep. Lima: La Molina, *Ferreira* 11,118 (US); Dep. Loreto: Aquaitia, Río Yurac Yacu, *Seibert* 2,076 (MO, US). PUERTO RICO: Monte Mesa, vicinity of Mayaguez, *A. Chase* 6,179 (US); vicinity of San Juan, SW of Bayamon, *A. Chase* 6,388 (US); Viequis Island, vicinity of Isabel Segunda, *Shafer* 2,474 (NY, US). RYUKYU ISLANDS: Daitoshima group, Rasa Island, *Kawagoe s.n.*, Oct 1919 (US); Okinawa, Borozino Island, *Amano* 5,756 (US). EL SALVADOR: Dep. Sonsonate: Acajutla, *Standley* 21,908 (US); Dep. de la Libertad: vicinity of Atecos, *Standley* 23,343 (MO, US). SURINAM: Lower Saramacca River, *Lanjouw* 263 (US). TOBAGO: Orange Hill, *Broadway* 4,649 (US). TRINIDAD: Santa Cruz, Cangrehal, *Broadway* 2,279 (MO, US). UNITED STATES: Hawaiian Islands, Oahu, Haumaman Bay, *A. Chase* 12,681

Table 13. Comparison of *Chloris arenaria*, *C. cubensis*, *C. ekmanii*, *C. halophila*, *C. pycnothrix*, *C. radiata*, and

Species	Culms	Mature inflorescence shape	Leaf Blade	
			Width (in mm)	Pubescence
<i>C. arenaria</i>	stout; 60-70 cm tall	spikes horizontally spreading or somewhat deflexed	1.5-3.0	scabrous to densely pilose above; densely pilose below
<i>C. cubensis</i>	stout; 50-60 cm tall	spikes erect, diverging no more than 45° from vertical axis	about 1.5 mm	glabrous, occasionally short pilose
<i>C. ekmanii</i>	slender, wiry; 30-45 cm tall	spikes horizontally spreading or deflexed	less than 1.0 mm, often less than 0.5 mm	sparsely to densely pilose, occasionally glabrous
<i>C. halophila</i>	stout; 15-50 cm tall	spikes in several verticils, horizontally spreading	2-3	glabrous or scabrous, sparsely pilose above the base
<i>C. pycnothrix</i>	stout	spikes ascending when young, diverging at maturity	3-5	glabrous to scabrous
<i>C. radiata</i>	stout	spikes ascending	5-10	usually pilose, occasionally glabrous or scabrous
<i>C. sagraeana</i>	stout	spikes horizontally spreading to somewhat deflexed	1.3-3.0	glabrous

(US); Oregon: Linnton, on ballast, *J. C. Nelson* 487, 9 Oct 1915 (US). VENEZUELA: Periveca, Capacho, Tachira, *Tamayo* 2,297 (UC, US). VIRGIN ISLANDS: St. Croix, *Britton and Cowell* 50 (NY); Tortola, *Britton and Shafer* 755 (NY, US). WINDWARD ISLANDS: Barbadoes, Maxwell coast, *Allan* 317 (K); Dominica, *Hitchcock* 16,440 (US); Grenada, Richmond Hill, *Broadway* 978 (US); St. George's, *Broadway s.n.*, 12 Nov 1905 (US); Martinique, *Hahn* 696 (NY, US); St. Lucia, *Hitchcock* 16,485 (US); St. Vincent, *Smith and Smith* 581 (K).

49. **CHLORIS PYCNOTHRIX** Trinius, Gram. Unifloris 234, 1824. (HOLOTYPE: "Chloris pycnothrix . . . Rhadd pycnothrix mi Sta. Cathar am Chamisso." Fragment, in US!, from Trinius Herbarium.) Fig. 74, A-E.

Chloris beyrichiana Kunth, Rev. Gram. 1:89. 1829; 2:289. pl. 56. 1830. (TYPE: ". . . Brasiliae graminosis, prope Rio-Janeiro . . ." Not seen, but description and plate clearly refer to this species.)

Chloris humilis Kunth, Rev. Gram. 1:89. 1829; 2:531, pl. 180. 1832. (TYPE: "prope

Rio-Janeiro." Not seen, but description and plate are definitive.)

Chloris obtusifolia Desvaux, Opuscules 73. 1831. (Type not seen, but description is clear.) *Non Trinius*, 1824.

Chloris intermedia Achille Richard, Tent. Florae Abyssinicae 2:407. 1850. (HOLOTYPE: "Abyssinia, Chire, Leg. Quartin Dillon and Petit" P!)

Chloris leptostachya Hochstetter ex Achille Richard, Tent. Florae Abyssinicae 2:407. 1850. (ISOTYPES: "Abyssinica, ad agrorum margines et in incultis prope Adoam. Schimper, Sectio secunda, 951." BM! G! K! P!)

Chloris salzmanii Steudel, Syn. Pl. Glum. 1:206. 1854. (HOLOTYPE: "Brazil, Bahia, in argillosis aridis . . . Salzmann 664." G!)

Chloris leptostachya var. *intermedia* (Achille Richard) Durand and Schinz, Conspectus Florae Africae 5:861. 1895. (Based on *Chloris intermedia* Richard.)

Chloris radiata var. *beyrichiana* (Kunth) Hackel in Stuckert, Anales Mus. Nac. Hist. Nat. Buenos Aires 6:489. 1906. (Based on *Chloris beyrichiana* Kunth; see also *Chloris*

C. sagracana.

Spikelets per cm of rachis	Fertile lemma				Sterile floret	
	Length (in mm)	Width (in mm)	Awn length (in mm)	Margin pubescence	Length (in mm)	Width (in mm)
5-7	3.5-3.7	ca 0.5	20-24	appressed-ciliate; hairs short	1.6-1.9	0.2-0.3
5-9	3.1-3.6	0.6-0.7	9-12	densely ciliate, at least some hairs more than 1 mm long	1.4-1.9	0.4-0.6
6-10	2.0-3.0	0.4-0.5	5.5-10	sparsely to densely appressed-pilose on upper margins; hairs short	0.4-1.1	less than 0.2 mm
4-7	3.8-5.5	0.6-0.8	9.0-26	appressed-pilose	1.5-2.5	0.2-0.4
12-17	2.5-3.0	0.4-0.5	10-45	glabrous, or with few scattered hairs near apex	0.3-1.6	0.2 mm or less
11-15	2.8-3.3	0.4-0.6	6-13	upper margins short-pilose with appressed hairs	0.4-0.7	ca 0.1
4-9	2.6-3.5	0.5-0.7	7-13	densely appressed-pilose with hairs less than 0.5 mm long	0.7-1.6	0.2-0.5

radiata var. *beyrichiana* Hackel in Kurtz under "Unidentified Names.")

Gymnopogon radiatus var. *beyrichiana* (Kunth) Parodi, *Physis* 4:173. 1918. (Based on *Chloris beyrichiana* Kunth.)

Gymnopogon haumani Parodi, *Physis* 4:183. 1918. (Type not seen, but description and illustration are conclusive.)

Gymnopogon beyrichianus (Kunth) Parodi, *Revista Centr. Estud. Agron. Vet. Univ. Buenos Aires* 18:148, *Fig.* 55. 1925. (Based on *Chloris beyrichiana* Kunth, possibly misapplied.)

Annuals with erect culms arising from short stolons, up to 45 cm tall; sheaths glabrous, occasionally becoming long-pilose near the collar; ligule ciliate, occasionally long-pilose; leaves 4 to 9 cm long, 3 to 5 mm wide, glabrous or scabrous, apex usually obtuse; spikes four to eleven (often three to nine), 3 to 8 cm long, usually borne in a single verticil, though occasionally with two; spikes ascending when young, becoming divergent at maturity; spikelets densely imbricate and tightly appressed to the inflorescence axis, averaging 12 to 17 per cm of the scabrous rachis; glumes thin, nar-

rowly lanceolate, glabrous except for the scabrous-hispid midnerve and the somewhat scabrous apex, rarely pilose; first glume 1.3 to 1.7 mm long, 0.1 to 0.3 mm wide; second glume 2.5 to 3.5 mm long, 0.2 to 0.3 mm wide; fertile lemma narrowly elliptic, 2.5 to 3.0 mm long, 0.4 to 0.5 mm wide, glabrous except occasionally a few scattered hairs near the apex, callus bearded, awn 10 to 45 mm long, usually 10 to 25; sterile floret greatly reduced, usually less than 1 mm long, occasionally up to 1.6 mm long, 0.2 mm or less wide, awn 4.5 to 11.0 mm long, caryopsis 1.2 to 1.4 mm long, 0.3 to 0.4 mm wide, narrowly ellipsoid; anthers ca 0.5 mm long; chromosome numbers $2n=30, 36, 40$.

Chloris pycnothrix most closely resembles *C. radiata* and, somewhat less so, *C. arenaria*, *C. cubensis*, *C. ekmanii*, and *C. sagraeana*. Table 13 presents the more important characteristics differentiating these species.

Plants combining various characteristics of *Chloris pycnothrix* and *C. radiata* are occasionally found in areas that are unquestionably within the range of *C. pycnothrix*. For example, collections from the Galápagos Islands have long awns, a characteristic of *C. pycnothrix*, but otherwise fit *C. radiata*. Specimens

with the short-ciliate lemma margins of *C. radiata*, from parts of Venezuela and North Africa, are referred to *C. pycnothrix* only because the preponderance of their characters belong to that species. Individual specimens from these areas may be difficult, if not impossible, to refer to one species or another on the basis of only a few key characters. These aberrant specimens must represent casual, random variation in spikelet features, for these plants otherwise maintain the distinctive epidermal features of the species (see Table 13; Fig. 1).

Chloris pycnothrix is widely distributed through Africa and northern South America (Fig. 77). Collection data indicate that these plants are frequently found as weeds in disturbed areas. While usually described as an annual, greenhouse specimens have persisted for over two years before dying, suggesting that this species might behave as a weak perennial under favorable conditions.

Representative specimens examined: AN-GOLA: Huila Dtr.: Posta Zootechnica, *Teixeira*

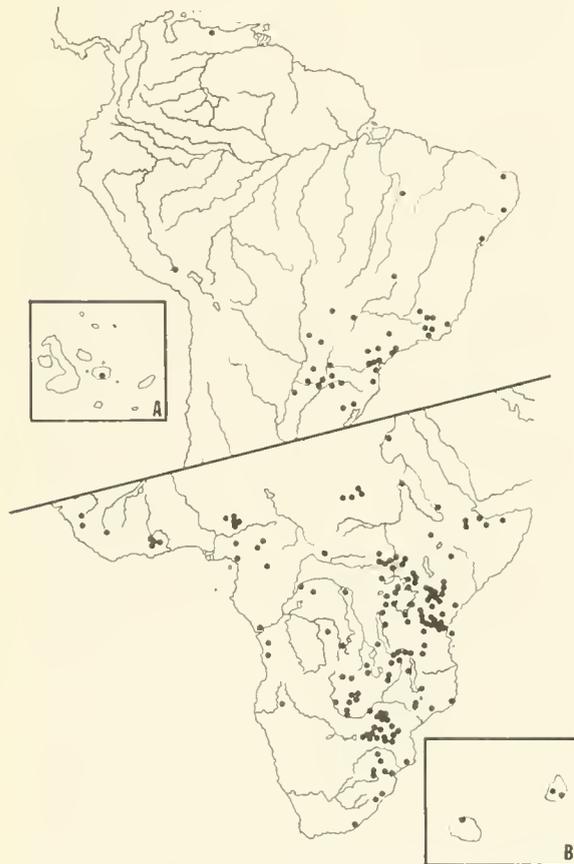


Fig. 77. Distribution of *Chloris pycnothrix*. Insets: (A) Galápagos Islands. (B) Reunion and Mauritius.

637 (K); Golungo Alto, *Wehritsch* 2,985b (K). ARGENTINA: Prov. Corrientes: Empedrado Dep., Estancia "Las Tres Marias" *Pedersen* 3,053 (US); Prov. Misiones: Posades, *Parodi* 4,017 (US); Prov. Formosa: without precise location, *Jorgensen* 43,053 (US). BRAZIL: Prov. Bahia: 39 km NE of Bahia, *A. Chase* 8,016 (F, MO, NY, US); Prov. Maranhao: Carolina to San Antonio de Balsas, *Swallen* 3,951 (US); Prov. Matto Grosso: Tres Lagoas, *A. Chase* 10,759 (US); Prov. Parana: Guaratuba, Morro do Brejatuba, *Hatschbach* 4,469 (US); Prov. Rio Grande do Sul: vicinity of Guaiba, *Beetle* 1,498 (UC); Prov. Catarina: Campo Ere, Fazenda São Vicente, *Castellanos* 24,742 (K). BURUNDI: environs de Karuzi, *Vander Ben* 2,075 (K). CAMEROONS: Bertoua, *Baldwin* 13,954 (US); Wakwa, 10 km S of N'Gaoundere, *Breteler* 488 (K); Nkambe Div.: Bamenda Highlands, 6°35'N, 10°40'E, *Hepper and Charter* 1,938 (K). CENTRAL AFRICAN REPUBLIC: 35 mi from Bambari, *Kyrle* FA10 (K). ETHIOPIA: Bagemeder Prov.: Lake Lana, Bahudur Gorge, *Grabham* 116/21 (K); Harar Prov.: NE of Lake Alemaya, 15 km NW of Harar, *Burger* 1,079 (K). GALÁPAGOS ISLANDS: Santa Cruz Island, Academy Bay, *Schimpff* 39 (NY, US). GHANA: Venchi, 7°49'N, 2°07'W, *Rose-Innes* 30,519 (K); Nzerekore, *Baldwin* 9,709 (US), 9,725 (K). GUINEA: Mamou, *Chevalier* 34,887 (K). IVORY COAST: Pakobo Nord, *Adjoussoun* 384A (K). KENYA: 8 mi N of Tsavo Falls, 6,300 ft, *Barney* 1,123 (K); Nairobi, *Bogdan* B44 (UC); Amboseli National Park, 50 mi E of Namanga, *Bogdan* AB 5,500 (K); S Lake Elmenteita, 6,000 ft, *Clayton* DC 27 (K); Mt. Suswa, *Glover* 3,785 (K). MALAGASY REPUBLIC: Mt. Belamboany, *Perrier de la Bathie* 14 (K). MALAWI: Shiri Highlands, *Buchanan* 55 (K); Mlanje, *Burt-Davy* 1962/29 (K); near Zomba, *Cormack* 165 (K). MARTINIQUE: roadside, *Velez* 3,447 (US). MAURITIUS: Curepipe, Vacoa, *Vaughan* A-29 (K). MOÇAMBIQUE: Mocuba Dtr.: Namagoa, *Faulkner* 18 (K), 145 (K, US); 26 km W of Lourenço Marques, *Gomes e Sousa* 3,247 (K). NIGERIA: Samaru, Zaria, *Clayton* DC 1,332 (K); Bauchi Plateau, *Lely* P769 (MO); Toro, 20 mi E of Jos, *Semple* 173 (US). PARAGUAY: Dep. Guáira: Villarica, *Jorgensen* 3,532, 3,533 (US); Dep. San Pedro: Primavera, *Woolston* 6.40 (K). PERU: Dep. Apurimac: Abancay, *Stordt*, without collection number and date (K). REPUBLIC OF THE CONGO: Marungu, *Dubois* 1,363 (K); Eala, *Lebrun* 454 (MO, US); Yangambi,

Louis 16,007 (K); Katanga, 25 km N of Lubumbashi (Elizabethville), *Schmitz 7,384* (K). RE-UNION: St. Denis, *Rivels*, without collection number and date (K). SOMALI REPUBLIC: Hargeisa, 9°33'N, 44°E, *Gillett 3,917* (K); Medishe, *Glover and Gilliland 941* (K, US). SOUTHERN RHODESIA: Salisbury, *Brain 440, 1,541* (MO); Stapleford Forest Reserve, *Gilliland 237* (K); Kariba Gorge, *Goldsmith 73/60* (K); Urungwe National Reserve, Zwipani area, *Goodier 513* (K); Victoria Falls, wet spray areas, *Parker 4,202* (K); near Sinoia, *Rodin 4,376* (F, MO, UC, US). SUDAN: Darfur Prov.: Gur Lambong, *Jebel Marra, Wickens 2,593* (K); Equatoria Prov.: Yei, *Harrison 488* (K); Khartoum Prov.: Khartoum, *Jackson 4,186* (K); Northern Prov.: Wadi Halfa, *Pettet 90* (K). TANZANIA: Kondoia Dtr.: near Sambala, *Burtt 2,603* (K); Ngorongoro Crater, *Burtt 4,338* (K); Musoma, *Emson 241* (K); Bukoba Dtr.: Ngono Bridge, *Gillman 67* (K); Kilimanjaro, Lyamungo, *Greenway 3,133* (K); Seronera, Serengeti, *Greenway 9,874* (K); Zanzibar, *Hitchcock 24,445* (US). UGANDA: Nabilatuk, near Emonagalaberi, *Dyson-Hudson 55* (K); Entebbe, *Hitchcock 24,874* (US); 7 mi W of Moroto Karamoja, *Langdale-Brown 1,572* (K); Busoga, Nawendwa, *Maitland 1,406* (K); Mbale, near Mt. Elgon, *Snowden 1,090 A* (K). UNION OF SOUTH AFRICA: Cape Provinces, East London, *McCallum-Webster N94* (K); Natal, SW of Mapumulo, Umtavi Valley, *Moll 1,843* (K); Transvaal, Kruger National Park, *de Winter and Codd 600* (US). VENEZUELA: E of La Guiana, *Curran and Haman 902* (NY). ZAMBIA: Chilonga, Mt. Makula Research Station, *Hinds 6* (K); Mpika Dtr.: Luangwa Game Reserve, Mfuwe, *Mitchell 2,945* (K); Kasama Dtr.: Mungwi, *Robinson 4,080* (K); Mazabuka Dtr.: Mochipapa to Mabwngombe Hills, *White 7,523* (K).

50. CHLORIS HALOPHILA Parodi, Rev. Argentina Agron. 12:45. Fig. 1. 1945. (ISO-TYPE: "Argentina, Buenos Aires, Pergamino . . . Parodi 2769" US!) Fig. 78.

Perennial 15 to 50 cm tall, sometimes up to 80 cm, weakly stoloniferous; sheaths glabrous, sometimes sparsely pilose above; ligule ciliate or a short, membranous crown; blades glabrous or scabrous, sometimes becoming sparsely pilose on upper surface near the base; spikes four to thirteen, 3.5 to 12.0 cm long (usually 7 to 8 cm), arranged in several verticils; spikelets appressed, somewhat distant, ca four to seven per cm of the scabrous rachis; glumes narrowly lanceolate, glabrous except for the scabrous mid-

nerves; first glume 1.5 to 3.0 mm long, 0.2 to 0.3 mm wide; second glume 3.7 to 5.3 mm long, 0.3 to 0.4 mm wide; fertile lemmas 3.8 to 5.5 mm long, 0.6 to 0.8 mm wide, narrowly lanceolate or elliptic, apex acute to acuminate, callus bearded, margins appressed-pilose, awn 9 to 26 mm long; sterile floret one, 1.5 to 2.5 mm long, 0.2 to 0.4 mm wide, lanceolate to elliptic, apex acute to acuminate, glabrous to somewhat scabrous, awn 7 to 13 mm long; anthers ca 0.7 mm long; caryopsis 1.9 to 2.4 mm long, 0.4 to 0.6 mm wide, ellipsoid, trigonous; chromosome number $2n=80$.

Chloris halophila is similar to *C. radiata* and *C. pycnothrix* in outward appearance but has a coarser inflorescence and larger spikelets (compare Fig. 75 and 78). Additional differences are given in Table 13.

For many years the names *Chloris beyrichiana*, *C. radiata* var. *beyrichiana*, and *Gymnopogon beyrichianus* were misapplied to this taxon, especially by Parodi. Parodi later (1945) recognized these names as being properly applied to *C. radiata* and provided a new name, *C. halophila*, for the plant described above.

Chloris halophila has been collected through a great altitudinal range from ca 2,000 feet elevation in Tucuman Province, Argentina, to over 11,000 feet in Bolivia (Fig. 71, circles). It occurs in grasslands, especially in saline conditions.

Representative specimens examined: ARGENTINA: Prov. Catamarca: Dep. Ambato, Camino al Rodeo, *Cristobal 406* (UC); Prov. Córdoba: S of de Mar Chiquita, *Burkart 20,457* (UC); Dep. Punilla La Cocha, *Stuckert 20,191* (G); Prov. Tucuman: valle de Tafi, *Bruch s.n.*, 1908 (NY); Dep. Burruyacu: Sal Morado, *Dias 799* (NY); Río de Nio, *Monetti 43,048* (US); Tapia, *Rodriguez 182* (US); Leales, Chamar Pojo, *Venturi 711* (K, US); Prov. Salta: Pasaje del Río Juaramendo, *Lorentz 344* (F); Rosario de Lerma, *Meyer 3,464* (NY); Dep. Agua Caliente: Cavelaria, *Venturi 3,773* (MO, US). BOLIVIA: Dep. Cochabamba: Cochabamba, *Cutter 7,381* (US); Mizque, *Eyerdam 24,987* (F, G, K, MO, UC); Río Tapacari, *Kuntz s.n.*, 1892 (NY); Dep. La Paz: vicinity of La Paz, ca 10,000 ft, *Baug 82* (BM, G, MO, NY, US). ECUADOR: Prov. Carchi: Pistu a la Palestina, *Acosta-Solis 16,557* (US); Prov. Loja: between Las Lomas and Loja, *Hitchcock 21,409* (US); Prov. Pichincha: descenso del Quincha a Guayllabamba, *Acosta-Solis 10,329* (F, US); Cajamarca Prov.: Cajamarca, 2,600 m, *Anderson 630* (UC, US). PERU: Dep. Cuzco: Cuzco, *Hitchcock 22,492* (US); 5 km S of Ollantaytambe,

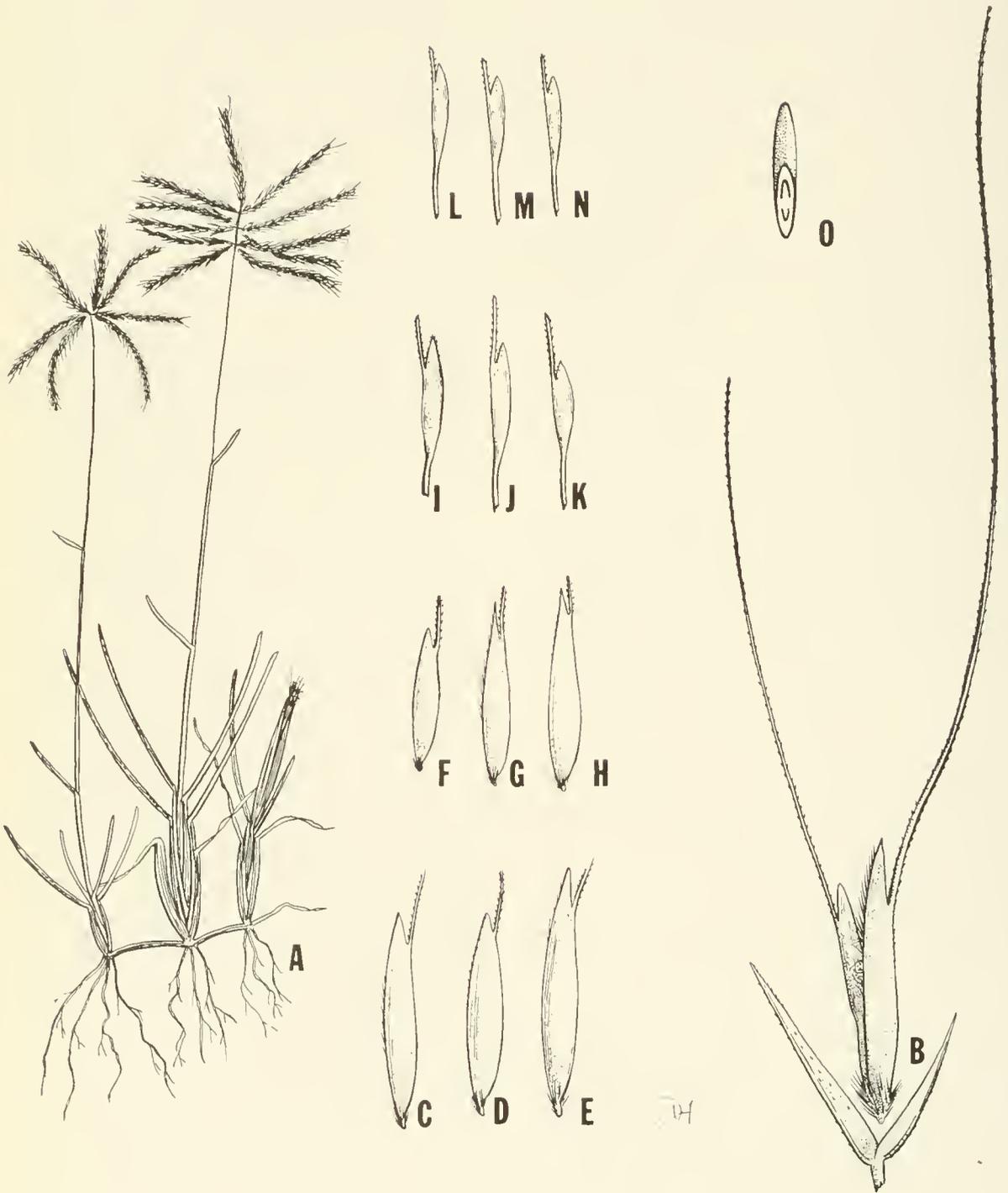


Fig. 78. *Chloris halophila*. (A) habit, x 1/5; (B) spikelet, partly dissected, x 7.5; (C-H) fertile florets, showing variation, x 5; (I-N) sterile florets, showing variation, x 7.5; (O) caryopsis, x 7.5.

Hitchcock 22,552 (K, NY, US); Dep. Haunceve-lia, Izcuchaca, entre Cuenca y La Mejorada, 3,100-3,150 m, *Tovar* 2,448 (US); Prov. Huancayo: Mantero, N of Huancayo, 3,300 m, *Anderson* 683 (UC, US).

51. **CHLORIS EKMANII** Hitchcock, U.S. Dept. Agric. Misc. Publ. 243:129. 1936. (HOLOTYPE: "Babujal, Jagüey Grande, prov. Matanzas, Cuba . . . Ekman . . . 16594." US!) Fig. 79, A-F.

Perennial 30 to 45 cm tall, occasionally up to 60 cm tall, tufted to short-stoloniferous; culms slender, wiry, somewhat geniculate at the base; sheaths compressed-keeled; blades up to 10 cm long, usually less than 1 mm wide, sparsely to densely pilose on both sides, occasionally glabrous; spikes three to six, 1.5 to 5.0 cm long, slender, flexuous, erect to appressed when young, at maturity spreading horizontally or becoming somewhat reflexed; spikelets imbricate, appressed when young, somewhat divergent at maturity, ca 6 to 10 per cm of the scabrous rachis; glumes lanceolate, glabrous except for the scabrous midnerve; first glume 1.1 to 2.0 mm long, 0.1 to 0.3 mm wide; second glume 2.3 to 3.6 mm long, 0.1 to 0.3 mm wide; fertile lemma 2 to 3 mm long, 0.4 to 0.5 mm wide, narrowly lanceolate to elliptic, callus bearded, sparsely to densely appressed-ciliate on upper margins, otherwise glabrous, awn 5.5 to 10.0 mm long; sterile floret one, 0.4 to 1.1 mm long, less than 0.2 mm wide, usually included in the fertile lemma, awn 3.3 to 6.0 mm long; caryopsis ca 1.4 mm long, ca 0.3 mm wide, ellipsoid, trigonous.

Chloris arenaria, *C. cubensis*, *C. ekmanii*, *C. radiata*, and *C. sagraeana* form a complex of species in the Caribbean region, the area to which all except *C. radiata* are restricted. While most specimens can be named with reasonable confidence, some either have intermediate features or else recombine characteristics of two species. These are often found in, but are not restricted to, areas of sympatry. Field studies are needed, especially in Cuba; and precise definitions of the taxa involved and evaluation of their biological significance must await further information. The treatment presented here will enable one to name most specimens. A further discussion of variation patterns is presented under the species most closely concerned. Table 13 presents a comparison of the characteristics of these species.

Chloris ekmanii is most similar to *C. sagraeana* but is a more delicate plant with wiry stems and, usually, very narrow leaves. The first

glume, less than 1.5 mm long, and the sterile floret are both smaller than any other species in this complex. Occasional specimens have glabrous rather than hairy leaves, but this character does not correlate with either geographic origin of the specimen or with other features.

This species is apparently widely distributed in Cuba, Jamaica, and Hispaniola (Fig. 80, circles) in a variety of ecological sites, such as along railways, roadways, and rivers, shrubby savannas, pastures, and pinelands. It is often collected in bright red clay soils, though other collections have been made on rocky or even serpentine soils.

Representative specimens examined: CUBA: Prov. Camagüey: Camagüey to Santayana, *Britton* 2,428 (NY); San Serapio, N of Camagüey City, *Leon* 16,927 (US); Prov. Havana: near Almandares River, *Leon* 287 (US); San Miguel, *Ekman* 10,912 (US); La Pitanill, San Miguel de Casanova, *Leon* 12,454, 19,517 (US); Guanabacoa, *Ekman* 13,645 (F, NY, US), *Hitchcock* 23,299 (K, US), 23,240 (US); Jata Hills, *Ekman* 856 (US); Isla de Piños, Nueva Gerona, along Río Los Casas, *Ekman* 11,682 (NY); Prov. Las Villas (Santa Clara): Trinidad, road to San Juan de Letran, *Ekman* 13,975 (US); Gara, *Leon* 1,480 (NY); vicinity of Sancti Spiritus, *Serguis* 2,569 (US); Pitajones to Ciegos de Ponciano, *Shafer* 12,225 (NY, US); Prov. Matanzas: Jagüey Grande, *Ekman* 16,954 (F); Prov. Oriente: Guamo, *Hitchcock* 23,412, 23,427 (US); Holguin, *Ekman* 3,229 (F); Prov. Pinar del Río: El Sabalo, Finca Sabanalamar, *Killip* 32,294 (US); Loma Pelada de Buenovista, Cayajabos, *Leon* 13,226 (US); Bahía Honda, *Wilson* 9,421 (NY). DOMINICAN REPUBLIC: Prov. Monte Cristi: Guayabin, *Abbot* 916 (US); Santiago Prov.: Licey al Medo, near Peña, *Jimenez* 3,910 (US). JAMAICA: Cornwall Co., Montego Bay, *Hitchcock* 9,695 (US); Middlesex Co.: Lititz, Manchester, *Harris* 12,434 (F, K, NY, US), *Harris* 12,697 (K, NY, US); Inverness, Lower Clarendon, *Harris* 12,727 (K, NY, US); between Ewarton and Linstead, *Hitchcock* 652 (F, K, MO, NY, UC, US); New Forest, Southern Manchester, *Hitchcock* 9,823, 9,847 (US).

52. **CHLORIS ARENARIA** Hitchcock & Ekman ex Hitchcock, U.S. Dept. Agric. Misc. Publ. 243:131. 1936. (HOLOTYPE: "Cuba, La Grifa, prov. Pinar del Río. Ekman 11253." US! ISOTYPES: F! K!) Fig. 79, G-K.

Chloris cleusinoides Grisebach var. *vestita* Greenman ex Combs, Trans. Acad. Sci. St. Louis 7:477, pl. 39. 1897. (Fragment of

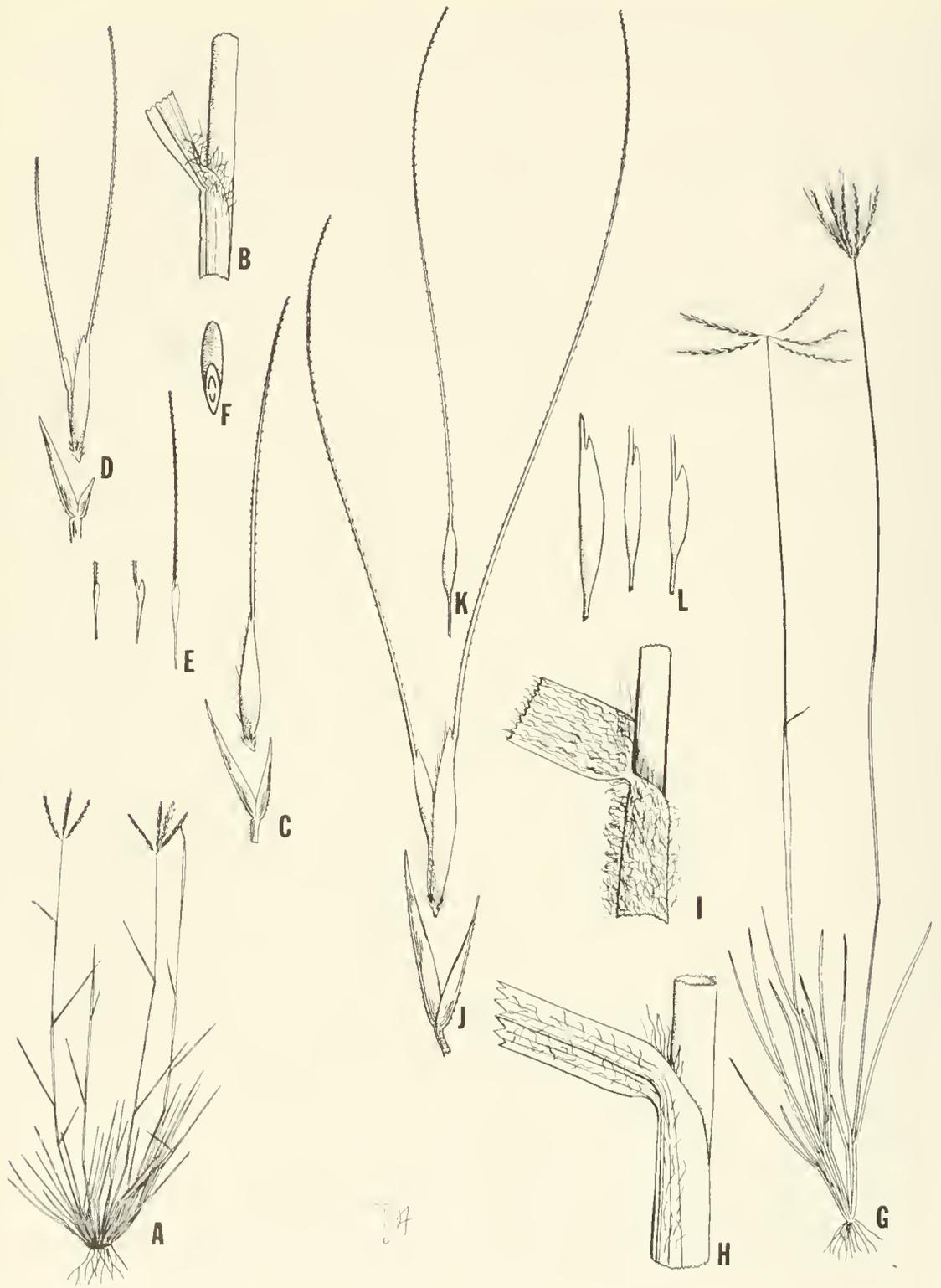


Fig. 79. *Chloris ekmanii* and *C. arenaria*. (A-F) *C. ekmanii*. (A) habit, x 1/3; (B) ligule region, x 5; (C,D) spikelets, partly dissected, x 7.5; (E) sterile florets, showing variation, x 10; (F) caryopsis, x 10. (G-L) *C. arenaria*. (G) habit, x 1/4; (H,I) ligule region, x 5; (J) spikelet, x 7.5; (K, L) sterile florets, showing variation, x 15.



Fig. 80. Distribution of *Chloris cubensis* (squares), *C. ekmanii* (circles), and *C. sagraeana* (triangles). Inset A: Puerto Rico and the Lesser Antilles.

type: "Rio Damuji, Rodas Cuba . . . Combs 631" US! Origin of fragment unknown.)

Perennial 60 to 70 cm tall; culms cespitose, erect to somewhat decumbent at base; sheaths compressed-keeled, puberulent, becoming densely so near the apex; ligule a dense tuft of hairs; lower leaves 5 to 10 cm long, 1.5 to 3.0 mm wide, becoming shorter upward on the culm; blades scabrous to densely pilose above, densely pilose below; spikes five to six, 4 to 6 cm long, digitate, ascending when young, becoming horizontal or somewhat reflexed at maturity; spikelets rather densely imbricate, appressed, ca five to seven per cm of the scabrous rachis; glumes narrowly lanceolate, acuminate, glabrous except for the scabrous midnerve; first glume 2.2 to 2.5 mm long, 0.2 to 0.3 mm wide; second glume 3.3 to 3.5 mm long, 0.2 to 0.4 mm wide; fertile lemma 3.5 to 3.7 mm long, ca 0.5 mm wide, lanceolate to elliptic, callus bearded, otherwise glabrous except for the short, appressed-ciliate margins, awn 20 to 24 mm long; sterile floret one, 1.6 to 1.9 mm long, 0.2 to 0.3 mm wide, narrowly cylindrical, glabrous, awn 15 to 20 mm long; caryopsis not seen.

Chloris arenaria may be separated from other species in this complex by its densely villous leaf blades and sheaths and by its long awns on the lemmas (20 to 24 mm).

Only one of the two specimens studied had collection information. This plant (*Ekman 11,253*) was collected in pineland on white sand.

Specimens examined: CUBA: without precise location, *Wright 3,819* (K, NY, US).

53. **CHLORIS SAGRAEANA** Achille Richard in Sagra, *Hist. Fisica Politica Natural Isla Cuba XI. Botanica* 315. 1850. (HOLO-

TYPE: "*Chloris sagraeana* nob. no. v. fol. obtusa Cuba. . . ." P! Fragment of type: US!) Fig. 81, 1-T.

Chloris morales-coelloi Leon ex Britton, *Bull. Torrey Bot. Club* 53:458. 1926. (ISO-TYPE: ". . . Cajobabo . . . not far from mouth of the Jojo River, Oriente . . . Leon . . . 12320." US!)

Perennial 15 to 80 cm tall, cespitose, erect or ascending from a geniculate base; sheaths glabrous, ligule short-ciliate; blades up to 15 cm long, 1.3 to 3.0 mm wide, glabrous; spikes three to six, 3.5 to 15.0 cm long (usually ca 4 to 9 cm long), becoming widely divergent or somewhat reflexed at maturity; glumes narrowly lanceolate, glabrous except for the scabrous midrib; spikelets appressed, ca four to nine per cm of the scabrous rachis; first glume 1.6 to 2.2 mm long, 0.2 to 0.4 mm wide; second glume 2.4 to 3.5 mm long, 0.5 to 0.7 mm wide; fertile lemma 2.6 to 3.5 mm long, 0.5 to 0.7 mm wide, elliptic, callus bearded, with hairs less than 0.8 mm long, margins strongly appressed-pilose, the hairs usually less than 0.5 mm long, keels glabrous, occasionally very sparsely pilose, awn 7 to 13 mm long; sterile floret one (occasionally two), 0.7 to 1.6 mm long, 0.2 to 0.5 mm wide, cylindrical, glabrous, apex acute, awn 3.3 to 9.0 mm long; caryopsis 1.6 to 1.7 mm long, 0.4 to 0.5 mm wide, ellipsoid, trigonous.

Chloris sagraeana is the most variable species within the complex that includes *C. arenaria*, *C. cubensis*, *C. ekmanii*, and *C. radiata*. This variation is especially noticeable with respect to the size of the fertile and sterile lemmas. Frequently specimens with exceptionally long lemmas will produce two sterile florets; and on occasion, the lowermost "sterile" floret will produce a caryopsis, though it otherwise resembles the upper sterile floret in morphology. This variation in structure may or may not be correlated with size. A specimen with two sterile florets, coincidentally very robust, was named *Chloris morales-coelloi* by Leon (in Britton, 1926).

Chloris sagraeana may be separated from *C. ekmanii* by its more robust stature and broader leaves and from *C. cubensis* in having shorter, appressed hairs on the lemma margins (Table 13).

This species has been collected from a variety of habitats, including pinelands, serpentine outcrops, coral rocks, and pastures (Fig. 80, triangles).

Representative specimens examined: BAHAMA ISLANDS: Fortune Island, *Hitchcock s.n.*, Nov 1890 (F, MO); Inagua Island, *Hitchcock*

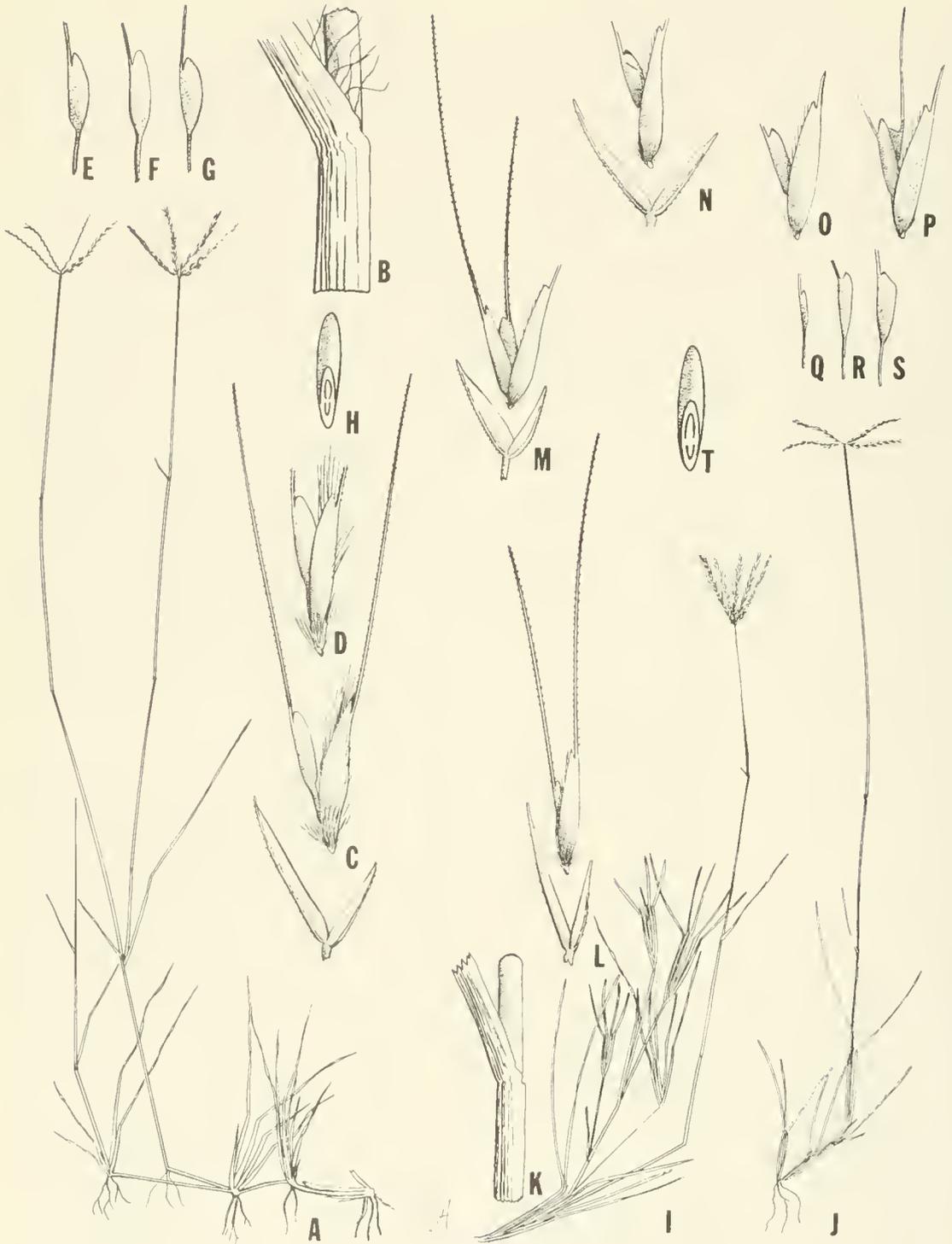


Fig. 81. *Chloris cubensis* and *C. sagracana*. (A-H) *C. cubensis*. (A) habit, x 1/3; (B) ligule region, x 3; (C) spikelet, partly dissected, x 7.5; (D) florets, x 7.5; (E-G) sterile florets, showing variation, x 10; (H) caryopsis, x 10. (I-T) *C. sagracana*. (I, J) habit, x 1/3; (K) ligule region, x 3; (L) spikelet, partly dissected, x 7.5; (M) spikelet with two sterile florets, partly dissected, x 7.5; (N) spikelet from type, partly dissected, x 7.5; (O, P) additional florets, showing variation, x 7.5; (Q-S) sterile florets, showing variation, x 10; (T) caryopsis, x 10.

s.n., 3 Dec 1890 (F, MO, NY); Nassau, *Britton and Brace* 596 (F, NY), *Curtiss* 81 (US). BARBADOS: *Allen s.n.*, Jan 1942 (K, NY). BARBUDA: S of Codrington, *Danforth* 3 (US). CUBA: Prov. Havana: vicinity of Havana, *Ansoñin* 779 (US); between Morro and Cojimar, *Ekman* 389 (US); Guanabacoa, Lomas de los Jatos, *Ekman* 10,902a (US); Near Marianas, *Leon* 1,965 (US); near Luzano, *Leon* 4,807 (US); Santa Fe, *Leon* 13,096 (US); Cuabal de Jesus Maria Minas, *Leon and Hioram* 4,783, 4,787 (US); Prov. Matanzas: Babiyal, *Ekman* 16,954 (US); Prov. Pinar del Río: La Grifa, *Ekman* 11,252 (US); Mariel, coral reef E of town, *Ekman* 12,837 (US); Prov. Oriente: pinelands, crest of Sierra Nipe, *Leonard and Leonard* 3,183 (US). DOMINICAN REPUBLIC: Prov. Monte Cristi: Valle de Cibao, Villa Vasquez, *Ekman* 13,128 (K, US); Prov. de Santiago: Mao, *Abbott s.n.*, 23 Feb 1921 (US). GUADELOUPE: without precise locality, *Duss* 4,110 (F, NY, US); *Les Pointes*, *Questal* 1,740 (US). HAITI: Pignon to San Rafael, *Cook* et al. 138 (US); Port-au-Prince, *Ekman* 2,107 (K, US); Tortue Island between La Vallée and Ravine-Rosetiere, *Ekman* 4,058 (K, US); Corail, Dutreuil, *Ekman* 11,0748 (K, US); Grande Cayemite, Pointe Macon, *Eyerdam* 336 (F, NY, US); vicinity of Petionville, *Leonard* 4,984 (NY, US); vicinity of Gros Morne, Dep. Artibonite, *Leonard* 9,839 (US); Port-de-Paix, *Leonard and Leonard* 11,051 (US); Baie des Moustiques, *Leonard and Leonard* 12,067 (US); vicinity of Jean Rabel, *Leonard and Leonard* 12,552 (K, MO, NY, US); vicinity of Mole St. Nicolas to Bombardopolis, *Leonard and Leonard* 13,225 (UC, US). JAMAICA: Cornwall Co., Savanna-la-Mar, *Hitchcock* 9,890 (F, MO, NY). Middlesex Co., Ashley Hall Savannah, Lower Clarendon, *Harris* 12,738 (F, NY, US).

54. **CHLORIS CUBENSIS** Hitchcock & Ekman ex Hitchcock, U.S. Dept. Agric. Misc. Publ. 243:131. 1936. (HOLOTYPE: "... Cuba, prov. Oriente, Gamboa . . . Ekman . . . 14960." US!) Fig. 81, A-H.

Perennial usually 50 to 60 cm tall, occasionally up to 90 cm, tufted to stoloniferous; sheaths glabrous, ligule a short-ciliate or naked crown up to 0.5 mm tall; leaves 10 to 15 cm long, ca 1.5 mm wide, often folded, scabrous to sparsely pilose above, glabrous below; spikes three to seven, 5.5 to 8.5 cm long, radiate, ascending; spikelets appressed, imbricate, ca five to nine per cm of the scabrous rachis; glumes narrowly lanceolate, membranous, glabrous except for the scabrous midnerve; first glume 1.7 to 2.4 mm

long, 0.2 to 0.3 mm wide; second glume 2.9 to 3.9 mm long, 0.2 to 0.4 mm wide; fertile lemma 3.1 to 3.6 mm long, 0.6 to 0.7 mm wide, lanceolate, callus long-bearded, upper 2/3 of margins long-ciliate with hairs up to 1 mm long, keel and sides sparsely pilose, lemma awn 9 to 12 mm long; sterile floret one, 1.4 to 1.9 mm long, 0.4 to 0.6 mm wide, cylindrical, apex obtuse, awn 6 to 9 mm long; caryopsis ca 1.3 mm long, ca 0.3 to 0.4 mm wide, ellipsoid.

Chloris cubensis is similar to *C. sagraeana*, from which it may be separated by its generally larger size, less divergent mature spikes, and by the long hairs on the lemma margins and, usually, on the lemma keel. (Fig. 81; Table 13).

Specimens have been collected on roadsides and open dry areas (Fig. 80, squares).

Representative specimens examined: ANTIGUA: Nonsuch Bay, Facey Creek, *Box* 556 (US). BARBADOS: without precise location, *Hitchcock* 16,499 (US). CUBA: Prov. Camagüey: Minas, *Ekman* 15,368 (F, NY, US); Prov. Havana: Loma de Tierra, *Ekman* 13,469 (K, US); Vibora, *Leon* 859 (US); Calvarco, *Leon* 860 (US); Prov. Las Villas: Loma de Belen, *Leon* 15,627 (US); Prov. Oriente: Holguin, *Ekman* 1,014 (F, K, MO, NY, UC, US), *Ekman* 15,715 (F, NY, US). HAITI: Tortue Island, vicinity of Basse Terre, *Leonard and Leonard* 12,538 (US). JAMAICA: Hanover Park, Bailey's Point, *Adams* 7,964 (BM); Cockpit, Vere, *Harris* 12,462 (F, MO, NY, US); Spanish Lower Road, *Harris* 12,476 (K). PUERTO RICO: Río Piedras, *Alberts* 273 (US).

55. **CHLORIS MOSSAMBICENSIS** Schumann, Notizbl. Bot. Gart. Berlin 1:104. 1895. (ISO-TYPE: "Mozambik, Cabareino Grande . . . No. 88. leg. Prelado." BM!) Fig. 82.

Tetrapogon mossambicensis (Schumann) Chippendahl ex B.S. Fisher in Meredith, Grasses and Pastures of South Africa 198. 1955. (Based on *Chloris mossambicensis* Schumann.)

Perennial, tufted to aggressively stoloniferous, 20 to 100 cm tall (usually 40 to 80 cm); sheaths glabrous to scabrous; ligule a short-ciliate crown, often with a few long hairs interspersed, especially near the margins; blades up to 30 cm long, ca 8 mm wide, obtuse to acuminate; spikes three to six (often four or five), 3 to 10 cm long, divaricate to horizontally spreading; spikelets sparsely inserted, imbricate, divergent, ca eight or nine per cm of the scabrous rachis; glumes narrowly lanceolate, thin, membranous, glabrous except for the scabrous mid-

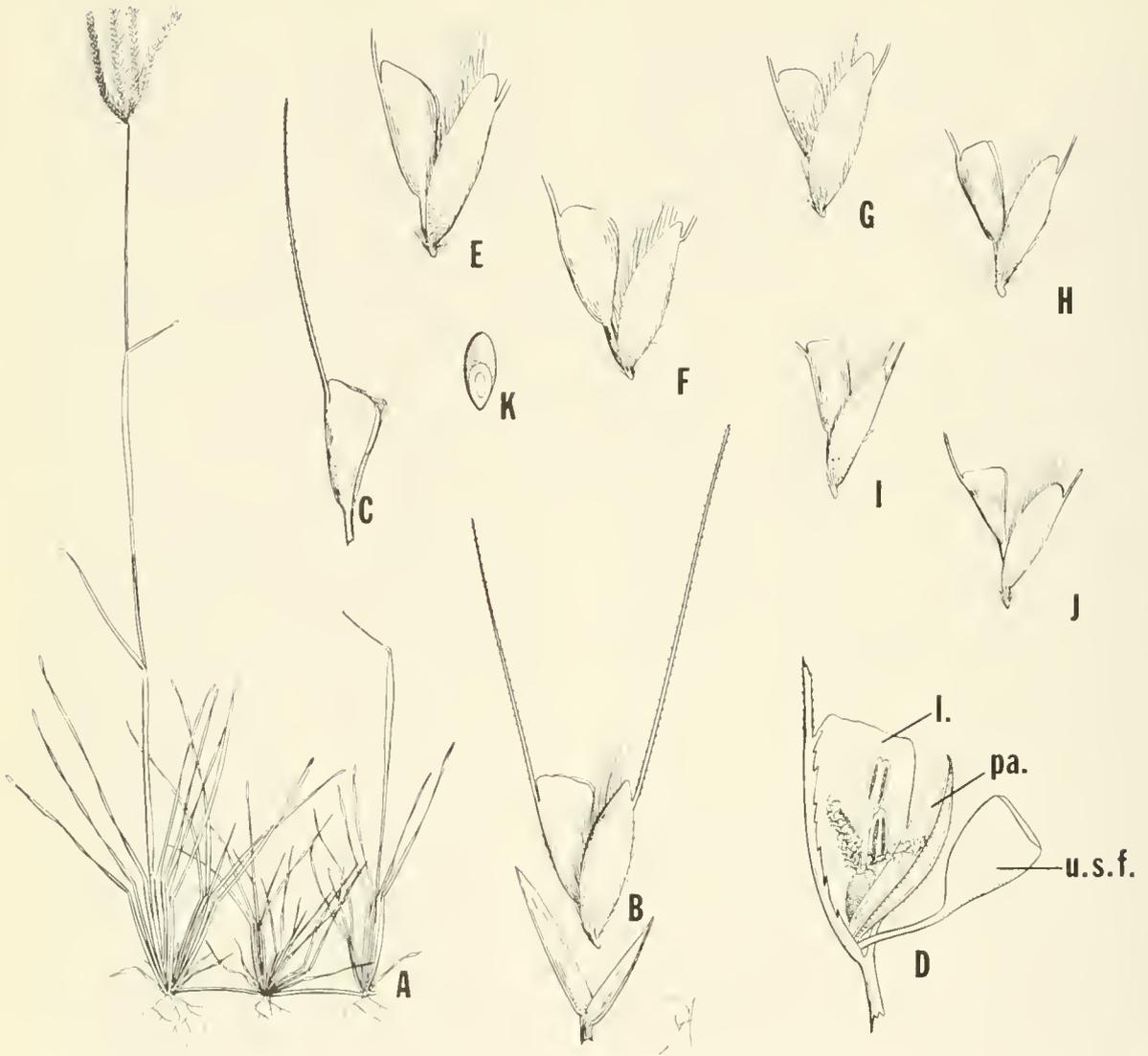


Fig. 82. *Chloris mossambicensis*. (A) habit, x 1/5; (B) spikelet, partly dissected, x 5; (C) sterile florets, x 7.5; (D) partly dissected "sterile" florets, showing upper sterile floret (u.s.f.), palea of lower "sterile" floret (pa.), lemma of lower "sterile" floret (l.), and flower, x 20; (E-J) florets, showing variation, x 5; (K) caryopsis, x 7.5.

nerve; first glume 1.6 to 2.6 mm long, ca 0.2 mm wide; second glume 3.0 to 4.4 mm long, 0.3 to 0.4 mm wide; fertile lemma 3.0 to 4.7 mm long, 0.8 to 1.2 mm wide, elliptic to ovate, apex acute to obtuse, callus densely bearded, margins appressed-pilose below, becoming ciliate near the apex with hairs ca 1 mm long, keel appressed-pilose, internerves glabrous, awn 3.5 to 12.0 mm long; sterile floret usually one (occasionally two), 1.5 to 3.3 mm long, 0.7 to 1.5 mm wide, narrowly to broadly triangular, usually barren, occasionally fertile and setting seed, apex truncate, usually glabrous, very occasionally sparsely

pilose, awn 2 to 9 mm long; caryopsis 1.2 to 1.3 mm long, 0.3 to 0.5 mm wide, ovoid to obovoid, rounded to trigonous.

This species has been treated variously as a member of *Chloris* or of *Tetrapogon*. As brought out in earlier discussion, the two genera are very closely related and must be somewhat arbitrarily separated. Essentially, *Tetrapogon* regularly has more than one basal fertile floret, while *Chloris* has just one. A sampling of nineteen specimens, from different locations in southern Africa, showed seventeen with a single fertile floret and two with two fertile florets. Because



Fig. 83. Distribution of *Chloris mossambicensis* (southern Africa).

of this and an overall resemblance to the preponderance of *Chloris* species, I am treating this species as a member of the genus *Chloris*.

Chloris mossambicensis is widely distributed in southern Africa (Fig. 83), where it has been collected in a variety of habitats. A more detailed and expanded distribution map may be found in Chippendall (1955).

Representative specimens examined: KENYA: I4 Falls, Athi River, near Doinyo Sapuk, *Bogdan AB 1,590* (K); Nairobi to Mombasa Road, near Samburu Station, *Bogdan AB 3,616* (K); Mariakani, *Bogdan AB 5,429* (K); Kwale Dtr., near Taru, between Samburu and MacKinnon Road, *Drummond and Hensley 4,189* (K). MOZAMBIQUE: Sul do Save, Maputo River, entre Changanane e Catuane, *Myre and Carvalho 1,440* (K); between Moamba and Boane, *Schwieckerdt 1,919A* (K); Lourenço Marques, Rio Limpopo, entre Mianga e Guija, *Torre 6,614* (K). SWAZILAND: 11 mi W of Stegi, *Codd and Dyer 2,863* (K). TANZANIA: Tanga Prov., Mkwaja, Pangani, banks of Bohomaia River, *van Rensburg 516* (K). UNION OF SOUTH AFRICA: Natal: 8 mi N of Mkuze on Candover Road, *Edwards 3,257* (K); Zululand, lower Umfolozi region, *Ward 2,442* (K); Transvaal: 16.5 mi SE of Pretoria Kop, *Acocks 16,713* (K); Barberton Dtr., near Krokodipoort siding, *Liebenberg 2,406* (K); Kruger National Park, 4 mi S of Skukuza, *de Winter and Codd 546* (K).

56. CHLORIS BURMENSIS sp. nov. Fig. 84.

Culmi inferiores cum foliis ignoti. Foliorum vaginae glabrae; ligulae breves \pm truncatae, scabrae vel breviterciliatae; laminae 10–18 cm longae, 5–16 mm latae, acuminatae, inferne glabrae, superne scabrae. Spicae 7–9, adscen-

descentes, 6–18 cm longae, dilute virides. Spiculae appressae, secus rachin scabram \pm 9–10 per utrumque cm dispositae. Glumae lanceolatae tenues membranaceae, praeter carinam scabram glabrae. Gluma prima 1.7–2.2 mm longa, 0.2–0.3 mm lata. Gluma secunda 2.5–3.2 mm longa, \pm 0.5 mm lata. Lemma fertile ellipticum, apice acutum, 2.5–2.8 mm longum, 0.8–0.9 mm latum, callo angusto barbato, secus margines carinamque dense appressepilosum; arista 1–2 mm longa. Flosculi steriles 2, inferior obovoideus obtusus vel acutus, 1.5–1.7 mm longus, 0.6–0.7 mm latus, praeter carinam sparsim appressepilosam, glaber, arista 0.7 to 1.6 mm longa, superior obovoideus apice $+$ truncatus 1.0–1.5 mm longus, 0.5–0.8 mm latus, versus apicem scaber ceterum glaber, arista \pm 0.5 mm longa. Caryopsis ignota.

Lower stems and leaves unknown. Leaf sheaths glabrous, ligule a densely scabrous or short-ciliate, truncate crown; upper leaf blades 10 to 18 cm long, 5 to 16 mm wide, scabrous above, glabrous below, acuminate; spikes seven to nine, 6 to 18 cm long, ascending, pale green; spikelets appressed, ca nine or ten per cm of the scabrous rachis; glumes lanceolate to narrowly ovate, thin and membranous, glabrous except for the scabrous midnerve; first glume 1.7 to 2.2 mm long, 0.2 to 0.3 mm wide; second glume 2.5 to 3.2 mm long, ca 0.5 mm wide; fertile lemma 2.5 to 2.8 mm long, 0.8 to 0.9 mm wide, elliptic, callus narrow, bearded, margins and keel densely appressed-pilose, apex acute, awn 1 to 2 mm long; sterile florets two; lower sterile floret 1.5 to 1.7 mm long, 0.6 to 0.7 mm wide, obovoid, keel lightly appressed-pilose, otherwise glabrous, apex acute to obtuse, awn 0.7 to 1.6 mm long, upper sterile floret 1.0 to 1.5 mm long, 0.5 to 0.8 mm wide, broadly obovoid, glabrous below, scabrous at the truncate to rounded apex, awn ca 0.5 mm long; anthers ca 0.4 mm long; caryopsis unknown.

HOLOTYPE: Burma, roadside between Meiktila and Pyawbye. On calcareous stiff clay. *U. Thein Lwin 311*. 23 Oct 1947. K!

Chloris burmensis is, without question, distinct from all other species in *Chloris*. The combination of awned sterile florets in pairs and the densely appressed-pubescent, elliptic fertile florets (Fig. 84) separates this taxon from all other species. The only specimen available—the holotype—is unfortunately without any basal parts; so information on height, habit, or longevity is not available. Superficially, *C. burmensis* resembles some species of *Tetrapogon*, but details of its spikelet structure place it definitely in *Chloris*.

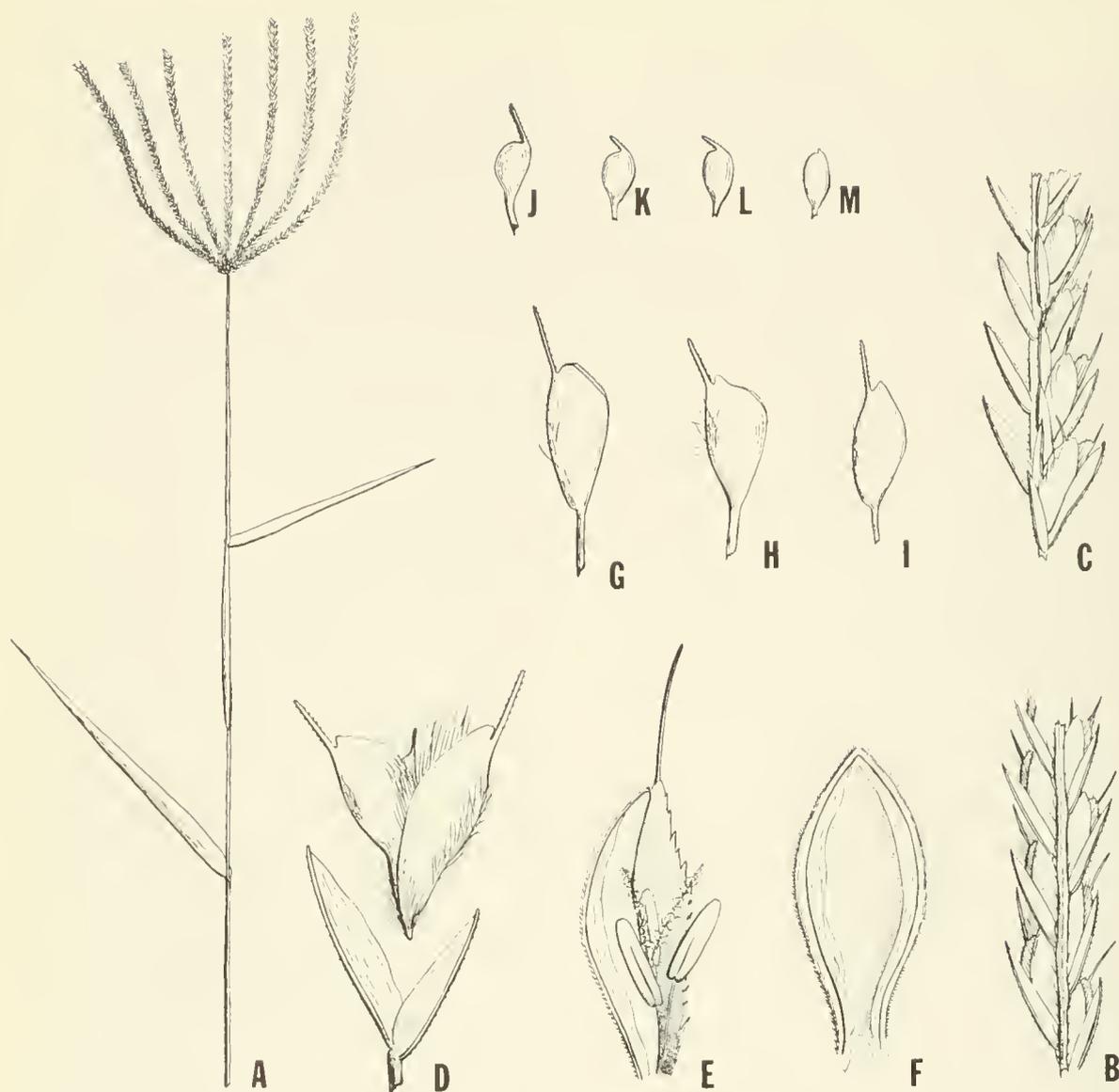


Fig. 84. *Chloris burmensis*. (A) inflorescence and upper culm, x 1/3; (B) ventral view of portion of rachis, x 3; (C) dorsal view of portion of rachis, x 3; (D) spikelet, partly dissected, x 10; (E) fertile floret with one half removed, showing palea and flower, x 15; (F) palea, ventral view, x 15; (G-I) lower sterile florets, showing variation, x 10; (J-M) upper sterile floret, showing variation, x 10.

UNIDENTIFIED, REJECTED, OR REASSIGNED NAMES

The following alphabetical list includes all names used in *Chloris* that are presently unidentifiable, not located, or assigned to other genera.

Chloris acicularis Lindley ex Mitchell, Jour. Exped. Interior Trop. Australia 33. 1848. Basis of *Enteropogon acicularis* (Lindley) Lazarides.

Chloris acicularis var. *queenslandiae* Domin, Biblioth. Bot. 85:368. 1915. = *Enteropogon acicularis* (Lindley) Lazarides, on basis of the description.

Chloris acuminata Trinius, Species Gram. Icon. 3:pl. 305. 1831. = *Eustachys distichophylla* (Lagasca) Nees.

Chloris affinis Caro and Sánchez, Kurtziana 6:224. 1971. Fig. 2. Specimens of this plant were not available in time to be considered in this publication. On the basis of the original description and accompanying illustration, it would seem to be most closely related to *Chloris pycnothrix* Trin.

Chloris agowensis Hochstetter ex Regel, Annotationes Bot. Index Seminum 26. 1862. *Nomen nudum*, synonym of *Chloris spathacea* Hochstetter.

Chloris anoplia (Nees) Fournier ex Hemslley, Biol. Cent.-Amer. Bot. 3:558. 1885. =?, possibly *Leptochloa* sp. Based on *Leptochloa anoplia* Nees.

Chloris argentina (Hackel) Lillo and Parodi, Physis 4:180. 1918. Based on *Chloris distichophylla* var. *argentina* Hackel which = *Eustachys retusa* (Lagasca) Kunth.

Chloris argentinensis Parodi, Rev. Fac. Agron. and Vet. Univ. Nac. Buenos Aires 2:283. 1919. Error for *Chloris argentina*?

Chloris aristida Salzmann ex Steudel, Syn. Pl. Glum. 1:218. 1854. *Nomen nudum*, as synonym of *Gymnopogon foliosus* Nees.

Chloris bahiensis Steudel, Syn. Pl. Glum. 1:208. 1854. = *Eustachys caribaea* (Sprengel) Herter.

Chloris bahiensis f. *glabrescens* Hackel, RePERT. Sp. Nov. 8:46. 1910. = *Eustachys caribaea* (Sprengel) Herter.

Chloris boivinii A. Camus, Bull. Soc. Bot. France 79:845. 1933. Basis of *Daknopholis boivinii* (A. Camus) Clayton.

Chloris brachyathera (Hackel) Herter, Revista Sudamer. Bot. 6:146. 1940. Based on *Chloris ciliata* Swartz var. *brachyathera* Hackel in Kurtz, which see.

Chloris brevipila Rosengurtt and Izaguirre de Artucio, Bol. Soc. Argentina Bot. 12:120. Fig. 2. 1968. = *Eustachys* sp., on basis of description and illustration.

Chloris calvescens Hackel in Chodat and Hassler, Bull. Herb. Boissier II. 4:279. 1904. = *Eustachys* sp., on basis of description.

Chloris campulodes Trinius ex Steudel, Nom. Bot. ed. 2. 1:353. 1840. *Nomen nudum*.

Chloris capensis (Houttyn) Thellung, RePERT. Sp. Nov. 10:289. 1912. Based on *Andropogon capensis* Houttyn, which is based on *Andropogon muticum* Linnaeus, a superfluous name. *Andropogon muticum* Linnaeus is unidentifiable.

Chloris capensis var. *bahiensis* (Steudel) Parodi, Revista Argentina Agron. 20:26. 1953. = *Eustachys caribaea* (Sprengel) Herter.

Chloris capensis var. *glabrescens* (Hackel) Parodi, Revista Argentina Agron. 20:20. 1953. = *Eustachys caribaea* (Sprengel) Herter.

Chloris caribaea Sprengel, Syst. Veg. 1:295. 1825. Basis of *Eustachys caribaea* (Sprengel) Herter.

Chloris castilloniana Lillo and Parodi var. *pubescens* Caro and Sánchez, Kurtziana 6:230.

1971. Specimens of this plant were not available in time to be considered in this publication. On the basis of the original description it would seem to be part of the variation pattern of *Chloris castilloniana* Lillo and Parodi.

Chloris cenchriformis (Achille Richard) Baillon ex Schweinfurth and Ascherson, Beitr. Flora Aethiopiens 310. 1867. Based on *Lepidopironia cenchriformis* Achille Richard. = *Tetrapogon cenchriformis* (Achille Richard) Pilger.

Chloris cheesmanii Hackel ex Cheesman, Trans. Linnean Soc. Bot. 6:305. 1903. = *Enteropogon unispiceus* (F. Mueller) Clayton on basis of description.

Chloris ciliata Swartz var. *brachyathera* Hackel ex Kurtz, Bol. Acad. Ciencias Córdoba (Rep. Argentina) 16:257. 1900. Without description. As described by Parodi (Rev. Fac. Agron. and Vet. Univ. Nac. Buenos Aires 2:271. 1919) = *Chloris ciliata* Swartz.

Chloris compressa De Candolle, Cat. Horti Monspeliensis 94. 1813. =? Specimens Pl., labeled as this species, of uncertain origin, are *C. radiata* Swartz. A photo, in US!, of a specimen in Montpellier labeled as *C. compressa*, perhaps in de Candolle's script, is also *C. radiata*. The protologue might apply equally to *C. radiata* or *C. virgata* Swartz.

Chloris confertifolia Trinius in Sprengel, Neue Entdeckungen 2:74. 1821. = *Eustachys distichophylla* (Lagasca) Nees.

Chloris ctenioides Steudel, Syn. Pl. Glum. 1:423. 1854. = *Dactyloctenium* sp., on basis of fragment of type (US!) from CN.

Chloris curtipendula Michaux, Flora Bor. Amer. 1:59. 1803. Basis of *Bouteloua curtipendula* (Michaux) Torrey in Emory.

Chloris cynodoidea Lagasca, Elenchus Plantarum 5. 1816. *Nomen nudum*.

Chloris cynodon (Linnaeus) Trinius, Gram. Unifloris 229. 1824. Based on *Panicum dactylon* Linnaeus = *Cynodon dactylon* (Linnaeus) Persoon.

Chloris delicatula Clarke in Hooker, f. Flora British India 7:290. 1896. Basis of *Gymnopogon delicatula* (Clarke) Bor.

Chloris dichanthioides Everist, Queensland Agric. Jour. 49:432. pl. 155, 1938. Basis of *Austrochloris dichanthioides* (Everist) Lazarides.

Chloris digitaria Humboldt, Bonpland. Kunth, Nov. Gen. and Sp. Pl. 1:168. 1816. = *Leptochloa* sp. on basis of description.

Chloris digitata (Roxburgh) Steudel, Syn. Pl. Glum. 1:207. 1854. Based on *Melica digitata* Roxburgh which = *Enteropogon dolichostachya* (Lagasca) Lazarides.

Chloris distachya Bojer, Hortus Mauritanus 371. 1837. = *Chloris filiformis* (Vahl) Poiret? An unnamed Bojer specimen from Mauritius (in G!) is *C. filiformis*. The protologue is incomplete.

Chloris distichophylla Lagasca, Gen. Sp. Nov. 4. 1816. Basis of *Eustachys distichophylla* (Lagasca) Nees.

Chloris distichophylla var. *acuminata* (Trinius) Hackel, Bull. Herb. Boissier II. 4:279. 1903. = *Eustachys distichophylla* (Lagasca) Nees.

Chloris distichophylla var. *argentina* Hackel in Stuckert, Anales Mus. Nac. Hist. Nat. Buenos Aires 11:113. 1904. = *Eustachys distichophylla* (Lagasca) Nees.

Chloris distichophylla var. *genuina* Hackel in Stuckert, Anales Mus. Nac. Hist. Nat. Buenos Aires 11:113. 1904. = *Eustachys distichophylla* (Lagasca) Nees.

Chloris dolichostachya Lagasca, Gen. Sp. Nov. 5. 816. Basis of *Enteropogon dolichostachya* (Lagasca) Lazarides.

Chloris dubia Humboldt, Bonpland, Kunth, Nov. Gen. and Sp. Pl. 1:169. 1816; pl. 694. 1825. Basis of *Leptochloa dubia* (Humboldt, Bonpland, Kunth) Nees.

Chloris durandiana Schultes, Mantissa 2:341. 1824. Based on *Chloris gracilis* Durand, which may equal *Chloris radiata* (Linnaeus) Swartz. See also *C. gracilis* Durand in this list.

Chloris dusenii Ekman, Arkiv för Botanik 10:26. 1911. = *Eustachys uliginosus* (Hackel) Herter; isotype in US!

Chloris elegans (Kunth) Roberty, Petite Flore Ouest.-Afrique 387. 1954. Basionym not cited.

Chloris elegans (Kunth) Roberty, Bull. Inst. Française Afrique Noire Ser. A. 17:51. 1955. Based on *Ctenium elegans* Kunth.

Chloris elcusinoides Grisebach, Flora British West Indian Islands 539. 1864. Unidentified. Type not seen, but description suggests *Chloris sagraeana* A. Rich.

Chloris emarginata Beauvois, Ess. Agrost. 79, 158. 1812. *Nomen nudum*.

Chloris equitans Trinius, Sp. Gram. Icon. 3. pl. 309. 1831. = *Eustachys paspaloides* (Vahl) Lanza and Mattei.

Chloris falcata Swartz, Ges. Naturf. Freunde Berlin Neue Schrift 3:160. pl. 1. Fig. 1. 1801. = *Harpachloa capensis* Kunth.

Chloris fasciculata Schrader in Schultes, Mantissa 2:339. 1824. = *Eustachys distichophylla* (Lagasca) Nees.

Chloris fasciculata (Linnaeus) Thellung, Repert. Sp. Nov. 10:289. 1912. *Non Chloris*

fasciculata Schrader in Schultes. Based on *Andropogon fasciculatum* Linnaeus = *Microstegium* sp. on basis of holotype (LINN!).

Chloris floccifolia (Forsk.) Poiret in Lamarek, Encycl. Method. Bot. Suppl. 2:238. 1811. Based on *Cynosurus floccifolius* Forsk. = *Eleusine floccifolia* (Forsk.) Sprengel.

Chloris floridana (Chapman) Wood, Amer. Bot. and Florist Pt. 2. 407. 1871. = *Eustachys floridana* Chapman.

Chloris foliosa Willdenow, Sp. Pl. 4:924. 1806. Basis of *Gymnopogon foliosus* (Willdenow) Nees. Fragment of type, from B, in US!

Chloris foliosa Lagasca, Gen. Sp. Pl. Nov. 5. 1816. *Non Chloris foliosa* Willdenow. Unidentified. A fragment, in US!, of a Lagasca specimen dated 1820, from M, is *Gymnopogon* sp.

Chloris geminata Hochstetter, Flora 38:205. 1855. = *Tetrapogon* sp. on basis of description.

Chloris glauca (Chapman) Wood, Amer. Bot. and Florist Pt. 2. 407. 1871. = *Eustachys glauca* Chapman.

Chloris glabrescens (Hackel) Rosengurt and Izaguirre, Bol. Soc. Argentina Bot. 12:123. 1968. Based on *Chloris bahiensis* var. *glabrescens* Hackel = *Eustachys caribaea* (Sprengel) Herter.

Chloris gracilis Durand, Chloridis Speciebus 10. 1808. =? Type not seen, description may be of *Chloris radiata* (Linnaeus) Swartz. *Non Chloris gracilis* Humboldt, Bonpland, Kunth, 1816.

Chloris gracilis Humboldt, Bonpland, Kunth, Nov. Gen. Sp. Pl. 1:168. 1816. *Non Chloris gracilis* Durand. = *Leptochloa* sp. on basis of description.

Chloris gryllus (Linnaeus) Honckeny, Syn. Pl. Germaniae 1:437. 1792. = *Chrysopogon gryllus* (Linnaeus) Trinius on basis of description. Based on *Andropogon gryllus* Linnaeus.

Chloris guineensis Schumacher, Beskr. Guineiske Planter 75. 1827. = *Dactyloctenium* sp. on basis of photograph of type (in US!) in the Isert and Thonning Herbarium.

Chloris hispida Durand, Chloridis Speciebus 17. 1808. = *Bouteloua* sp. on basis of description.

Chloris imberbis Desfontaines, Cat. Pl. Parisiensis ed. 3. 15. 1829. *Nomen nudum*.

Chloris incompleta Roth ex Roemer and Schultes, Syst. Veg. 2:607. 1817. = *Enteropogon dolichostachya* (Lagasca) Lazarides on basis of photograph of type in K!

Chloris lepidopironia Desveaux ex Regel, Annotationes Bot. Index Seminum 26. 1862.

Nomen nudem, herbarium name published as a synonym.

Chloris longibarbis Michaux ex Beauvois, Ess. Agrost. 79, 158. 1812. *Nomen nudem*.

Chloris macrantha Desvieux, Opuscles 73. 1831. = *Tetrapogon* sp. on basis of description.

Chloris macrantha Jaubert and Spach, Illustr. Pl. Orient. 4:42. pl. 328. 1851. *Non Chloris macrantha* Desvieux. = *Tetrapogon* sp. on basis of description.

Chloris macrostachya Hochstetter ex Achille Richard, Tent. Florae Abyssinicae 2:408. 1850. Basis of *Enteropogon macrostachyus* (Hochstetter ex Achille Richard) Munro ex Benthiam.

Chloris maritimus (Kunth) Trinius, Gram. Unifloris 235. 1824. Based on *Cynodon maritimus* Kunth. = *Cynodon* sp.

Chloris mearnsii Merrill, Philippine Jour. Sci. 3:220. 1908. = *Enteropogon* sp. on basis of description.

Chloris monostachya Michaux, Flora Bor. Amer. 1:59. 1803. = *Ctenium* sp. on basis of description.

Chloris monostachya (Vahl) Poirlet in Lamarck, Encycl. Method. Bot. Suppl. 2:238. 1811. *Non Chloris monostachya* Michaux. Basis of *Enteropogon monostachyos* (Vahl) K. Schumann ex Engl. (Based on *Cynosurus monostachyus* Vahl.)

Chloris moorei F. Mueller, Linnaea 25:444. 1852. Unidentified. A specimen at K!, collected and labeled as *C. moorei* by von Mueller, though not the type, is *Enteropogon acicularis* (Lindley) Lazarides.

Chloris mucronata Michaux, Flora Bor. Amer. 1:59. 1803. = *Dactyloctenium* sp. on basis of description.

Chloris multiradiata Hochstetter var. *ragazzii* Pirota, Anales Ist. Reale Bot. Roma 6:157. 1896. Unidentified, possibly a variant of *Chloris virgata* Swartz.

Chloris neglecta Nash, Bull. Torrey Bot. Club 22:423. 1895. Basis of *Eustachys neglecta* (Nash) Nash.

Chloris obtusifolia Trinius, Gram. Unifloris 233. 1824. Unidentified, description suggests *Eustachys tener* (Presl) A. Camus.

Chloris obtusifolia Balansa, Jour. de Bot. (Morot) 4:166. 1890. *Non Chloris obtusifolia* Trinius 1824. = *Eustachys tener* (Presl) A. Camus.

Chloris pallida Willdenow, Sp. Pl. 4:293. 1806. Based on *Andropogon provinciale* Retz. = ?. The letter name unidentified, though description is not of a *Chloris*.

Chloris pallida (Edgeworth) Hooker, f., Flora British India 7:289. 1896. *Non Chloris*

pallida Willdenow. = *Schoenefeldia pallida* Edgeworth, on basis of description.

Chloris panicea Willdenow, Sp. Pl. 4:923. 1806. = *Enteropogon dolichostachya* (Lagasca) Lazarides. Type not seen, but description strongly suggests this species.

Chloris parva G. Mimeur, Bull. Mus. Hist. Nat. (Paris) 22:128. 1950. = *Chloris prieurii* Kunth? Mimeur cites a specimen sent in 1880, Talmy 86, from Senegal and deposited in P. This cannot be located, but another specimen sent by Talmy, also from Senegal, but in 1882, is *Chloris prieurii*. The original description likewise strongly suggests this species.

Chloris parvispicula Caro and Sánchez, Kurtziana 6:227. 1971. Fig. 3. Specimens of this plant were not available in time to be considered in this publication. On the basis of the original description and accompanying illustration it would seem to be most closely related to *Chloris dandlyana*.

Chloris paspaloides Hochstetter, Flora 38:206. 1885. = *Eustachys paspaloides* (Vahl) Lanza and Mattei.

Chloris pauli-ducis Schweinfurth, Beitr. Flora Aethiopiensis 298. 1867. *Nomen nudum*.

Chloris paytensis Steudel, Syn. Pl. Glum. 1:207. 1854. = *Cynodon dactylon* on basis of fragment of type (in US!) from Urville Herbarium.

Chloris pedicellata Steudel, Flora 33:232. 1850. *Nomen nudum*, as synonym of *Schellingia tenera* Steudel.

Chloris pendula Salzmann ex Steudel, Syn. Pl. Glum. 1:208. 1854. *Nomen nudum*, as synonym of *Chloris bahiensis* Steudel.

Chloris penicellata (Vahl) Persoon, Syn. Pl. 1:87. 1805. = *Tetrapogon* sp.? on basis of description of *Cynosurus penicillatus* Vahl, upon which it is based.

Chloris penicillata Jan. ex Trinius, Gram. Uniflores 231. 1824. *Non Chloris penicillata* (Vahl) Persoon. *Nomen nudum*, as synonym of *Chloris compressa* De Candolle.

Chloris perrieri A. Camus, Bull. Soc. Bot. France 96:93. 1949. = *Daknopholis boivinii* (A. Camus) Clayton on basis of holotype in P!

Chloris peregrina Durand, Chlorides Speciebus 11. 1808. Unidentified. Type not seen, description suggests *Chloris inflata* Link.

Chloris petraea Swartz, Prodr. Veg. Ind. Occ. 25. 1788. Basis of *Eustachys petraea* (Swartz) Desfontaines.

Chloris piperita Michaux ex Steudel, Nom. Bot. ed. 2. 1:353. 1840. *Nomen nudum*, as synonym of *Campulosus monostachyus* Beauvois.

Chloris poaeformis Humboldt, Bonpland,

Kunth, Nov. Gen. and Sp. Pl. 1:169. 1816. = *Leptochloa* sp. on basis of description.

Chloris polydactyla Swartz var. *breviaristata* Hackel in Kurtz, Bol. Acad. Ciencias, Córdoba (Rep. Argentina) 16:257. 1899. Unidentified. Type specimen not seen, but description suggests *Chloris ciliata* Swartz.

Chloris polydactyla Swartz f. *major* Regel, Annotationes Bot. Index Seminum 25. 1862. Unidentified. Type not seen. Description inconclusive.

Chloris polydactyla Swartz f. *media* Regel, Annotationes Bot. Index Seminum. 25. 1862. *Nomen nudum*.

Chloris polydactyla Swartz f. *minor* Regel, Annotationes Bot. Index Seminum 25. 1862. Based on *Chloris elegans* Humboldt, Bonpland, Kunth, which = *Chloris virgata* Swartz. Probably misapplied to *Chloris polydactyla* Swartz.

Chloris polystachya Lagasca, Elenchus Plantarum 5. 1816. *Nomen nudum*.

Chloris procumbens Durand, *Chlorides Speciebus* 16. 1808. = *Bouteloua* sp. on basis of description.

Chloris prostrata (Willdenow) Poirlet in Lamarck, Encycl. Method. Bot. Suppl. 2:239. 1811. Based on *Dactyloctenium prostratum* Willdenow. = *Dactyloctenium* sp.

Chloris pubescens Peyritsch in Wawra and Peyritsch, Akad. Wiss. Wien Sitzungsber. Math.-Naturwiss. Klasse 38:385. 1860. *Non C. pubescens* Lagasca, 1805. = *Eustachys* sp. on basis of description.

Chloris pulchra Schumacher, Beskr. Guineiske Planter 76. 1827. = *Ctenium* sp. Photograph of type, in US!, from Isert and Thonning Herbarium.

Chloris queenslandiae Domin, Biblioth. Bot. 85:368. 1915. *Nomen nudum*, as synonym of *Chloris acicularis* var. *queenslandiae* Domin.

Chloris radiata Heyne ex Roth, Nov. Pl. Indiae Orientalis 61. 1821. *Non Chloris radiata* Swartz. *Nomen nudum*, as synonym of *Chloris incompleta* Roth, which = *Enteropogon dolichostachya* (Lagasca) Lazarides.

Chloris radiata Swartz var. *beyrichiana* (Hackel) Kurtz in Rio and Achával, Geog. Prov. Córdoba 1:331. 1904. Attributed incorrectly to Hackel by Kurtz, presumably based on *Chloris beyrichiana* Kunth, but basionym not cited.

Chloris ramosissima A. Camus, Not. Syst. Mus. Hist. Nat. Paris 12:155. 1946. = *Daknopholis boivinii* (Camus) Clayton on basis of holotype in P!

Chloris repens Steudel, Nom. Bot. ed. 2. 1:353. 1840. *Nomen nudum*, as synonym of *Eleusine indica* (Linnaeus) Gaertner.

Chloris retusa Lagasca, Elenchus Plantarum 5. 1816. = *Eustachys retusa* (Lagasca) Kunth on basis of fragment and photograph of type in US!

Chloris rhachitricha Steudel, Syn. Pl. Glum. 1:205. 1854. = *Eulalia* ? on basis of type specimen in P!

Chloris ridleyi Hackel, Oesterr. Bot. Zeitschr. 52:237. 1902. = *Eustachys tener* (Presl) A. Camus. Isotype at K!

Chloris roxburghii Edgeworth, Jour. Asiatic Soc. Bengal 21:183. 1851. Based on *Melica digitata* Roxburgh which = *Enteropogon dolichostachya* (Lagasca) Lazarides.

Chloris rufescens Lagasca, Var. Ciencias Lit. and Artes (Madrid) 4:143. 1805. Type not located. Original description too meager for recognition of plant.

Chloris savatieri Baillon, Bull. Soc. Linn. (Paris) 2:1070. 1893. *Nomen nudum*, given as an herbarium name in a discussion of *Tetrapogon* sp.

Chloris scariosa Beauvois, Ess. Agrost. 79, 158. 1812. *Non Chloris scariosa* F. Mueller. *Nomen nudum*.

Chloris secundus (Pursh) A. Eaton, Manual Bot. North Amer. ed. 5. 173. 1829. Based on *Cynosurus secundus* Pursh. = *Bouteloua* sp. on basis of description.

Chloris septentrionalis C. Mueller, Bot. Zeitung (Berlin) 19:340. 1861. = *Eustachys petraea* (Swartz) Desveaux on basis of description.

Chloris simplex Schumacher, Beskr. Guineiske Planter 74. 1827. = *Enteropogon* sp. on basis of photograph (in K!) of type specimen in Isert and Thonning Herbarium.

Chloris spathacea Hochstetter ex Steudel, Syn. Pl. Glum. 1:204. 1854. = *Tetrapogon cenchriformis* on basis of isotype at K!

Chloris spathacea Baillon, Bull. Soc. Linn. (Paris) 2:1070. 1893. *Non Chloris spathacea* Hochstetter, 1854. = *Tetrapogon* sp. on basis of type in P!

Chloris subaequigluma Rendle, Cat. African Plants collected by Dr. F. Welwitsch 2:222. 1899. Basis of *Bracteola subaequigluma* (Rendle) C. E. Hubbard.

Chloris swartziana Doell in Martius, *Flora Brasiliensis* 23:68. 1878. = *Eustachys petraea* (Swartz) Desveaux, on basis of description.

Chloris swartzii C. Mueller, Bot. Zeitung (Berlin) 19:341. 1861. = *Eustachys petraea* (Swartz) Desveaux. Based on *Chloris petraea* Swartz.

Chloris tenella Koen ex Roxburgh, Hortus Bengalensis 82. 1814. *Nomen nudum*. *Chloris*

tenella Roxburgh, Flora Indica ed. Carey, 1:330.

1820. = *Tetrapogon* sp. on basis of description.

Chloris tenera (Presl) Scribner, Ann. Rept. Missouri Bot. Gard. 10:41. pl. 40. 1899. = *Eustachys tener* (Presl) A. Camus.

Chloris tenuior Poiret ex Schultes, Mantissa 2:321. 1824. *Nomen nudum*, as synonym of *Leptchloa cynosuroides* Roemer and Schultes.

Chloris tetrameris Trinius, Gram. Uniflores 235. 1824. = *Enteropogon dolichostachya* (Lagasca) Lazarides on basis of description.

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Chloris triangulata Hochstetter ex Achille Richard, Tent. Florae Abyssinicae 2:409. 1850. = *Tetrapogon* sp. on basis of description.

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(Hackel) Herter.

Chloris unispicea F. Mueller, Fragm. Phytogr. Australiae 7:118. 1870. Basis of *Enteropogon unispicea* (Mueller) Clayton.

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Chloris villosa var. *sinaica* Decaisne, Ann. Sci. Nat. Bot. (Paris) II. 2:12. 1834. = *Tetrapogon* sp. on basis of description.

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**A COMPARISON OF METEOROLOGIC
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A COMPARISON OF METEOROLOGIC MEASUREMENTS FROM IRRIGATED AND NON-IRRIGATED PLOTS, PROVO, UTAH, 1970-1972

by

Ferron L. Andersen¹, Phil D. Wright², and J. Carl Fox³

ABSTRACT

A comparative study of micrometeorologic conditions on irrigated and non-irrigated pasture plots was conducted at Provo, Utah, from 1970 to 1972. Daily measurements were taken of the following: precipitation either as rain or snow, new snowfall and total snow depth during the winter; relative humidity in a standard weather shelter; number of hours at maximum relative humidity; cloud cover each morning; potential evaporation; total wind 1 m above ground level; temperature extremes in a standard weather shelter; and temperatures both on irrigated and non-irrigated plots with sensing devices located 5 cm beneath soil surface under grass cover, at soil surface under grass cover, and at soil surface on bare ground. During the pasture months of May through October, weekly soil moisture measurements from irrigated and non-irrigated plots were gravimetrically determined. All data were entered on columnized work sheets, key punched, and subsequently assimilated and tabulated by a FORTRAN IV program with the IBM 360/65 computer. Graphical representations of all daily measurements for the three years, as well as others depicting the effect of irrigation and snow cover for selected weeks, were completed.

The total precipitation for 1970, 1971, and 1972 was 491.0, 726.4, and 390.1 mm, respectively, and the average monthly mean temperatures in a standard weather shelter for the three years were 9.2, 8.8, and 9.4°C. Other representative yearly values for 1970, 1971, and 1972, respectively, were total snowfall: 1165.9, 1877.1, and 909.3 mm; average maximum and minimum rela-

tive humidity: 97 and 43, 97 and 46, and 97 and 46 percent; average hours at maximum relative humidity each day: 7, 8, and 8 hr; average cloud cover each morning: 3-, 3-, and 3-tenths of covered sky; total potential evaporation and daily average for May through October: 983.8 and 5.3, 1030.7 and 5.6, and 1274.2 and 6.9 mm; average monthly soil moisture content for both irrigated and non-irrigated plots for May through October: 16.1 and 8.4, 16.3 and 5.8, and 8.1 and 3.8 percent; wind totals and daily averages: 19,315 and 52, 22,691 and 61, and 22,255 and 60 km; average annual temperatures 5 cm beneath soil surface on irrigated and non-irrigated plots for 1971 and 1972: 8.4 and 9.0 and 8.2 and 10.4°C; average annual temperatures at soil surface under grass cover on irrigated and non-irrigated plots for 1971 and 1972: 9.7 and 10.6 and 10.9 and 12.8°C; and average annual temperatures at soil surface on bare ground on irrigated and non-irrigated plots for 1971 and 1972: 12.9 and 16.5 and 14.9 and 15.0°C. Temperature extremes on irrigated plots during the pasture season were moderated considerably from those recorded on the non-irrigated plots, and irrigation, when done routinely, provided adequate soil moisture throughout the entire pasture season. These findings are especially obvious when data other than yearly and monthly means are examined. Irrigation is undoubtedly the major factor in providing optimum moisture and temperature conditions for the development and survival of all types of pastureland biological organisms in creating optimum microenvironments in otherwise desolate, arid regions.

INTRODUCTION

Micrometeorology, the study of atmospheric conditions in microclimates, entails numerous difficulties, not the least of which is the lack

of a uniform definition of the zone in question. Reference can be made to both horizontal and vertical measurements, which may vary from

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a few millimeters to many meters in both directions. Sutton (1964) stated that micrometeorology deals with atmospheric phenomena "in the first few hundred feet above the earth's surface," whereas Holmes and Dingle (1965) stated that the microclimatic zone consists generally of the layer of air which is markedly altered by the surface of the earth or other surfaces thereon, and that the microclimate of a tree, therefore, is that area extending several meters out from the branches which acquires unique properties because of the tree. Whitman and Wolters (1965) defined microclimate as that zone beneath the level of a standard weather shelter (about 1.5 m). Andersen, Levine, and Boatman (1970) stated that the microclimate of the free-living stages of ruminant nematodes is the layer of space between the ground surface and the top of the pasture vegetation. Since the project described herein dealt with measurements on irrigated and non-irrigated pasture plots, the definition used is that given by the latter authors.

The practice of irrigation is the single most important process which permits maximum utilization of agricultural lands in arid regions of the earth. In the United States, of a total of 2,322,016,000 acres, 340,998,000 are cultivated, of which 33,022,000, or approximately 10 percent are irrigated (Israelsen and Hansen, 1967). In Utah, however, of 52,721,550 total acres, 2,155,186 are cultivated and 1,348,627, or about 63 percent, of that amount are irrigated. In Utah County, 76 percent of all cropland is irrigated (Utah Agricultural Statistics, 1972). Thus, we see that irrigation is far more important to agriculture in Utah and other western arid states than in areas where sufficient precipitation is accumulated through rain or snow only.

While irrigation is the most important factor toward creating cultivatable lands in arid regions, indiscriminate usage of available water often leads to soil erosion, alkalization, or high water tables, with resultant reduction in plant growth and productivity. In addition to these undesirable effects, irrigation may create suitable microhabitats for the development and survival of detrimental biological organisms, many of which could not exist or at least could not reach such high population levels on otherwise arid lands. The creation of desert bridges from one irrigation field to another may allow harmful insects to traverse broad expanses of arid regions (Rainy and Hess, 1967), and faulty irrigation may fill borrow pits or other depressions for long periods of time, thereby creating favorable breeding grounds for numerous arthropod or molluscan vectors of disease. Mosquitoes,

for example, are by far the most important of all arthropods of public health significance, since several species are vectors of malaria and encephalitis. In spite of extensive eradication campaigns, malaria is still the most important infectious disease in the world; however, arboviral encephalitis is far more significant in the United States proper. In 1970, only sixteen persons acquired malarial infections in the United States (Center for Disease Control, Malaria Surveillance, 1971), whereas during the same year, 110 cases of arboviral encephalitis were reported (Center for Disease Control, Neurotropic Viral Diseases Surveillance, 1972). *Anopheles freeborni*, the primary vector for malaria in the western part of the United States, and *Culex tarsalis*, (the "irrigation mosquito"), the primary vector for western and St. Louis encephalitis, both breed in water impoundments and seepage areas, such as those associated with faulty or inefficient irrigation (Rainy and Hess, 1967). The breeding habitats of both species generally decrease each summer with the recession of surface waters, except where irrigation waters maintain their breeding sites. Surtees (1970) showed a 70-fold increase in malaria vectors in an irrigated area in Kenya, and Reeves and Hammon (1962) demonstrated that human infections with encephalitis were definitely associated with work on irrigated agricultural lands in California.

Snails, which serve as intermediate hosts for the blood flukes that cause schistosomiasis (bilharziasis) in humans in many tropical and subtropical regions, have reproduced extensively in newly created habitats associated with massive irrigation projects. The first report by the study group on schistosomiasis in Africa (World Health Organization, 1950) stated that: "The introduction or development of irrigation schemes, as well as the change from basin to perennial irrigation, has always resulted in a considerable increase in the incidence and intensity of bilharziasis wherever that infection existed or was introduced by outside laborers. The severity of the infection may be such as to cause the abandonment of an irrigation scheme created at considerable expense."

Irrigation also creates favorable microenvironments in pastures for the free-living stages of many parasitic nematodes which otherwise could not exist in overall arid zones. As early as 1944, Furman pointed out that irrigational practices in the dry interior Sacramento Valley regions of California resulted in increased populations of nematode larvae parasitic to sheep. Honess and Bergstrom (1966) showed comparable results for populations of nematode larvae parasitic to cattle in Wyoming. Surveys in cen-

tral Utah have shown that 68 to 71 percent of all cattle and 90 to 96 percent of all sheep raised on irrigated pastures harbor parasitic helminths of at least one species (Fox, Andersen, and Hoopes, 1970; and Wright and Andersen, 1972). During the past decade numerous workers have shown that there is a positive correlation between optimum micrometeorologic conditions and the development and survival of many parasites (See Crofton, 1963; Levine, 1963; Kates, 1965; Williams and Mayhew, 1967; An-

dersen, Levine, and Boatman, 1970; Williams and Bilkovich, 1971; Gibson, 1973; and Levine and Andersen, 1973).

Because of the importance of irrigation to agriculture and animal husbandry in central Utah and the demonstrated high prevalence of parasites in domestic animals, a study was undertaken to measure microenvironmental conditions on irrigated and non-irrigated pasture plots in that area.

MATERIALS AND METHODS

A 9m x 9m experimental weather station designed to yield measurements from irrigated and non-irrigated plots was established at the Brigham Young University Animal Science Farm located at Provo, Utah (Fig. 1). Coordinates for the station are 111° 39' 1" W. longitude and 40° 16' 1" N. latitude. Elevation at the site is 4,653 feet (1163 m) above sea level. Meteorologic measurements from the area were either recorded or manually observed each day for 1970, 1971, and 1972. The plot was fenced with 5-foot (150 cm) chain link fence from the center of a 2-acre (.8-hectare) sheep pasture at the farm. The existing vegetation at the site consisted predominantly of meadow fescue (*Festuca elatior*), alfalfa (*Medicago sativa*), clover (*Trifolium repens*), and dandelion (*Leontodon taraxacum*). The vegetative cover was mowed weekly to an approximate height of 3 to 4 in (7.5 to 10 cm) and the clippings discarded. The soil was characterized as the Keigley series (1 percent slope, dark brown, deep, well-drained,

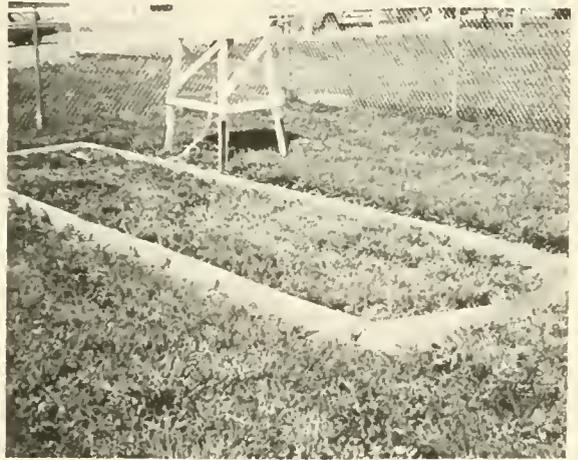


Fig. 2. Non-irrigated plot separated by a 5' x 20' metal frame.

silty clay loam) (Soil Survey of Utah County, Utah, 1972). The average volumetric moisture content at field capacity ($\frac{1}{3}$ rd bar) was 2.2 in (5.5 cm) of water per foot (30 cm) of soil, and at the permanent wilting point (15 bars) was 1.6 in (4.0 cm) per foot (30 cm) of soil (Soil Conservation Service, Utah, 1972).

A non-irrigated section near the center of the plot was established by placing a 5 ft by 20 ft (150 by 600 cm) rectangular galvanized metal frame into the ground to an approximate depth of 3 ft 8 in (110 cm), with about 4 in (10 cm) protruding above the ground (Fig. 2) in order to keep the water from that part of the plot during periods of irrigation. The pasture and the irrigated portion of the weather station were usually irrigated every 8 to 10 days during the warmer part of each pasture season; however, irrigation could only be performed by personnel not associated with the research project and the intervals between irrigations were not always consistent. During 1972, the timing was further disrupted until mid-June by road and ditch con-



Fig. 1. Weather station for measurement of meteorologic conditions on irrigated and non-irrigated pasture plots at BYU Animal Science Farm, Provo, Utah.



Fig. 3. Standard non-recording rain gauge.

struction in areas directly adjacent to our experimental plot. In spite of these limitations, irrigation times are indicated on the precipitation and soil moisture graphs for each of the three years of the study (Fig. 12, 13, and 14) and hopefully give some indication of the effects produced.

Precipitation as rain was measured in a standard non-recording rain gauge (Fig. 3) in hundredths of an inch. During the winter, the total snow cover was determined with an ordinary ruler by measuring in inches the total depth of snow to the soil surface at several representative sites, and the daily snowfall was likewise determined by measuring the depth to the previous day's crust. Precipitation in the daily snowfall was calculated as one-tenth that of the measured new snow depth, since that is the average reported snow depth to water equivalent ratio (McIntosh and Thom, 1969).

During the six months from 1 May through 31 October, soil moisture content from both irrigated and non-irrigated plots was determined gravimetrically by taking 6-in (15-cm) core samples each Monday with a 1-in (2.5-cm) diameter soil auger. The samples were immediately taken to the laboratory, where they were weighed, dried at 105°C for four days, and then reweighed.

Relative humidity (RH) was measured in a standard U.S. Weather Bureau shelter (Steven-



Fig. 4. Hygrothermograph for daily measurement of temperature (top graph) and relative humidity (bottom graph) recorded in a standard weather shelter.

son screen) located approximately 5 feet (1.5 m) above ground level with a standard hygrothermograph which gave a dual record of both temperature and relative humidity on the same curvilinear chart (Fig. 4). The humidity element consisted of multiple strands of specially treated hygroscopic hairs which expanded over the 0-100 percent scale range with 3 percent accuracy between 20 to 80 percent RH and 5 percent beyond those points. The instrument was calibrated periodically by adjusting the recording arm to 100 percent RH during rainy periods, and it was checked occasionally with a sling psychrometer or Assman spring-driven psychrometer. The number of hours each day when the relative humidity was at maximum (98-100 percent) was also noted and recorded.

Potential evaporation over the irrigated plot was measured by an evaporimeter consisting of a metal pan with a 250-sq cm evaporating surface resting over a spring-loaded device and recording arm (Fig. 5). Since the clock revolved



Fig. 5. Evaporimeter for daily measurement of potential evaporation.

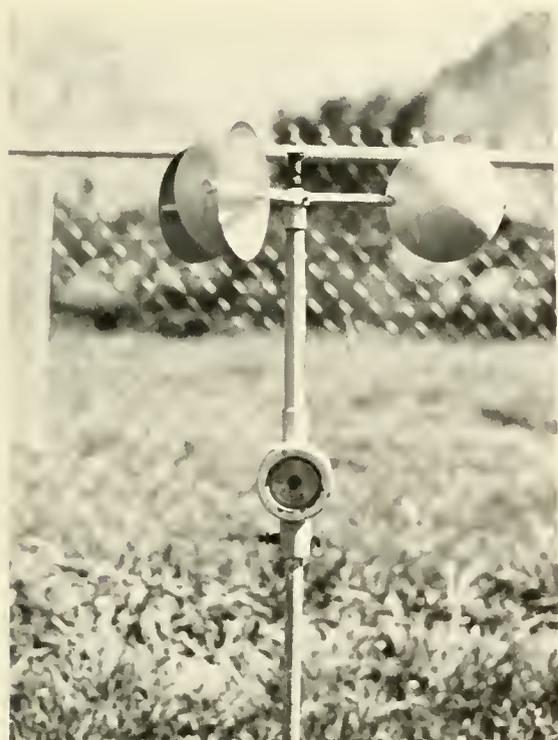


Fig. 6. Non-recording anemometer for measurement of daily wind total.

daily, the recorded spiral pattern was difficult to read once the chart had been removed; hence, the evaporation pan was filled daily and the potential evaporation read from the scale each morning.

Total wind movement at the site was read daily from a non-recording totalizing anemometer positioned 1 m above the vegetative surface (Fig. 6). Cloud cover for each day was estimated visually in tenths of sky covered so as to cast a shadow from the sun at the time the instruments were read.

Daily temperature measurements were taken with standard maximum and minimum thermometers in the weather shelter (Fig. 7) and also recorded by the hygrothermograph at that

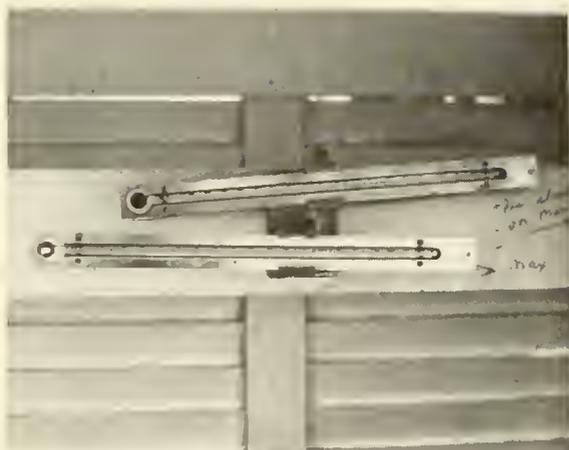


Fig. 7. Maximum and minimum thermometers located in a standard weather shelter.

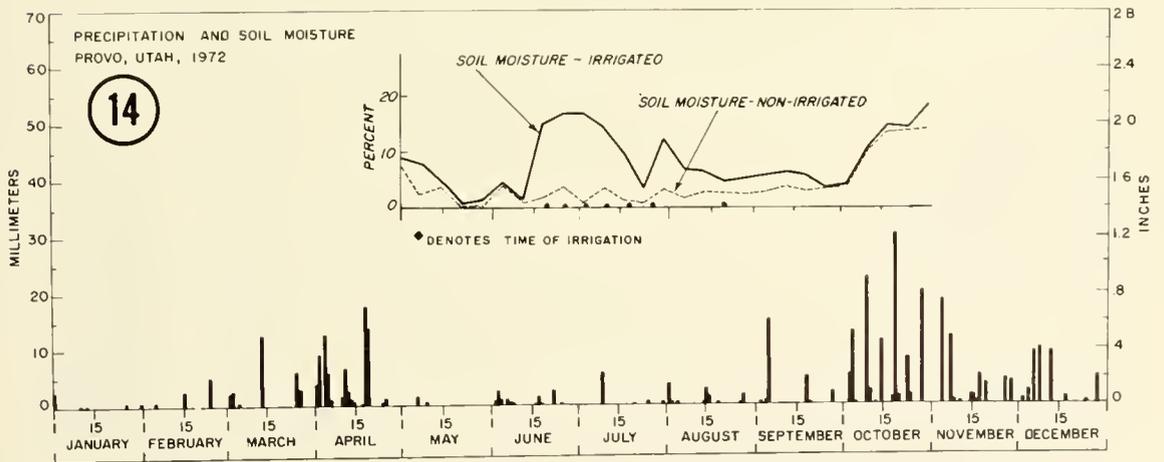
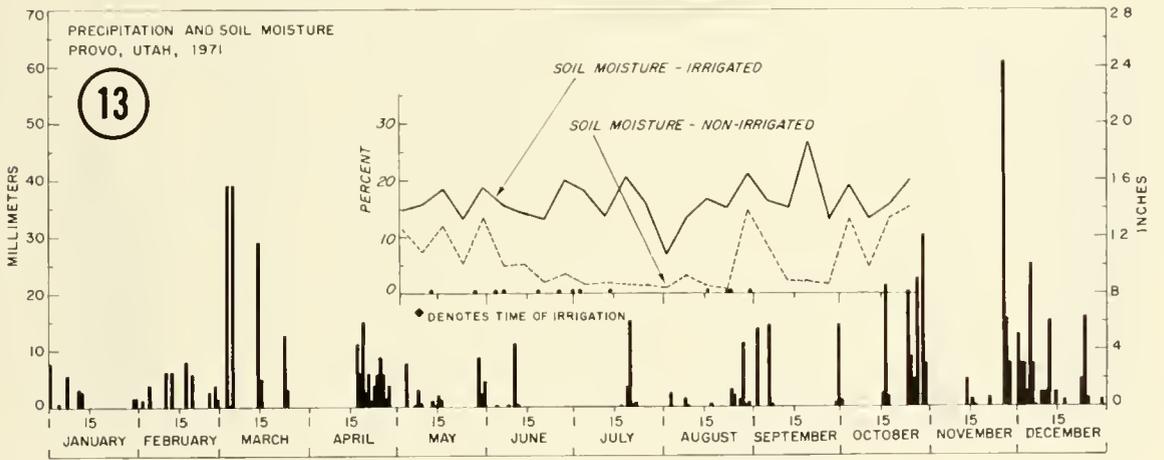
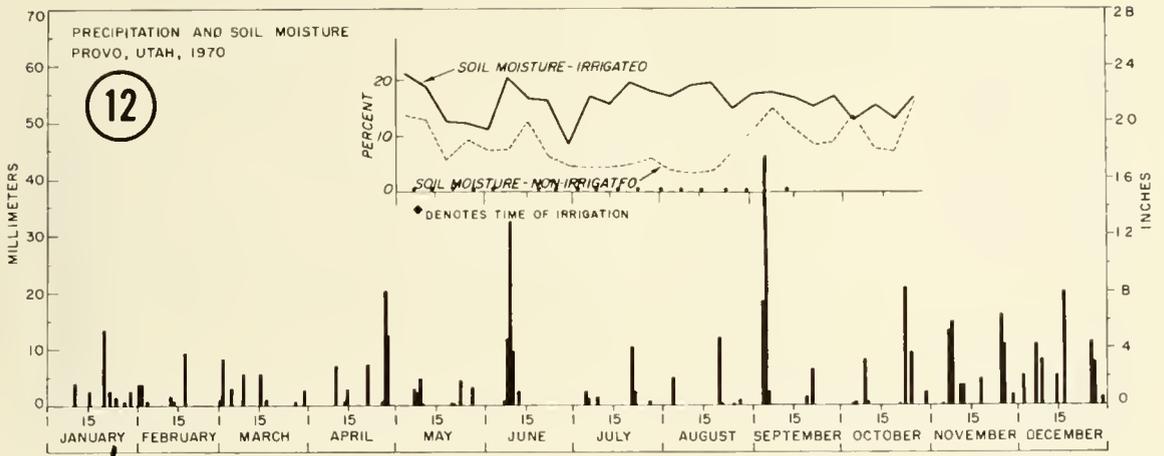
location as described above. Temperatures were also recorded on the irrigated and non-irrigated plots by three-lead distance thermographs (Fig. 8) with mercury bulb sensors located 2 in (5 cm) beneath soil surface under 3 to 4 in (7.5 to 10 cm) of grass cover, at soil surface under grass cover, and at soil surface on bare ground (Fig. 9).

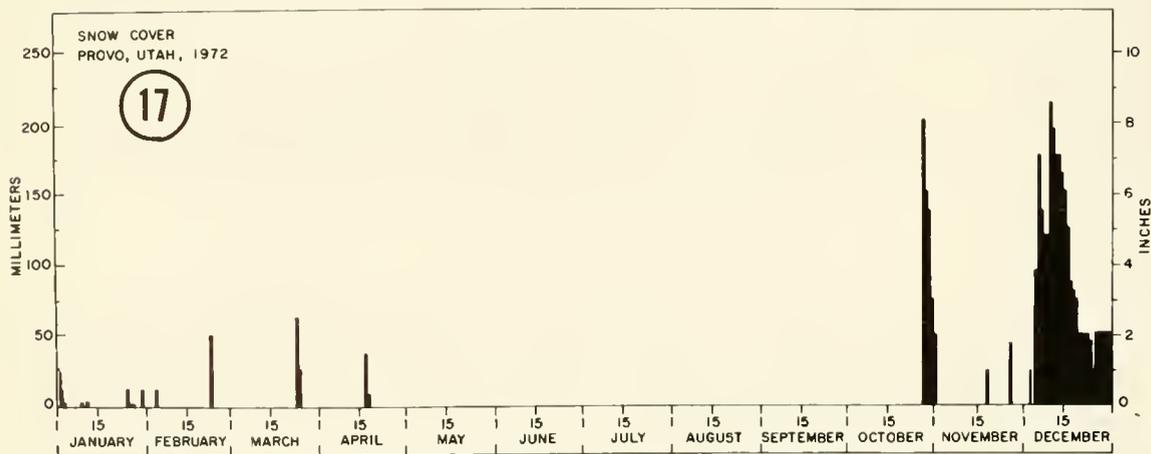
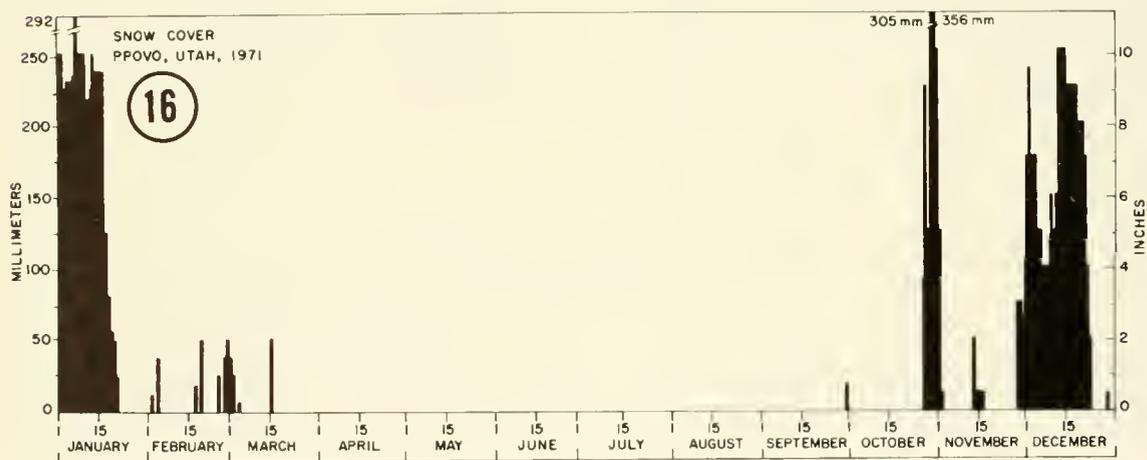
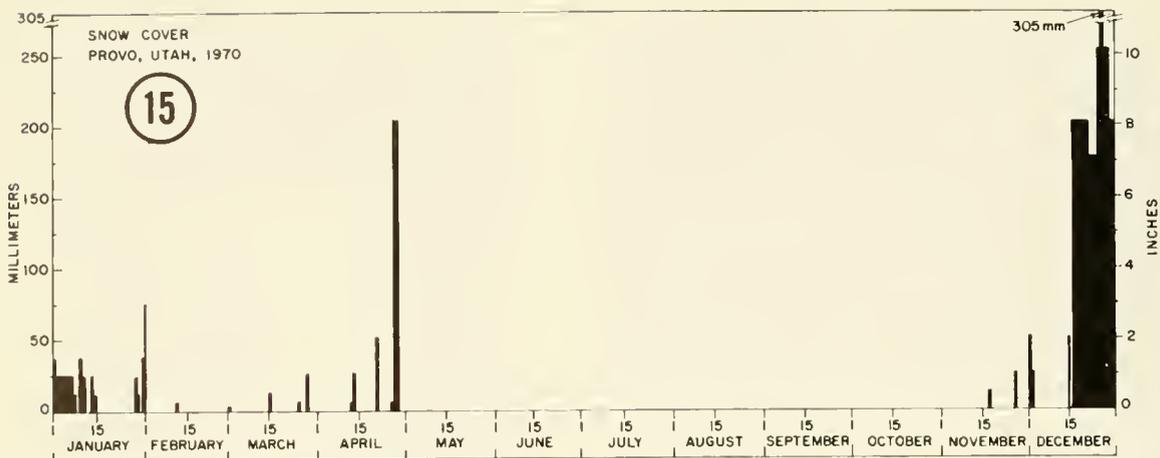
All meteorologic observations were taken daily at approximately 8:00 a.m. M.S.T., and charts for the recording instruments were changed each Monday morning. All data were entered on specially designed worksheets (Fig. 10 and 11) columnized for a FORTRAN IV program, keypunched on 80-column IBM cards, and then transferred to tape for storage and subsequent assimilation and tabulation of daily, monthly, and yearly summaries with the IBM 360/65 computer. All mensural data not already in the metric system were so transposed by appropriate subroutines. Daily measurements of most of the moisture and temperature totals or extremes recorded over the three-year period were graphed manually and photographed for reproduction herein.

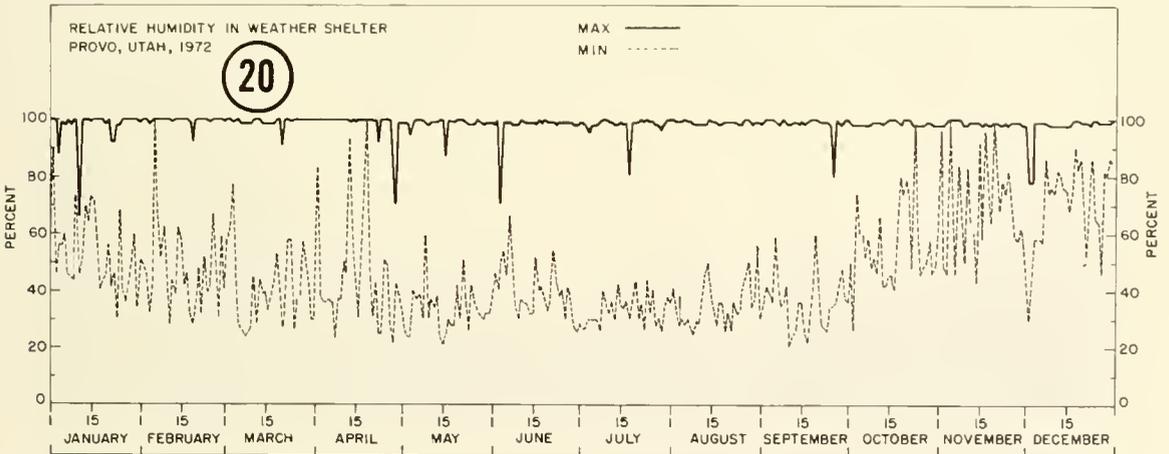
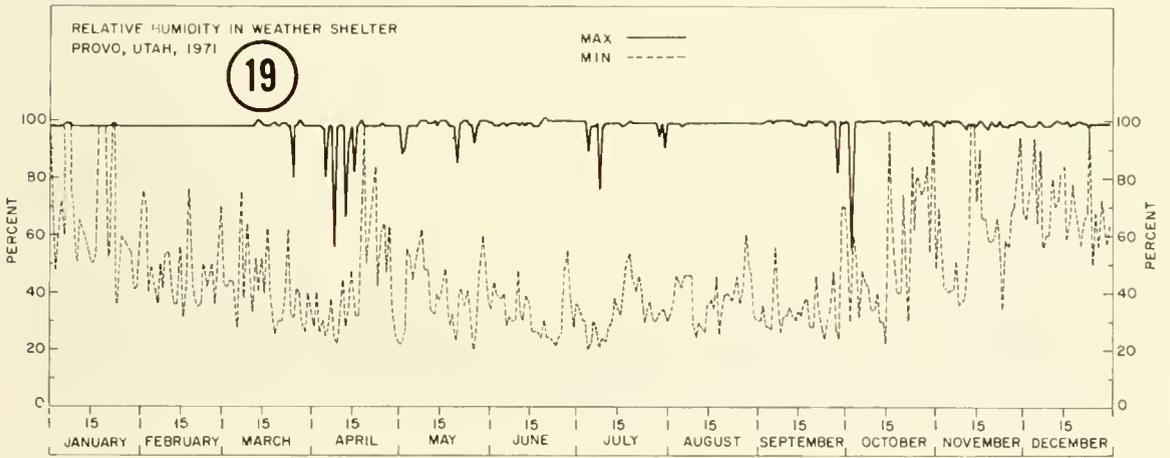
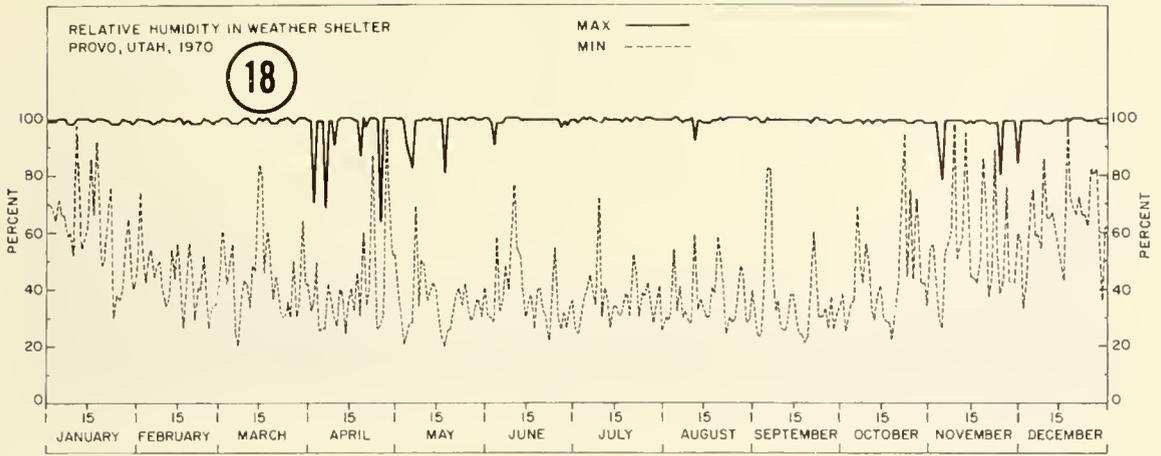
RESULTS AND DISCUSSION

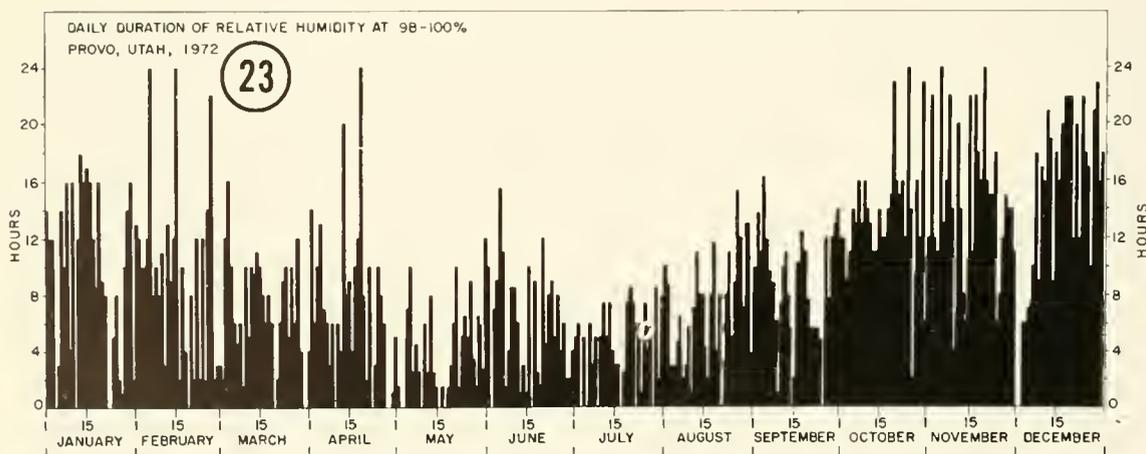
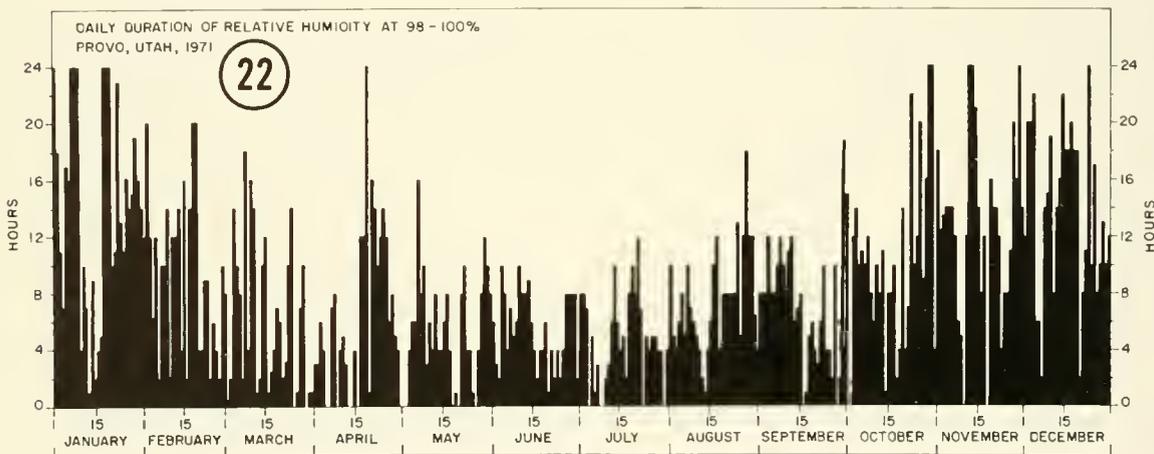
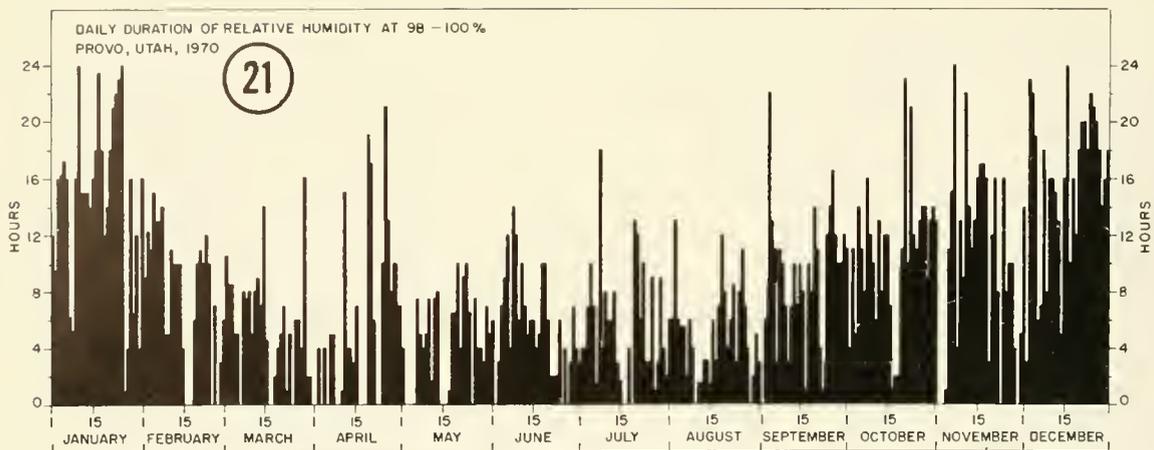
Meteorologic measurements of all data collected during the three-year study period as described above are tabulated as daily, monthly, and yearly summaries. However, since the daily summaries for any one month require three computer sheets per month, or 108 total pages, they are not included in this paper. Copies of these computer tabulations and the FORTRAN IV program are available upon request for

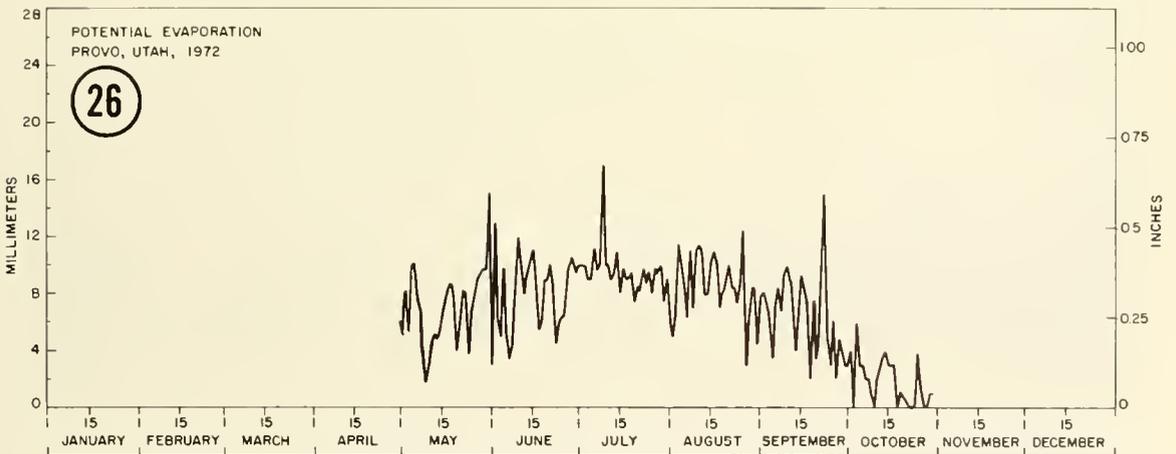
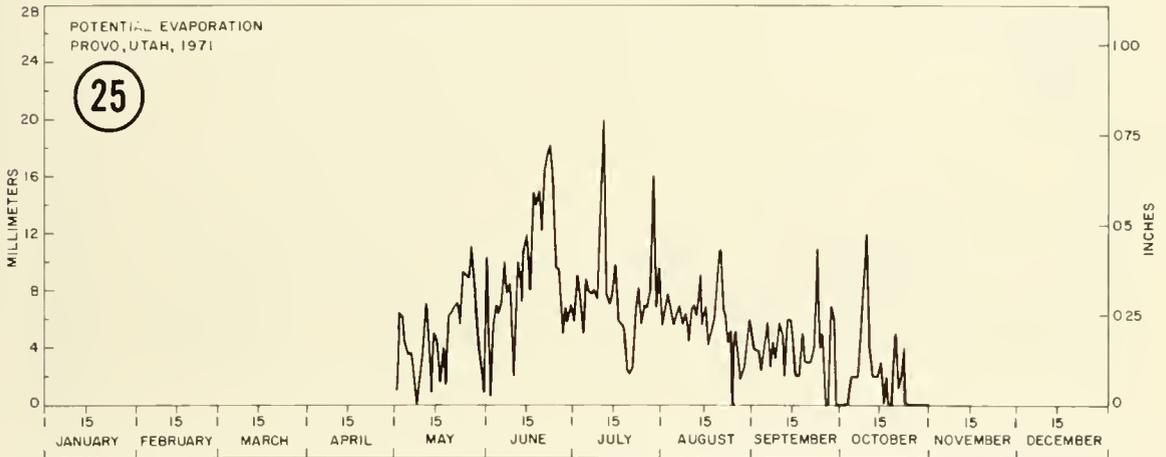
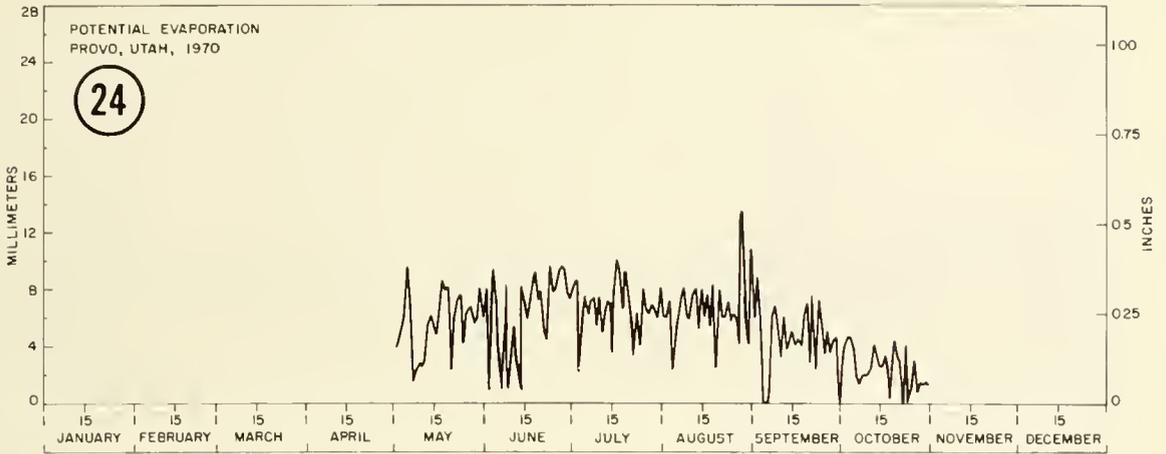
the cost of reproduction. Monthly and yearly totals and means are included herein as Tables 1 to 3, 4 to 6, and 7 to 9 for 1970, 1971, and 1972, respectively. Tables 10 and 11 give the monthly precipitation and the average monthly mean temperatures, respectively, as recorded for these three years at the official weather station for Provo (KOVO radio station), located approximately 6 km south of our station.

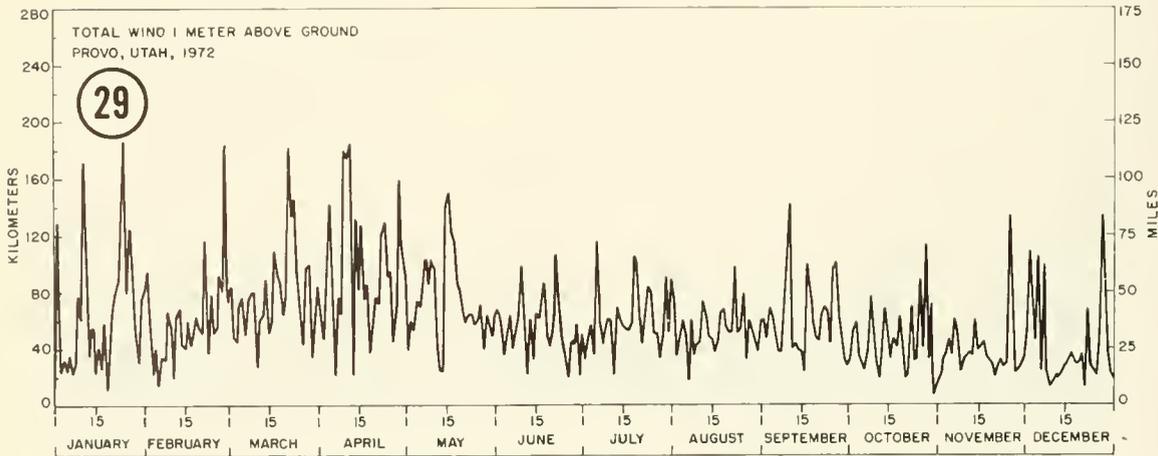
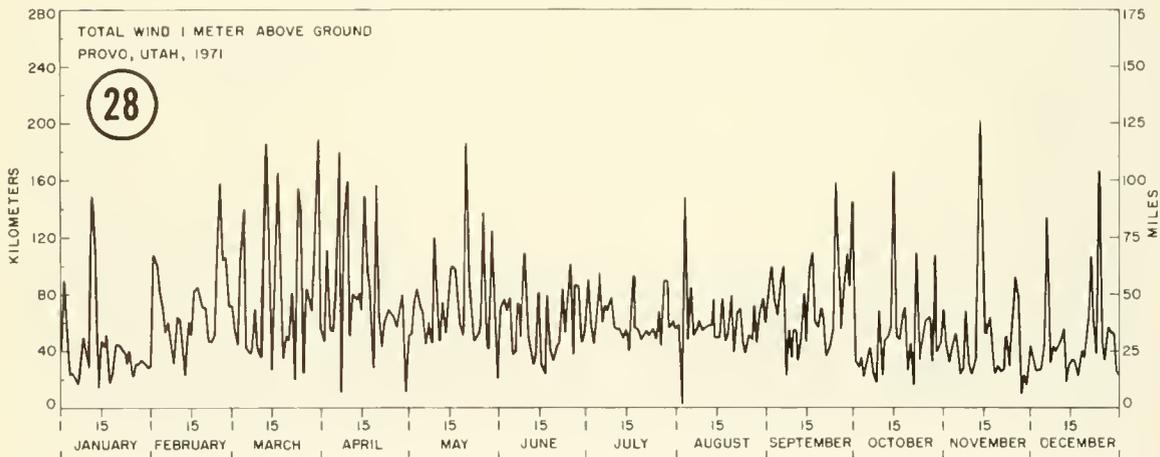
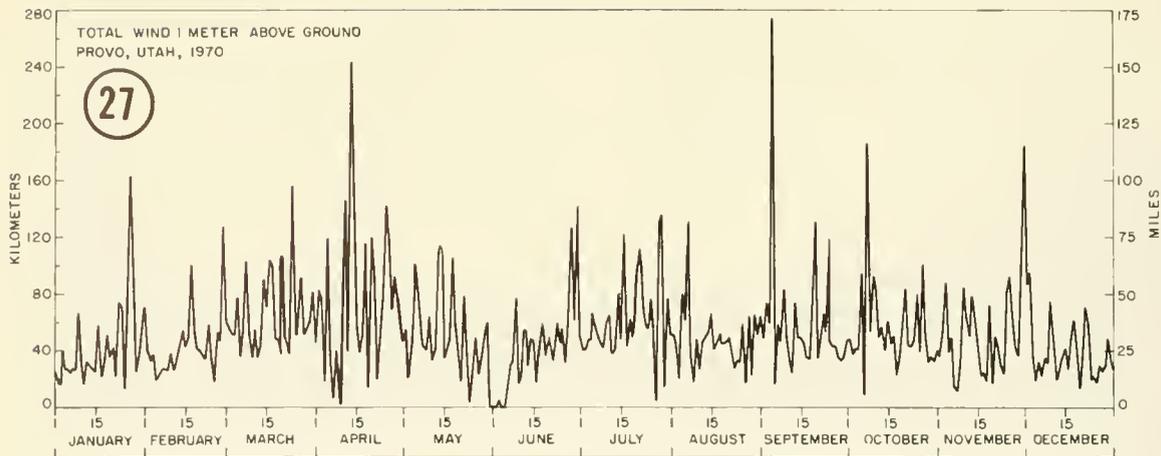


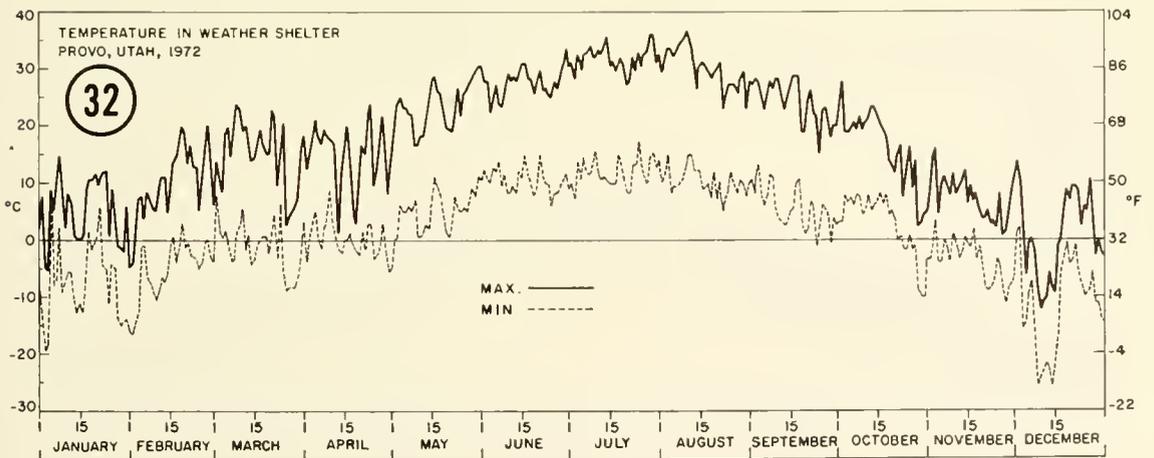
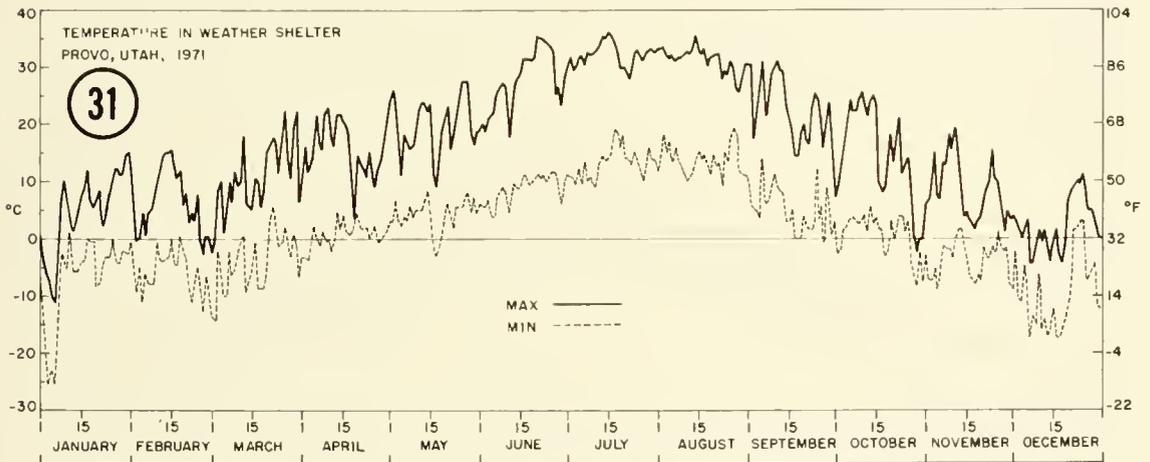
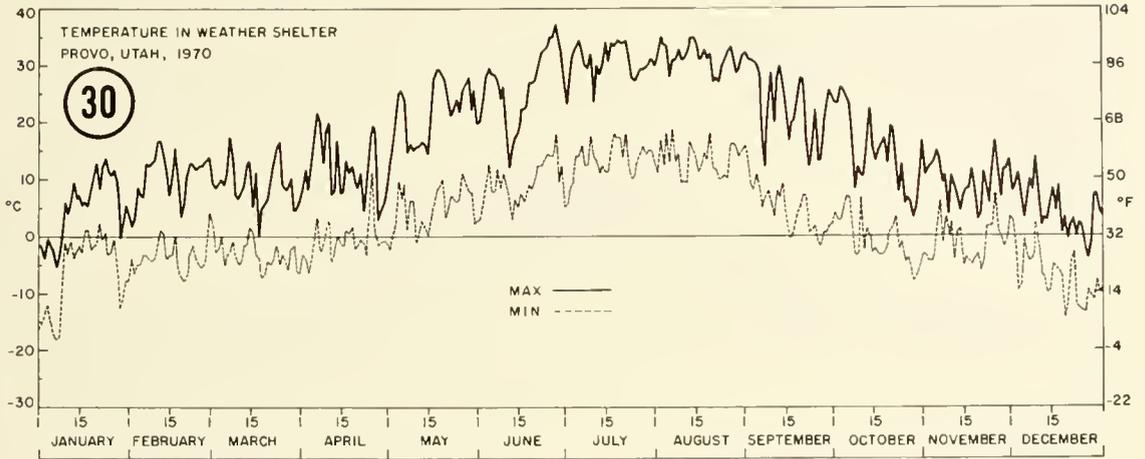


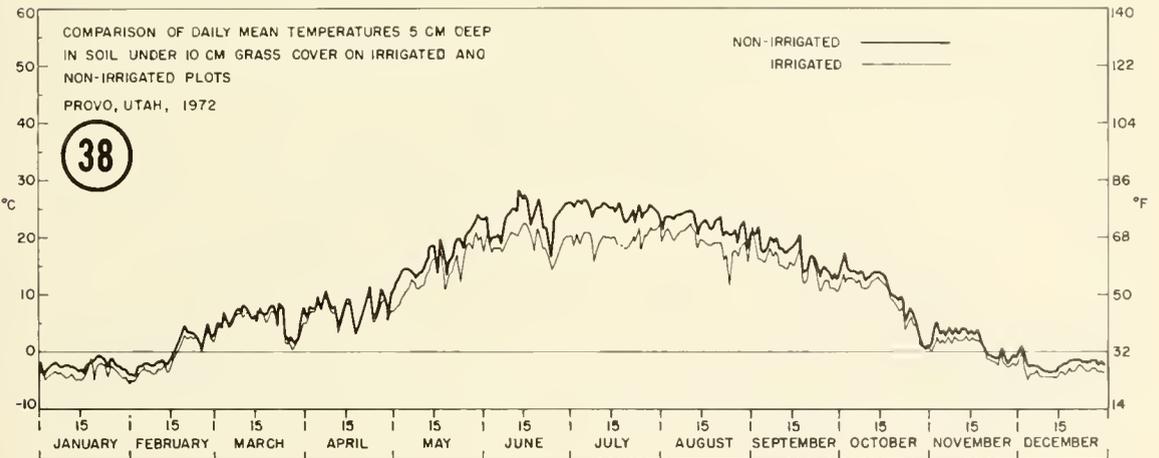
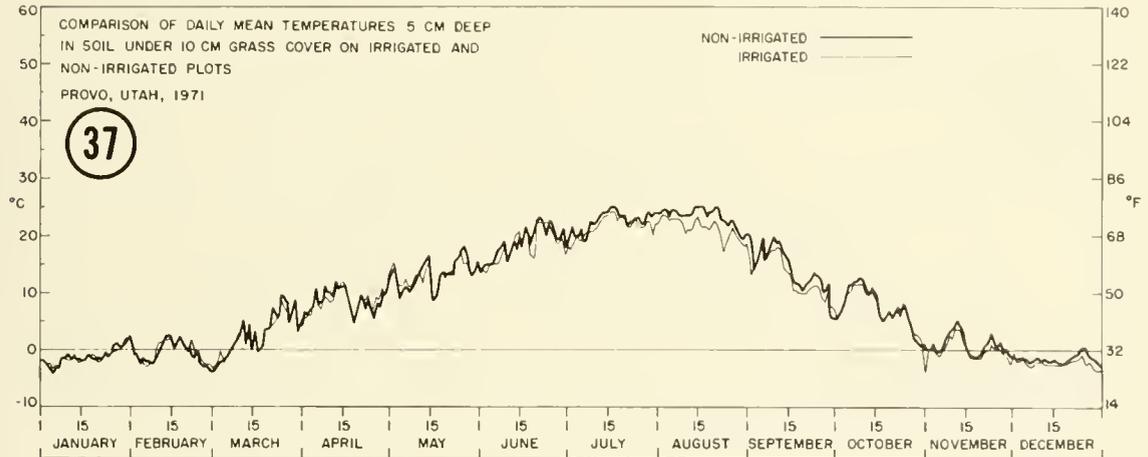
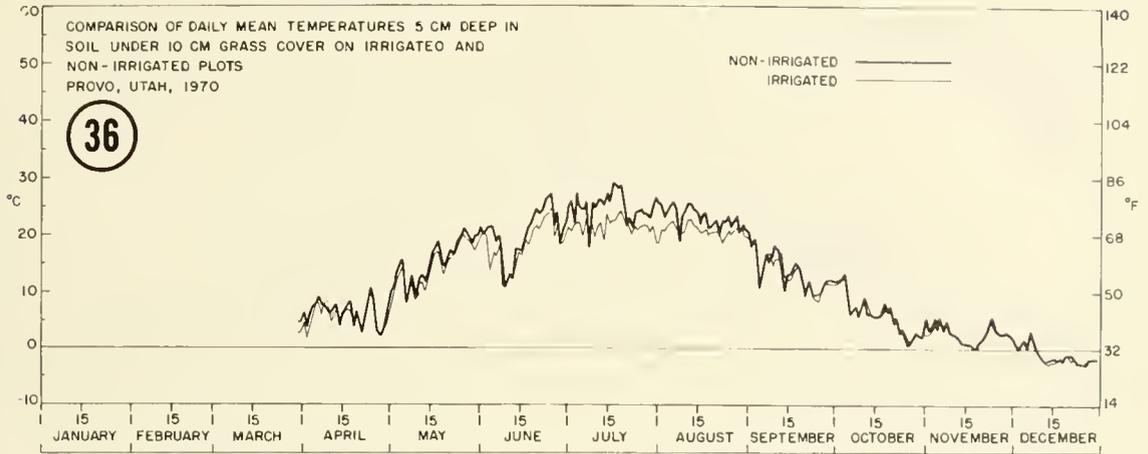


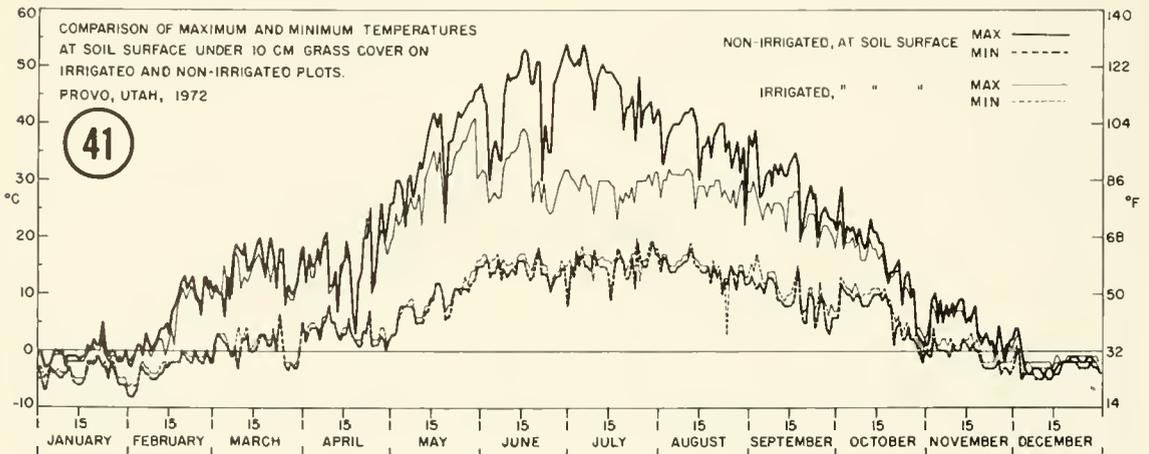
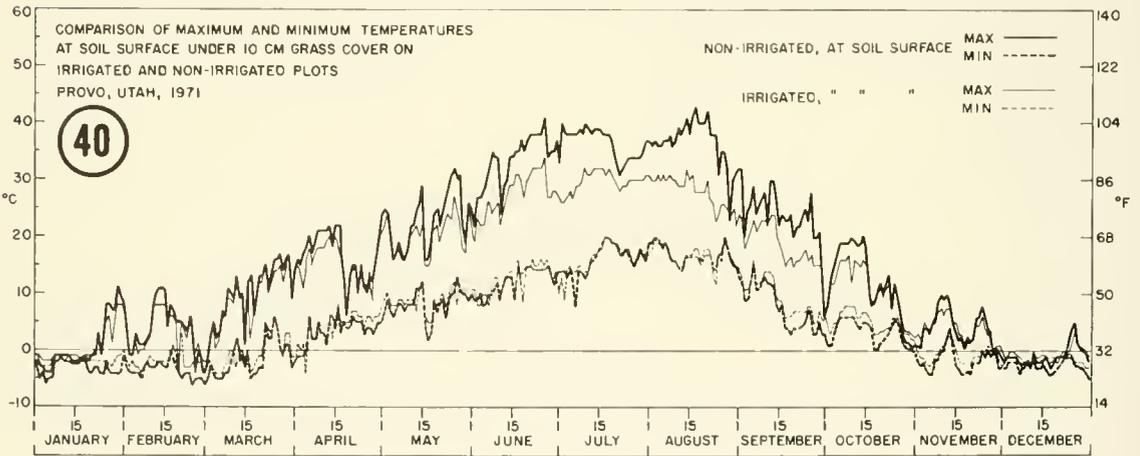
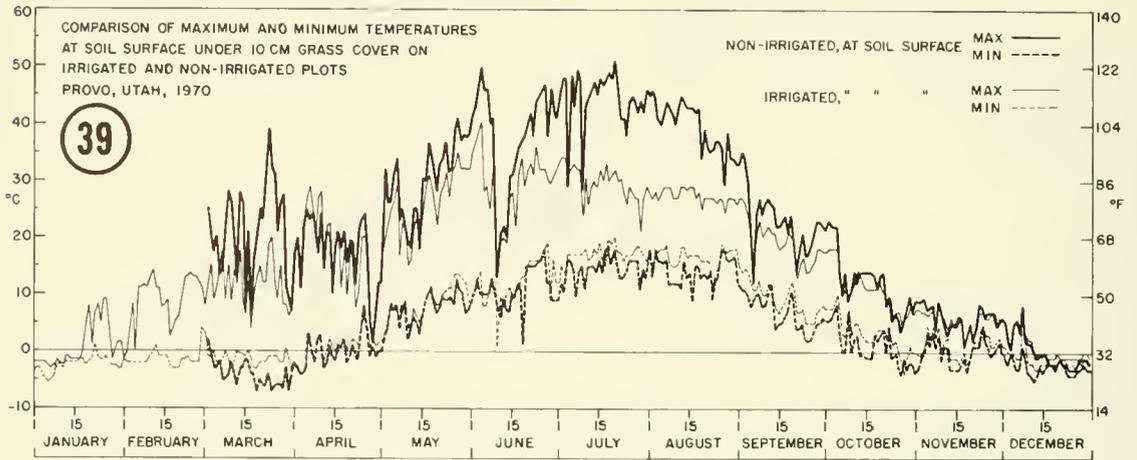


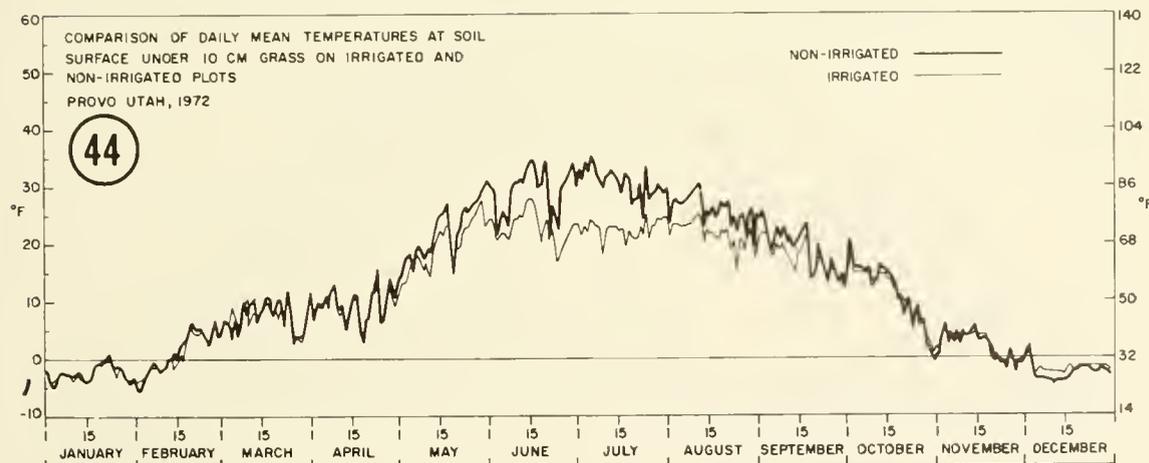
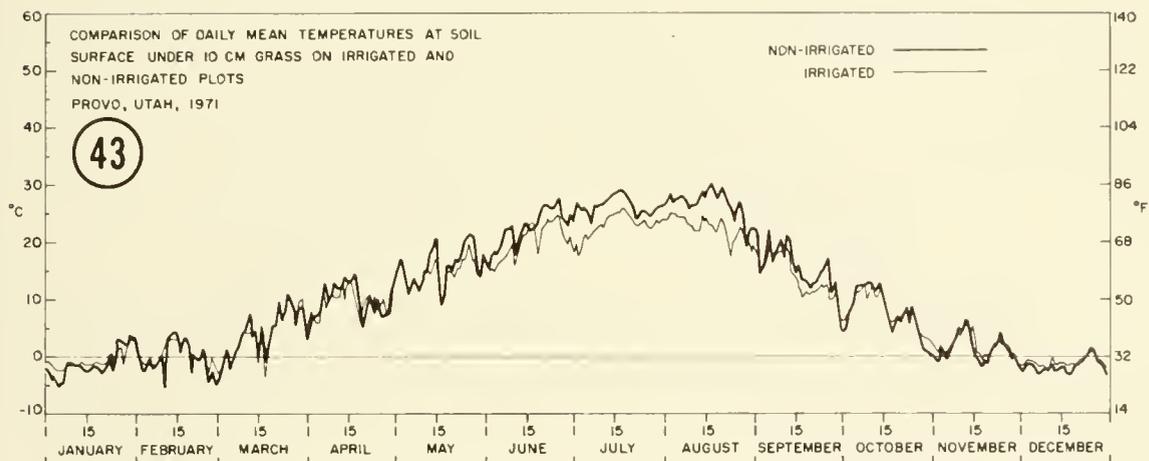
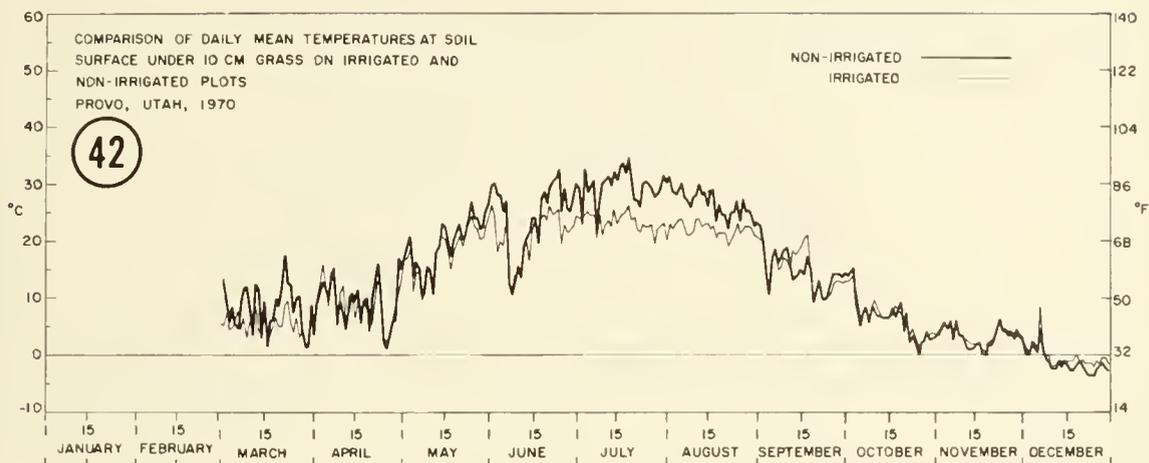


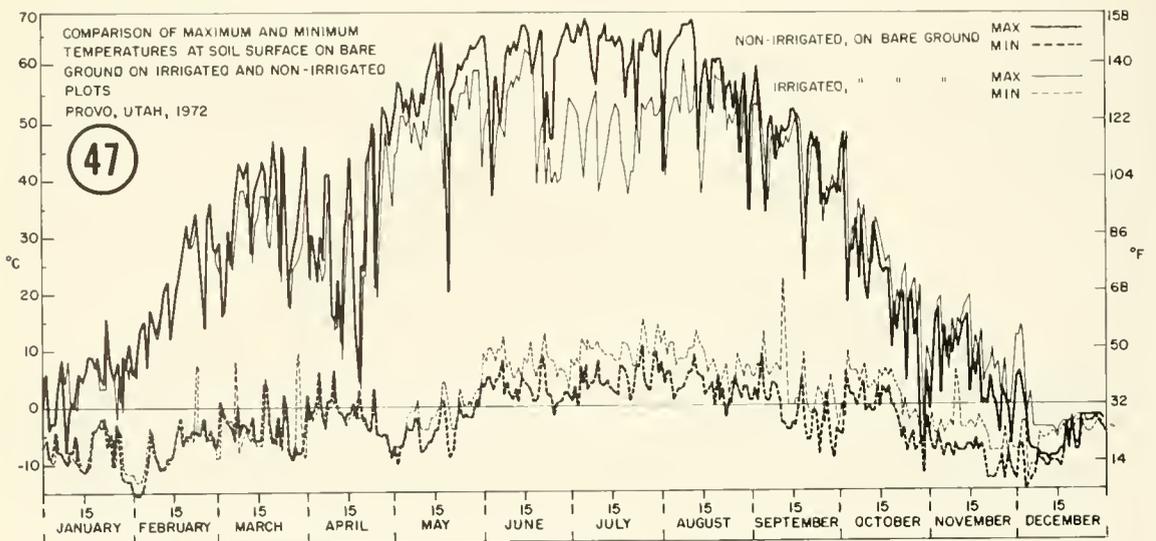
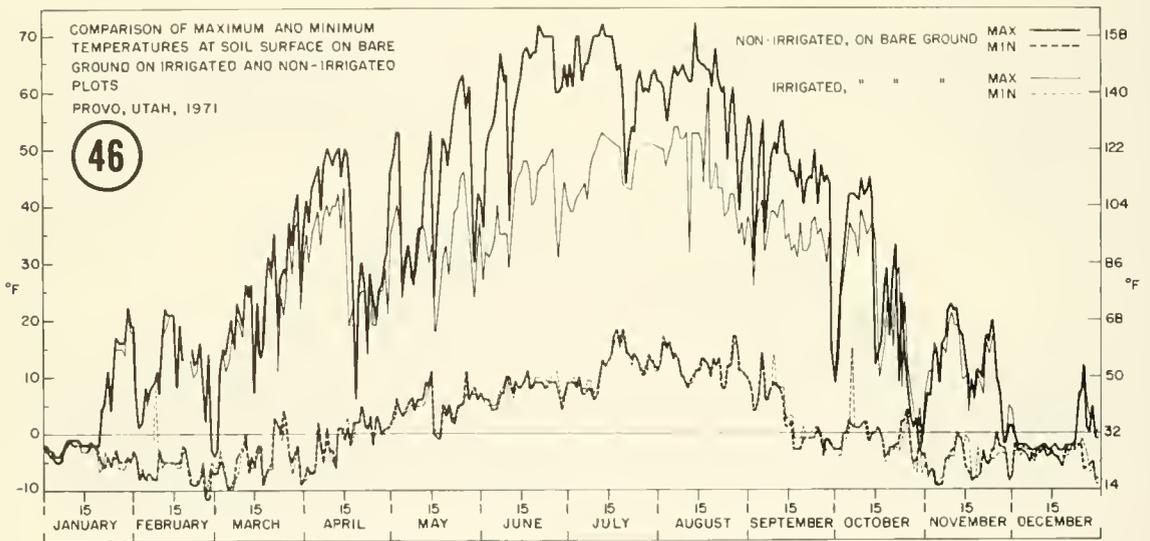
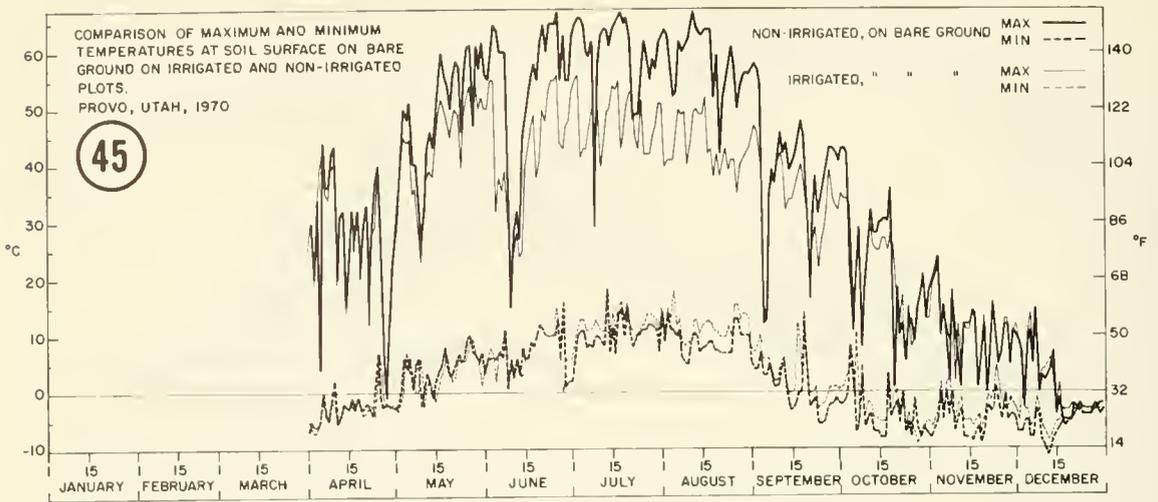


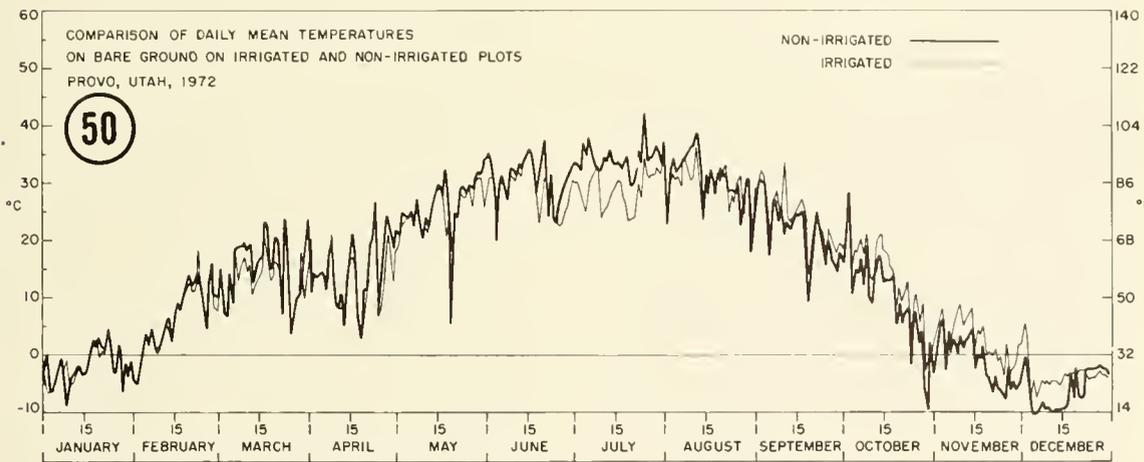
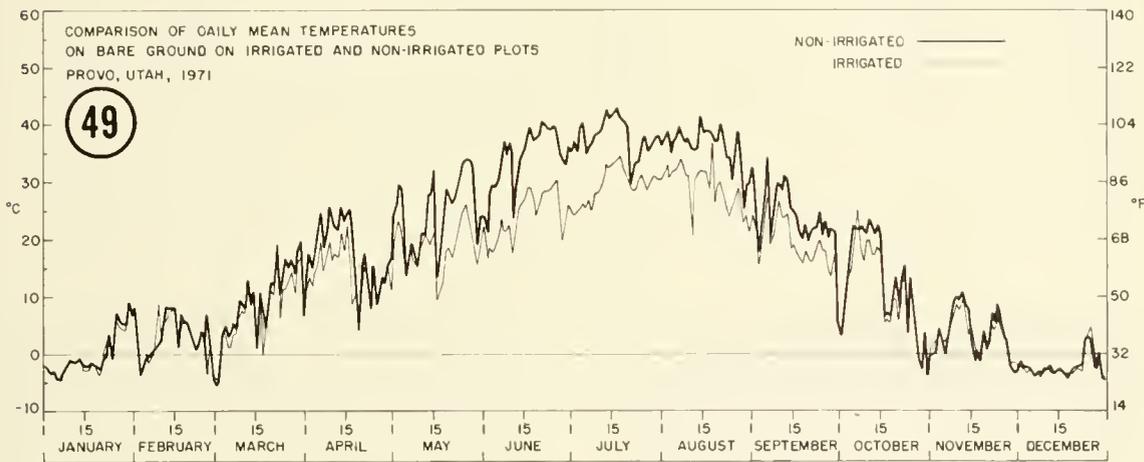
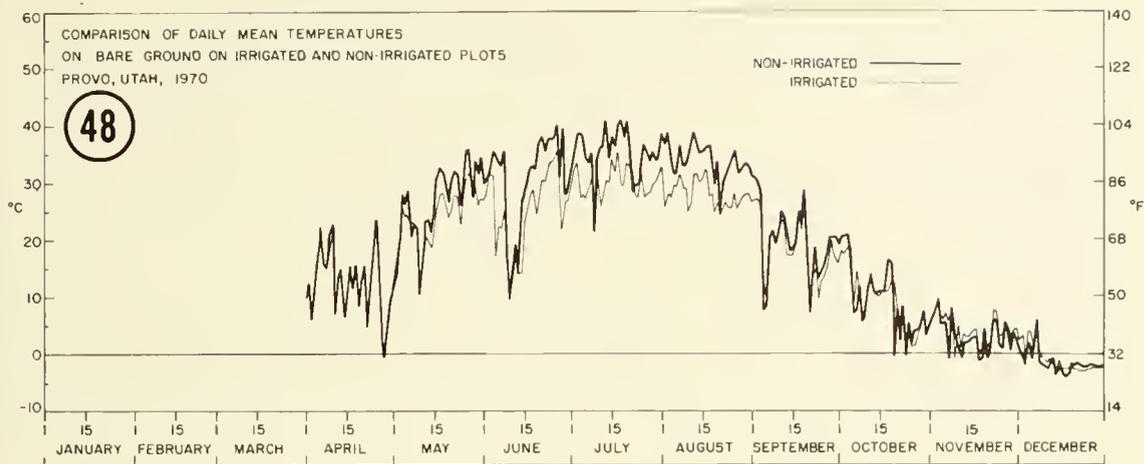


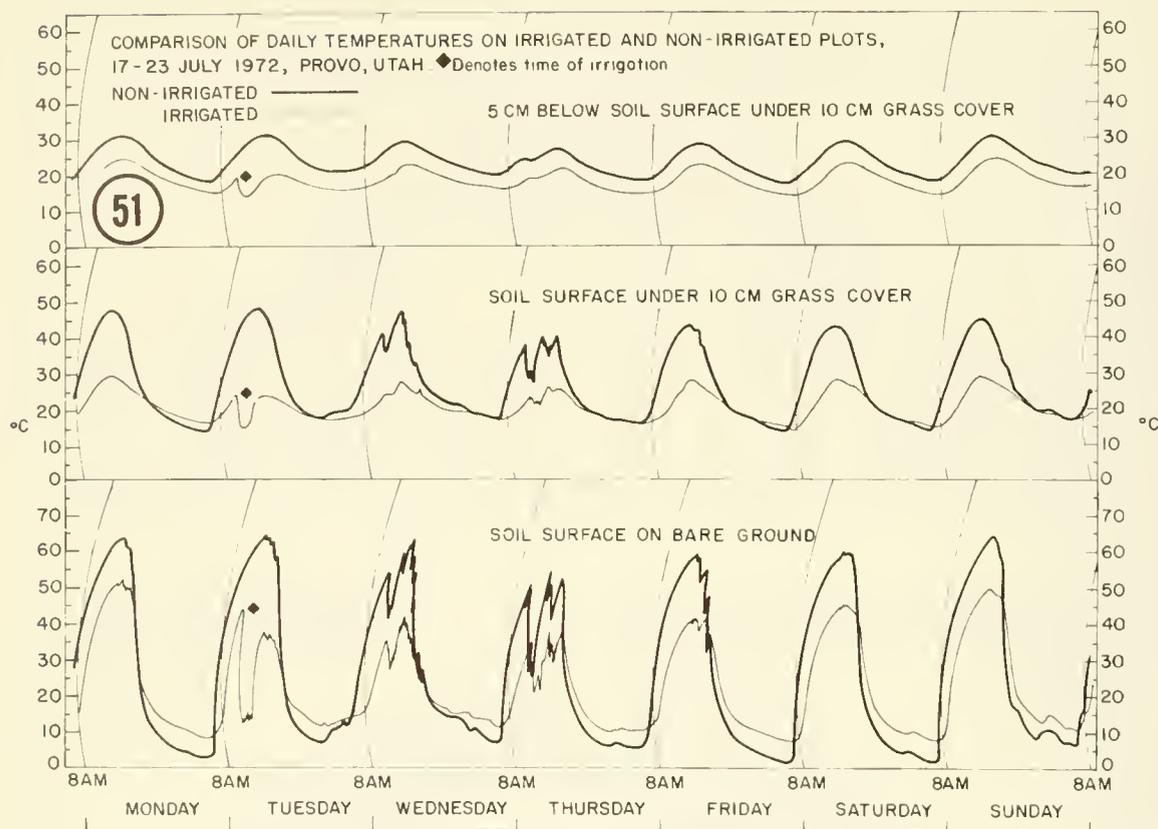








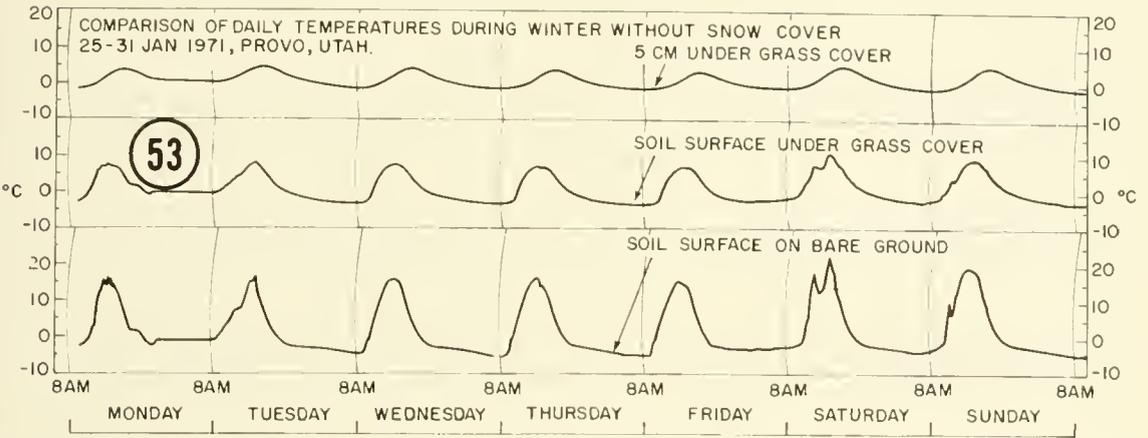
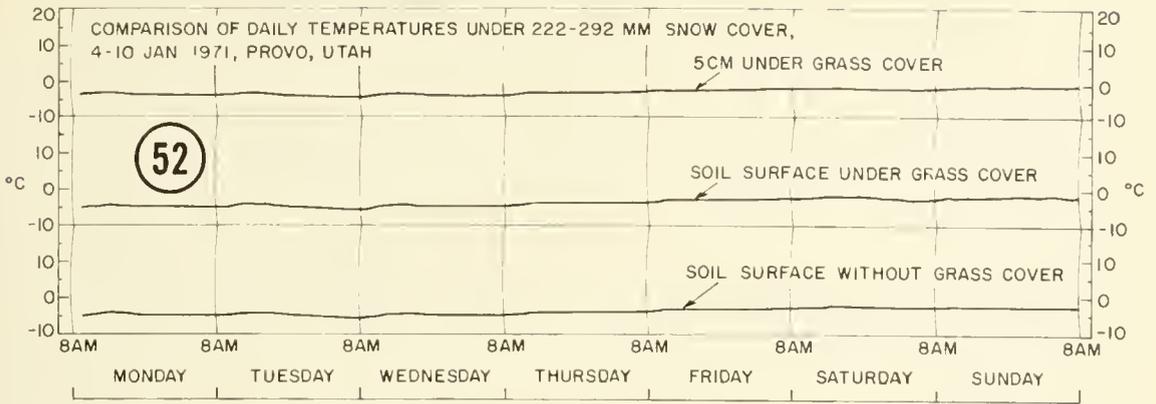




7) with the highest monthly amount of 125.7 mm received during March 1971 and the lowest amount of 2.0 mm recorded during May 1972. The yearly precipitation totals at the official Provo weather station (KOVO) were 494.8, 323.5, and 274.8 mm, respectively, for the three years indicated (Table 10). Whereas the totals for 1970 and 1972 were quite similar for the two sites, the total amount recorded for 1971 at our station was more than twice that reported at KOVO. Even though the rainfall may be irregular in distribution for any one storm, such a discrepancy for an entire year's total is difficult to explain. The fact that KOVO radio station is located more toward the center of Utah Valley, whereas our station is to the north and considerably closer to the surrounding mountains, may have contributed significantly to this difference. Also, since the main differences recorded occurred during the months of March, October, November, and December of that year, some of the discrepancy may be attributed to the fact that different methods were employed at the two stations to determine the precipitation in snow. As mentioned above, we measured snowfall with an ordinary ruler and calculated precipitation therein as one-tenth that of the depth of each snowfall. Official weather

stations either invert the rain gauge cone over the new snow cover to the last preceding crust or collect snowfall directly into the rain gauge at 1 m height. The collected snow is then melted and the water content therein measured directly with the rain gauge ruler. Collection of snow in the rain gauge canister at 1 m height is more subject to errors associated with concurrent wind movements, whereas reliability of our method suffers from the fact that the amount of moisture in snow may vary between 1/6th to 1/30th of the total snow depth for any one storm. Since we had no way of conveniently melting the snow at our station, we felt it best to use the approximation as described.

In addition to this measured precipitation, as stated earlier, the amount of water applied to the station via flood irrigation was not measured; however, such water was usually applied for one to two hours during each irrigation period. Since our station was located at the end of an irrigation ditch that was used solely for that pasture, our plot was never excessively irrigated at any time during the study. When cultivated lands are located at the ends of main irrigation ditches where excess water cannot be transferred or shut down, or when located adjacent to laterals which run continuously dur-



ing the irrigation season, such lands can often receive far more water than is optimum. Holmes and Watson (1967) stated that farmers in certain areas of southern Australia customarily use too much water for irrigation and often apply water crest depths of about 20 cm in order to cover high spots on lands in that area. As a result, as much as 50 percent of the water applied through irrigation must be pumped back into the river. DeVries and Birch (1961) compared environmental measurements in Australia on three irrigation pastures to that of an adjacent dry lot east of Rochester, Victoria, where the frequency of irrigation was approximately once every 15 days, and found that the drainage from irrigation lands in that area varied from 3 to 26 percent of the irrigational inflow. They assumed an average of 10 percent of irrigational water supplied would eventually leave as drainage. To our knowledge, the only comparable data for irrigational lands in central Utah is that by Israelsen, et al., who showed that in 1944 the average efficiency of flood irrigation was 40 percent for 11 farms they tested in Utah County. Presumably the overall efficiency has improved since then, especially in areas in which sprinkler irrigation is used, but it is not uncommon to

find pasture lands continually flooded with flows from drain streams during every day of the summer, and even into winter months in this area.

The impact of the precipitation pattern and the accompanying irrigation of pasture plots on the creation of suitable microenvironments for biological organisms is more apparent if one examines the precipitation data of this current study for June, July, August, and September, since irrigation in Utah is done routinely only during that approximate period of the year. During the three-year study period the total precipitation for those four months and the monthly averages over that period were 167.3 and 41.8 mm for 1970; 101.9 and 25.5 mm for 1971; and 53.9 and 13.5 mm for 1972. The long-term precipitation total and the monthly averages for those four months (based on all data collected from 1931 through 1960), as reported from the official Provo weather station, are 70.2 mm total and 19.5, 14.2, 21.0, and 15.5 mm for June, July, August, and September, respectively (Table 10). The normal values for all other months of the year average more than 25 mm of precipitation per month, whereas these four months all average below 25 mm per month. Parasitic nematodes, which are prevalent in cen-

Table 1. Monthly precipitation, relative humidity, cloud cover, potential evaporation, soil moisture, and total wind recorded at BYU Animal Science Farm, Provo, Utah, 1970.

Month	Precipitation (mm)						Relative Humidity		Hrs of		Pot Evap (mm)	Soil Moisture		Wind (km)
	Total Prec	Rain Prec	Snow Prec	Snow Fall	Snow Cover	Snow Cover	Max	Min	98-100 Rel Hum	Cloud Cover		Irrig	Non-Irrig	
January	Total	28.7	16.0	12.7	127.0	355.6	ND	1283
	Mean	0.9	0.5	0.4	4.1	11.5	99	60	14	5	ND	ND	ND	41
February	Total	16.8	12.4	4.3	43.2	81.3	ND	1226
	Mean	0.6	0.4	0.2	1.5	2.9	98	43	8	3	ND	ND	ND	43
March	Total	27.2	22.6	4.6	45.7	45.7	ND	2048
	Mean	0.9	0.7	0.1	1.5	1.5	99	43	5	4	ND	ND	ND	66
April	Total	48.8	7.1	41.7	416.6	492.8	ND	2187
	Mean	1.6	0.2	1.4	13.9	16.4	95	41	5	4	ND	ND	ND	72
May	Total	19.3	19.3	0.0	0.0	0.0	173.1	1484
	Mean	0.6	0.6	0.0	0.0	0.0	97	34	4	1	5.6	16.3	10.6	47
June	Total	57.1	57.1	0.0	0.0	0.0	187.3	1328
	Mean	1.9	1.9	0.0	0.0	0.0	98	38	5	3	6.2	14.6	7.9	44
July	Total	18.8	18.8	0.0	0.0	0.0	207.7	1881
	Mean	0.6	0.6	0.0	0.0	0.0	99	36	5	2	6.7	17.3	4.9	60
August	Total	18.8	18.8	0.0	0.0	0.0	200.7	1508
	Mean	0.6	0.6	0.0	0.0	0.0	99	36	4	2	6.5	17.3	4.6	48
September	Total	72.6	72.6	0.0	0.0	0.0	138.0	1792
	Mean	2.4	2.4	0.0	0.0	0.0	98	35	8	1	4.6	16.5	11.1	59
October	Total	42.2	42.2	0.0	0.0	0.0	77.0	1744
	Mean	1.4	1.4	0.0	0.0	0.0	98	44	10	3	2.5	14.5	11.4	56
November	Total	72.4	68.6	3.8	38.1	38.1	ND	1638
	Mean	2.4	2.3	0.1	1.3	1.3	96	54	10	5	ND	ND	ND	54
December	Total	68.3	18.8	49.5	495.3	3556.0	ND	1196
	Mean	2.2	0.6	1.6	16.0	114.7	99	63	15	4	ND	ND	ND	38
Yearly Total	491.0	374.4	116.6	1165.9	4569.5	983.8°	19315
Grand Mean	1.3	1.0	0.3	3.2	12.4	97	43	7	3	5.3°	16.1°	8.4°	52	

ND = Not determined

°Calculated 1 May through 31 October only

Table 2. Average monthly temperatures (°C) in weather shelter and 5 cm beneath soil surface under grass cover recorded at BYU Animal Science Farm, Provo, Utah, 1970.

Month	Weather Shelter Temperatures						5 cm beneath Soil Surface					
	Thermometer			Hygrothermograph			Irrigated			Non-Irrigated		
	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean
January	5.0	-6.1	-0.5	4.2	-5.9	-0.9	-0.9	-3.3	-2.1	ND	ND	ND
February	10.6	-3.6	3.5	9.7	-3.3	3.2	5.1	-1.7	1.7	ND	ND	ND
March	9.1	-3.3	2.9	8.3	-3.4	2.5	8.4	-1.1	3.6	ND	ND	ND
April	11.7	-0.7	5.5	10.9	-0.6	5.2	8.9	1.5	5.2	10.0	2.1	6.1
May	21.3	4.7	13.0	20.5	4.8	12.7	18.6	8.5	13.6	19.7	9.4	14.6
June	26.4	9.3	17.9	24.5	8.5	16.5	23.2	12.4	17.8	25.3	14.4	19.8
July	31.0	13.5	22.2	29.2	12.5	20.9	25.8	16.8	21.3	30.8	18.5	24.6
August	31.4	13.4	22.4	29.9	12.5	21.2	24.8	16.5	20.6	28.9	17.3	23.1
September	22.4	4.2	13.3	20.8	3.2	12.0	17.3	9.7	13.5	18.2	9.4	13.8
October	14.4	-1.0	6.7	12.8	-1.5	5.6	8.9	3.2	6.0	9.6	3.0	6.3
November	9.7	-0.7	4.5	8.3	-1.1	3.6	4.0	0.8	2.4	4.6	0.9	2.7
December	4.5	-7.4	-1.4	2.7	-7.7	-2.5	-0.2	-1.6	-0.9	0.0	-1.6	-0.8
Grand Mean	16.5	1.9	9.2	15.2	1.5	8.3	12.0	5.1	8.6	ND	ND	ND

Table 3. Average monthly temperatures (°C) at soil surface under grass cover at soil surface on bare ground recorded at BYU Animal Science Farm, Provo, Utah, 1970.

Month	Soil Surface under Grass Cover						Bare Soil Surface					
	Irrigated			Non-irrigated			Irrigated			Non-Irrigated		
	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean
January	0.9	-2.4	-0.8	ND	ND	ND	ND	ND	ND	ND	ND	ND
February	8.6	-1.4	3.6	ND	ND	ND	ND	ND	ND	ND	ND	ND
March	11.6	-1.2	5.2	ND	ND	ND	21.1	4.4	8.4	ND	ND	ND
April	16.8	0.6	8.7	17.6	-0.2	8.7	26.4	-2.5	11.9	28.0	-2.4	12.8
May	25.6	8.0	16.8	29.5	6.9	18.2	42.6	3.1	22.9	48.3	3.6	26.0
June	29.2	12.2	20.7	37.7	10.9	24.3	41.8	7.2	24.5	53.5	7.2	30.4
July	29.7	16.8	23.3	44.4	14.2	29.3	47.2	11.9	29.6	60.1	9.9	35.0
August	27.4	16.6	22.0	39.7	14.2	27.0	43.5	12.1	27.8	58.7	9.0	33.8
September	19.2	9.4	14.3	23.1	7.0	15.0	33.8	3.5	18.6	39.3	0.8	20.1
October	10.9	3.2	7.1	12.2	1.3	6.8	21.5	-2.3	9.6	24.0	-3.9	10.1
November	5.6	1.1	3.3	6.0	-0.1	3.0	11.2	-2.6	4.3	10.6	-4.6	3.0
December	0.8	-1.0	-0.1	0.2	-2.5	-1.1	1.7	-4.1	-1.2	1.0	-5.5	-2.3
Grand Mean	15.5	5.2	10.3	ND	ND	ND	ND	ND	ND	ND	ND	ND

ND = Not determined

Table 4. Monthly precipitation, relative humidity, cloud cover, potential evaporation, soil moisture, and total wind recorded at BYU Animal Science Farm, Provo, Utah, 1971.

Month	Precipitation (mm)			Relative Humidity		Hrs of 98-100 Rcl Hum	Cloud Cover	Pot Evap (mm)	Soil Moisture		Wind (km)
	Total Prec	Rain Prec	Snow Prec	Max	Min				Irrig	Non-Irrig	
January	Total	3.0	19.6	195.6	4264.6	ND	...	1303	...
	Mean	0.1	0.6	6.3	137.6	98	65	14	5	ND	42
February	Total	19.0	19.6	195.6	233.7	ND	...	2002	...
	Mean	0.7	0.7	7.0	8.3	98	47	9	4	ND	71
March	Total	120.1	5.6	55.9	119.4	ND	...	2566	...
	Mean	3.9	0.2	1.8	3.9	97	42	6	4	ND	82
April	Total	70.9	0.0	0.0	0.0	ND	...	2325	...
	Mean	2.4	0.0	0.0	0.0	94	43	6	4	ND	77
May	Total	31.7	0.0	0.0	0.0	146.9	...	2317	...
	Mean	1.0	0.0	0.0	0.0	97	39	5	4	16.1	9.9
June	Total	12.4	0.0	0.0	0.0	284.2	...	1724	...
	Mean	0.4	0.0	0.0	0.0	98	32	5	2	15.6	3.7
July	Total	20.1	0.0	0.0	0.0	242.8	...	1924	...
	Mean	0.6	0.0	0.0	0.0	97	33	4	1	17.1	1.4
August	Total	23.4	0.0	0.0	0.0	178.8	...	1822	...
	Mean	0.8	0.0	0.0	0.0	98	38	7	2	14.7	4.2
September	Total	44.2	1.8	17.8	17.8	119.0	...	2151	...
	Mean	1.5	0.1	0.6	0.6	98	34	6	2	17.3	3.5
October	Total	61.5	61.0	609.6	1270.0	59.0	...	1666	...
	Mean	2.0	2.0	19.7	41.0	98	54	10	4	17.1	11.7
November	Total	84.3	14.0	139.7	431.8	ND	...	1414	...
	Mean	3.3	0.5	4.7	14.4	99	60	12	6	ND	47
December	Total	48.0	66.3	662.9	4089.4	ND	...	1477	...
	Mean	3.7	2.1	21.4	131.9	98	68	13	6	ND	47
Yearly Total	726.4	538.7	187.7	1877.1	10426.7	1030.7°	...	22691	...
Grand Mean	2.0	1.5	0.5	5.1	28.1	97	46	8	3	16.3°	5.8°

ND = Not determined

°Calculated 1 May through 31 October only

Table 5. Average monthly temperatures (°C) in weather shelter and 5 cm beneath soil surface under grass cover recorded at BYU Animal Science Farm, Provo, Utah, 1971.

Month	Weather Shelter Temperatures						5 cm beneath Soil Surface						
	Thermometer			Hygrothermograph			Irrigated			Non-Irrigated			
	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
January	4.8	-1.2	-7.2	2.7	-6.2	-6.2	-0.7	-1.8	-2.2	-0.7	-1.5	-2.2	-0.5
February	6.2	0.2	-5.7	4.3	-6.6	-6.6	1.0	-1.2	-2.3	1.0	-0.7	-2.0	0.9
March	10.5	3.3	-4.0	8.9	-4.1	-4.1	5.4	2.4	-0.7	5.4	2.3	-0.2	5.2
April	15.5	8.0	0.4	14.1	-0.1	-0.1	11.9	7.0	4.5	11.9	8.2	4.9	12.1
May	19.7	12.0	4.2	18.0	4.1	4.1	16.8	11.0	9.1	16.8	13.0	9.1	17.0
June	27.4	17.9	8.5	25.6	7.3	7.3	23.5	16.5	12.6	23.5	18.0	13.3	24.4
July	32.2	22.6	13.0	30.1	11.6	11.6	26.0	20.8	16.6	26.0	21.3	17.1	27.6
August	31.3	22.4	13.5	29.3	12.0	12.0	25.5	20.6	17.2	25.5	21.3	18.6	28.3
September	22.8	13.9	5.0	20.9	3.6	3.6	17.0	12.3	9.6	17.0	13.3	10.0	19.1
October	14.8	7.7	0.7	13.0	-0.2	-0.2	9.6	6.4	4.9	9.6	7.2	4.6	10.1
November	8.5	2.5	-3.5	6.9	-3.9	-3.9	1.7	1.5	-1.5	1.7	0.1	-0.5	2.4
December	2.2	-3.7	-9.5	0.4	-9.5	-9.5	-1.6	-4.6	-2.6	-1.6	-2.1	-1.9	-0.9
Grand Mean	16.3	8.8	1.3	14.5	0.7	0.7	11.3	7.6	5.4	11.3	8.4	5.9	12.1

Table 6. Average monthly temperatures (°C) at soil surface under grass cover and at soil surface on bare ground recorded at BYU Animal Science Farm, Provo, Utah, 1971.

Month	Soil Surface under Grass Cover						Bare Soil Surface						
	Irrigated			Non-Irrigated			Irrigated			Non-Irrigated			
	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
January	0.4	-0.7	-1.9	0.4	-3.1	-3.1	2.7	-1.3	-3.9	2.7	-0.6	-3.6	3.0
February	3.0	0.4	-2.1	3.7	-3.4	-3.4	10.3	0.2	-5.7	10.3	11.1	-6.3	2.4
March	8.5	4.0	-0.6	9.1	-1.6	-1.6	19.7	3.8	-4.9	19.7	7.4	-4.4	8.9
April	15.1	9.5	3.9	16.3	3.3	3.3	29.5	9.8	-1.4	29.5	14.0	-0.9	17.5
May	20.2	14.6	9.0	23.0	8.1	8.1	32.5	15.6	4.7	32.5	18.6	4.8	24.6
June	27.2	20.0	12.8	33.2	12.0	12.0	40.0	22.6	8.0	40.0	24.0	7.6	34.0
July	29.7	22.9	16.1	36.5	16.0	16.0	46.9	26.2	11.6	46.9	29.3	11.6	37.6
August	28.2	22.6	17.0	36.7	16.6	16.6	46.4	26.7	11.8	46.4	29.1	12.0	36.2
September	18.8	14.2	9.6	24.3	7.8	7.8	34.5	16.0	3.5	34.5	19.0	2.6	24.0
October	10.8	8.0	5.1	12.0	3.2	3.2	21.8	7.6	-1.0	21.8	10.4	-0.8	12.1
November	3.7	1.6	-0.4	4.0	-1.5	-1.5	11.3	1.3	-4.7	11.3	3.3	-4.8	3.5
December	-0.4	-1.0	-1.6	-0.8	-2.6	-2.6	-0.5	-1.7	-4.1	-0.5	-2.3	-3.8	-2.2
Grand Mean	13.8	9.7	5.6	16.5	4.6	4.6	24.6	10.6	1.2	24.6	12.9	1.2	16.5

Table 7. Monthly precipitation, relative humidity, cloud cover, potential evaporation, soil moisture, and total wind recorded at BYU Animal Science Farm, Provo, Utah, 1972.

Month	Precipitation (mm)						Relative Humidity		Hrs of 98-100 Rel Hum		Pot Evap (mm)	Soil Moisture		Wind (km)
	Total Prec	Rain Prec	Snow Prec	Snow Fall	Snow Cover	Max	Min	Rel Hum	Cloud Cover	Irrig		Non-Irrig		
January	Total 5.6 Mean 0.2	0.0 0.0	5.6 0.2	55.9 1.8	73.7 2.4	97 53	97 53	9 9	6 6	ND ND	ND ND	ND ND	2044 65	
February	Total 8.9 Mean 0.3	2.5 0.1	6.3 0.2	63.5 2.2	63.5 2.2	99 47	99 47	9 9	4 4	ND ND	ND ND	ND ND	1742 60	
March	Total 27.2 Mean 0.9	18.3 0.6	8.9 0.3	88.9 2.9	88.9 2.9	99 40	99 40	6 6	3 3	ND ND	ND ND	ND ND	2443 78	
April	Total 79.5 Mean 2.7	74.9 2.5	4.6 0.2	45.7 1.5	45.7 1.5	97 45	97 45	7 7	4 4	ND ND	ND ND	ND ND	2756 91	
May	Total 2.0 Mean 0.1	2.0 0.1	0.0 0.0	0.0 0.0	0.0 0.0	98 33	98 33	3 3	2 2	218.6 7.1	4.7 2.4	4.7 2.4	2279 73	
June	Total 11.2 Mean 0.4	11.2 0.4	0.0 0.0	0.0 0.0	0.0 0.0	97 39	97 39	5 5	3 3	240.3 8.0	9.4 2.4	9.4 2.4	1631 54	
July	Total 7.4 Mean 0.2	7.4 0.2	0.0 0.0	0.0 0.0	0.0 0.0	98 33	98 33	4 4	1 1	297.8 9.6	11.3 1.8	11.3 1.8	1853 59	
August	Total 11.2 Mean 0.4	11.2 0.4	0.0 0.0	0.0 0.0	0.0 0.0	98 35	98 35	7 7	1 1	263.9 8.5	5.8 2.2	5.8 2.2	1661 53	
September	Total 24.1 Mean 0.8	24.1 0.8	0.0 0.0	0.0 0.0	0.0 0.0	98 36	98 36	8 8	2 2	197.2 6.6	5.3 3.2	5.3 3.2	1857 61	
October	Total 119.6 Mean 3.9	99.3 3.2	20.3 0.7	203.2 6.6	571.5 18.4	98 55	98 55	13 13	5 5	56.4 1.8	12.3 10.9	12.3 10.9	1435 46	
November	Total 54.1 Mean 1.8	47.2 1.6	6.9 0.2	68.6 2.3	119.4 4.0	98 69	98 69	14 14	6 6	ND ND	ND ND	ND ND	1183 39	
December	Total 39.4 Mean 1.3	1.0 0.0	38.4 1.2	383.5 12.4	2702.6 87.2	97 69	97 69	14 14	5 5	ND ND	ND ND	ND ND	1371 44	
Yearly Total	390.1	299.2	90.9	909.3	3665.2	97	97	8	3	1274.2°	8.1°	8.1°	22,255	
Grand Mean	1.1	0.8	0.2	2.5	9.9	97	97	8	3	6.9°	8.1°	8.1°	60	

ND = Not determined

°Calculated 1 May through 31 October only

Table 8. Average monthly temperatures (°C) in weather shelter and 5 cm beneath soil surface under grass cover recorded at BYU Animal Science Farm, Provo, Utah, 1972.

Month	Weather Shelter Temperatures						5 cm beneath Soil Surface						
	Thermometer			Hygrothermograph			Irrigated			Non-Irrigated			
	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
January	5.3	-1.1	-7.5	3.5	-2.2	-7.9	-3.1	-3.8	-4.4	-1.7	-2.4	-3.1	-1.7
February	9.9	2.3	-5.2	8.1	1.2	-5.7	0.7	-1.3	-3.2	1.6	-0.2	-2.0	1.6
March	14.8	6.7	-1.3	13.3	5.6	-2.1	8.8	5.0	1.1	9.0	5.7	2.4	9.0
April	14.8	7.5	0.3	13.5	6.7	0.0	10.6	6.9	3.2	11.1	7.7	4.3	11.1
May	23.1	13.9	4.7	22.3	13.5	4.7	19.2	13.7	8.2	21.9	16.2	10.6	21.9
June	27.8	19.1	10.4	26.5	18.3	10.2	23.5	18.8	14.1	29.4	23.2	16.9	29.4
July	31.8	21.8	11.8	30.5	21.0	11.6	23.9	19.4	14.9	27.6	24.7	17.1	27.6
August	30.2	20.3	10.4	29.0	19.8	10.5	23.7	18.9	14.1	30.8	24.7	18.5	30.8
September	24.4	15.1	5.9	23.4	14.8	6.1	19.4	14.7	10.0	22.3	22.3	11.9	22.3
October	16.6	9.8	2.9	15.2	9.4	3.6	11.4	9.0	6.6	13.4	10.5	7.6	13.4
November	7.2	1.8	-3.6	5.9	1.5	-2.9	1.9	0.5	-0.9	3.3	1.7	0.1	3.3
December	1.1	-5.0	-11.2	-0.1	-5.2	-10.3	-3.0	-3.5	-3.9	-1.6	-2.1	-2.7	-1.6
Grand Mean	17.3	9.4	1.5	15.9	8.7	1.5	11.4	8.2	5.0	13.9	10.4	6.8	13.9

Table 9. Average monthly temperatures (°C) at soil surface under grass cover and at soil surface on bare ground recorded at BYU Animal Science Farm, Provo, Utah, 1972.

Month	Soil Surface under Grass Cover						Bare Soil Surface						
	Irrigated			Non-Irrigated			Irrigated			Non-Irrigated			
	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
January	-1.2	-2.3	-3.5	-0.5	-2.3	-4.2	4.2	-2.0	-8.1	4.4	-1.6	-7.7	4.4
February	4.1	0.8	-2.4	5.6	1.2	-3.2	19.8	6.2	-7.5	30.2	6.4	-7.5	30.2
March	12.7	7.0	1.4	14.6	7.6	0.5	30.1	13.1	-3.9	34.2	15.2	-3.8	34.2
April	14.4	9.1	3.8	15.9	9.5	3.1	28.2	13.1	-2.1	31.6	15.1	-1.3	31.6
May	29.8	19.4	8.9	35.6	21.9	8.3	50.6	24.9	-0.9	55.9	26.1	-3.7	55.9
June	30.5	22.8	15.2	44.4	29.2	13.9	49.9	28.7	7.6	59.2	31.1	3.0	59.2
July	28.9	22.5	16.1	46.4	30.7	14.9	47.9	28.8	9.8	63.0	33.7	4.5	63.0
August	29.0	21.9	14.9	37.3	25.8	14.2	51.8	29.7	7.6	58.1	30.7	3.4	58.1
September	24.2	17.6	10.9	29.4	19.2	9.0	44.3	23.9	3.6	44.6	21.7	-1.2	44.6
October	14.6	11.2	7.8	16.4	11.4	6.5	24.4	13.1	1.8	21.1	9.7	-1.6	21.1
November	4.2	2.3	0.3	4.6	1.8	-1.0	9.8	2.7	-4.4	5.8	-1.5	-8.8	5.8
December	-1.2	-1.7	-2.3	-1.8	-2.5	-3.3	-1.7	-3.5	-5.4	-4.6	-6.2	-7.7	-4.6
Grand Mean	15.8	10.9	5.9	20.7	12.8	4.9	30.0	14.9	-0.2	32.8	15.0	-2.7	32.8

Table 10. Total monthly precipitation for Provo, Utah (KOVO radio station).

	1970				1971				1972					
	Normal °		Amount		Departure		Amount		Departure		Amount		Departure	
	mm	in	mm	in	mm	in	mm	in	mm	in	mm	in	mm	in
January	36.00	1.44	47.00	1.88	11.00	.44	16.00	.64	-20.00	-.80	4.25	.17	-31.75	-1.27
February	32.25	1.29	18.25	.73	-14.00	-.56	53.75	2.15	21.50	.86	2.50	.10	-29.75	-1.19
March	31.25	1.25	27.50	1.10	-3.75	-.15	2.50	.10	-28.75	-1.15	14.50	.58	-16.75	-.67
April	29.75	1.19	59.50	2.38	29.75	1.19	56.50	2.26	26.75	1.07	31.50	1.26	1.75	.07
May	28.25	1.13	17.00	.68	-11.25	-.45	29.25	1.17	1.00	.04	.25	.01	-28.00	-1.12
June	19.50	.78	46.75	1.87	27.25	1.09	9.50	.38	-10.00	-.40	18.50	.74	-1.00	-.04
July	14.25	.57	21.50	.86	7.25	.29	11.75	.47	-2.50	-.10	5.25	.21	-9.00	-.36
August	21.00	.84	31.00	1.24	10.00	.40	18.25	.73	-2.75	-.11	19.50	.78	-1.50	-.06
September	15.50	.62	63.25	2.53	47.75	1.91	33.25	1.33	17.75	.71	16.25	.65	.75	.03
October	33.50	1.34	37.25	1.49	3.75	.15	53.25	2.13	19.75	.79	100.50	4.02	67.00	2.68
November	27.75	1.11	84.25	3.37	56.50	2.26	15.25	.61	-12.50	-.50	40.25	1.61	12.50	.50
December	32.75	1.31	41.50	1.66	8.75	.35	24.25	.97	-8.50	-.34	21.50	.86	-11.25	-.45
Total	321.75	12.87	494.75	19.79	173.00	6.92	323.50	12.94	1.75	.07	274.75	10.99	-47.00	-1.88

°Normals based on data from 1931-1960.

Table 11. Average monthly mean temperatures recorded from Provo, Utah (KOVO radio station).

	Normal°		1970		1971		1972	
	°C	°F	°C	°F	°C	°F	°C	°F
	January	-3.5	25.7	-2.1	28.1 M	-2.0	28.3	-1.3
February	.1	32.1	3.6	38.5	1.2	34.2 M	2.4	36.4 M
March	4.4	40.0	3.4	38.2	4.9	40.9 M	7.9	46.3 M
April	9.6	49.2	6.8	44.4 M	9.1	48.5	8.8	48.0 M
May	13.8	56.9	14.0	57.2	13.0	55.4	14.8	58.8 M
June	18.1	64.6	18.6	65.6	18.9	66.1	19.5	67.1 M
July	22.8	73.0	22.7	72.9 M	22.5	72.5 M	22.4	72.4 M
August	21.6	70.9	23.2	73.9 M	22.3	72.2 M	21.2	70.3 M
September	16.7	62.1	14.0	57.3 M	13.8	56.9 M	15.6	60.2 M
October	10.9	51.6	7.6	45.7	7.9	46.3 M	10.5	51.0 M
November	3.4	38.2	5.0	41.1	2.7	36.9 M	2.7	37.0 M
December	-1.3	29.7	-1.7	28.8	-4.4	24.0 M	-5.2	22.5 M
Annual	9.7	49.5	9.6	49.3	9.1	48.5	10.0	50.0

° = Normals based on data from 1931-1960

M = Some data missing during month

°° = No data for Provo; data taken from Pleasant Grove, Utah

Table 12. Total monthly potential evaporation° at Utah Lake station, Lehi, Utah.

Month	1970		1971		1972	
	mm	in	mm	in	mm	in
May	187.00	7.48	164.25	6.57	221.75	8.87
June	206.00	8.24	229.00	9.16	225.25	9.01
July	232.25	9.29	272.00	10.88	293.00	11.72
August	220.50	8.82	226.50	9.06	218.25	8.73
September	115.00	6.20	171.00	6.84	151.00	6.04
October	86.75	3.47	ND	ND	ND	ND
Total	1,047.50	43.50	1,062.75**	42.51**	1,109.25**	44.37**

° Measured from standard 4-ft (120-cm) diameter evaporating pan

** 5-month total only

ND = Not determined

Table 13. Total monthly wind movement° at Utah Lake station, Lehi, Utah.

Month	1970		1971		1972	
	km	miles	km	miles	km	miles
May	3,563	2,227	2,990	1,869	3,373	2,108
June	2,941	1,838	2,850	1,781	2,963	1,852
July	2,626	1,641	2,397	1,498	2,624	1,640
August	2,045	1,278	2,338	1,461	1,877	1,173
September	3,402	2,126	3,438	2,149	2,547	1,592
October	2,632	1,645	3,291	2,057	2,566	1,604
Total	17,209	10,755	17,304	10,815	15,950	9,969

° Measured with standard wind-totalizing anemometer located 6 inches (15 cm) above standard 4-ft (120-cm) diameter evaporating pan

Table 14. Average monthly soil temperatures° at Salt Lake City, Utah.

Month	1970		1971		1972	
	°C	°F	°C	°F	°C	°F
January	1.3	34.4	1.6	34.8	0.0	32.0
February	3.0	37.4	2.4	36.3	1.7	35.1
March	5.1	41.1	4.2	39.6	8.3	46.9
April	7.2	44.9	9.6	49.3	9.3	48.7
May	13.4	56.2	13.4	56.1	16.1	61.0
June	18.4	65.2	19.4	66.9	22.5	72.5
July	21.9	71.4	26.4	79.6	26.5	79.7
August	23.3	74.0	26.3	79.4	26.3	79.3
September	16.3	61.3	17.9	64.2	19.6	67.2
October	10.3	50.5	9.6	49.3	13.2	55.8
November	5.7	42.2	3.1	37.5	4.8	40.6
December	2.2	36.0	-0.5	31.1	1.1	33.9
Yearly Mean	10.7	51.2	11.2	52.1	12.4	54.4
Yearly Maximum	27.8	82.0	33.9	93.0	30.0	86.0
Yearly Minimum	-1.7	29.0	-2.8	27.0	-1.7	29.0

° Recorded 10 cm deep in barren, level, sandy-loam soil

tral Utah and which are picked up by animals grazing on pasture, reportedly require a minimum monthly average of 50 mm precipitation (Levine, 1963) in order for the free-living stages to develop and survive. Thus, it appears that irrigation is the factor which supplies the additional moisture needed to create optimum microenvironments for these parasites.

The total snowfall for each of the three years of this study was 1165.9, 1877.1 and 909.3

mm (Tables 1, 4, 7), and the percentage of total moisture received as snow during those years was 23.7, 25.8, and 23.3 percent for 1970, 1971, and 1972, respectively. The number of days with at least 25 mm of snow cover on the ground was 38, 62, and 39 days, respectively. Snowfall during winter months is important to this geographic area as the major source of water to be used in irrigation during the following summer season. The impact of snowfall on bio-

logical organisms in microenvironments comes about through the moderating effect it has on temperature extremes. This effect can be readily seen by examining Fig. 52 and 53, which depict temperature fluctuations at soil surface with and without snow cover. For those parasitic organisms with free-living stages outside their normal hosts, this moderation may be an important factor in their extended winter survival. Andersen, Levine, and Boatman (1970) showed that free-living infective larvae of certain nematodes parasitic in sheep could survive twice as long when placed on plots during winter months than during the warmer periods of the year, which fact may have been due in part to the moderating effect of snow cover. The impact of snow cover on temperature at ground level under snow cover compared to that in a standard weather shelter was also demonstrated by Andersen and Levine (1967) who recorded a range during one day in January 1965, at Urbana, Illinois, of 0 and -2.2°C under 10 cm snow cover compared to -6.1 and -17.8°C in a standard weather shelter. In the study herein reported, we found that the temperature on 4 January 1971 at soil surface under 22 cm of snow (Fig. 52) varied only from -3 to -4°C (mean of -3.5°C), whereas that in the weather shelter at the same location ranged from -7.8 to -25.6°C (mean of -16.7°C). Three weeks later on 25 January 1971, with no snow cover (Fig. 53), the temperature at soil surface on bare ground varied from 15 to -3°C (mean of 6°C), whereas that in the weather shelter ranged from 12.2 to 0.0°C (mean of 6.1°C).

The extremes in relative humidity measured in the weather shelter fluctuated markedly throughout the year in the present study, but the daily maximum recorded was generally high even during warm summer periods. The average maximum and minimum humidity percentages recorded for the three years were 97 and 43 percent, 97 and 46 percent, and 97 and 46 percent, respectively (Tables 1, 4, and 7). Percentages less than 98 to 100 percent were recorded only 18 days during each of the three years. In a comparable study of meteorologic measurements on pasture lands at Urbana, Illinois, Andersen, Levine, and Boatman (1970) recorded average daily maximum and minimum relative humidities of 96 and 56 percent for 1965 and 94 and 60 percent for 1966.

Whereas in our current study we measured relative humidity only over the irrigated plot, deVries and Birch (1961) compared relative humidity in a Stevenson screen (approximately 150 cm above soil surface) located over weather stations in three irrigated pastures in Australia

with that measured over a dry lot area approximately 6 km away. By rotating hygrothermographs at 4 to 6 week intervals over a two-year study in order to eliminate systematic errors, they found that relative humidities were 5 to 10 percent higher in summer in the irrigated fields than in the non-irrigated region. The evaporation of moisture and increased transpiration from the higher vegetation in the irrigated stations undoubtedly contributed to this elevated reading and would naturally hold for any geographical region where such comparison could be made. Since our non-irrigated plot was confined within the irrigated section of the weather station, we were unable to make such a measurement. A comparison of relative humidities recorded within Stevenson screens on adjacent wet and dry plots would be meaningless as an adequate reflection of environmental influences emanating from the surface atmosphere, since as Halstead (1958) stated, meteorologic conditions may differ more from the instrument shelter to the ground below than might exist between weather stations located 100 miles apart.

Since the evaporimeter we used could not be read during freezing weather, data are given only for the pasture period of May through October. The totals and the daily averages of those periods for the three years were: 983.8 and 5.3 mm, 1030.7 and 5.6 mm, and 1274.2 and 6.9 mm, respectively (Tables 1, 4, and 7). Potential evaporation was generally highest during the months of July and August, except in 1971 when the greatest amount was recorded in June. Information on actual evaporation is preferred to that of potential evaporation, but as Holmes and Watson (1967) pointed out, the measurement of actual evaporation is one of the most difficult of all water budget components to obtain. Formulae are available for calculation of potential evapotranspiration—evaporation and transpiration—(Hamon, 1961) for indications of the overall water balance at specific locations, but they are not used herein, since our project dealt with basic actual measurements only. Levine (1963), however, pointed out that one should carefully differentiate between actual and potential evapotranspiration. The actual evapotranspiration amount would be low indeed over arid desert soils, but the potential there would be extremely high. This would be realized under conditions of irrigation such as occurred in our study. Burman and Loudon (1968) showed that potential evapotranspiration was 20 percent greater for irrigated ryegrass-alfalfa pastures in Wyoming highlands than that for wheatgrass-alfalfa pastures but did not propose an explanation for this.

Potential evaporation recorded from our station compared to that at the Utah Lake Station near Lehi, Utah (Table 12), was 983.8 and 1047.5 mm, respectively, for May through October 1970; 971.7 and 1,062.75 mm for May through September 1971; and 1217.8 and 1,109.25 mm for May through September 1972. These comparisons suggest that the measured potential evaporation is similar throughout Utah Valley. However, since the wind totals for those periods at the Utah Lake Station (Table 13) were nearly twice that measured at our station, one would expect correspondingly higher potential evaporation measurements instead of such comparable levels as recorded. A partial explanation of this apparent discrepancy might relate to the fact that we used a recording instrument with an 18-cm-diameter evaporating pan, whereas the Utah Lake Station used a standard non-recording 120-cm-diameter evaporating pan. A reliable comparison between stations is further complicated in that the water level in our instrument was routinely within 1 cm of the surface of the pan, whereas it is not infrequent for water levels in large standard non-recording evaporimeters to be 10 to 15 cm below the surface. Such a difference would influence greatly the effect of wind movements upon the resultant evaporation recorded.

Daily cloud cover was only rated visually each morning and thus was the most subjective of all data taken during this study. Nevertheless, this showed a general pattern of approximately 40 to 60 percent average daily cover during the early and later parts of each year and 10 to 30 percent during the pasture season (Tables 1, 4, and 7). These data were accumulated in order to approximate the degree to which cloud cover might affect conditions at microenvironments, and in turn affect such factors as temperature and evaporation at that site. The amount of solar energy reaching the soil surface would naturally be the same on either irrigated or non-irrigated plots, providing the amount and type of vegetation were similar. Since vegetation is consistently less on non-irrigated pastures in such a region as central Utah, and since vegetation moderates the microclimate by providing a barrier between the soil and immediate atmosphere above (Caborn, 1973), one would generally expect warmer microenvironments on non-irrigated plots than on irrigated ones. The amount of solar energy available to warm the soil would depend further on such factors as the reflective properties of the soil (albedo), soil moisture, and the amount of water leaving the soil upward through evapotranspiration. Andersen, Levine, and Boatman

(1970) measured solar radiation during June through November with a recording pyrheliometer over pasture lands at Urbana, Illinois, in 1965 and 1966 and noted this decreased gradually in the fall, naturally coincident with the decrease in daily sunlight hours. The average daily gram calories per cm^2 measured at their station for 1965 and 1966 were highest in July for both years (848 and 542) and lowest in November (385 and 188) for all months during the periods indicated. To our knowledge, comparable field data are not available for other sites near central Utah. The immediate effect of cloud cover upon temperatures can readily be seen by examining Fig. 51 herein. With the exception of the impact of .3 mm precipitation on Thursday of that week indicated, all other jagged lines in the temperature curves are attributed mainly to changes in cloud cover. While this effect is most marked in the temperatures recorded at soil surface on bare ground, the decrease in temperature during heavy cloud cover is detectable on the recordings at soil surface under grass cover as well.

Soil moisture measurements were taken weekly during May through October of each year. The yearly averages of soil moisture content on a dry-weight basis for those months for the irrigated and non-irrigated plots respectively were 16.1 and 8.4 percent for 1970, 16.3 and 5.8 percent for 1971, and 8.1 and 3.8 percent for 1972 (Tables 1, 4, and 7). In general, the percent soil moisture varied in accordance with times of irrigation or rainy periods (Fig. 12, 13, and 14), with the difference between irrigated and non-irrigated plots most apparent during 1970 and 1971. During 1972, road and ditch construction adjacent to the weather station prevented irrigation of the pasture until mid-June, at which time the moisture level on the irrigated plot climbed to 15.0 percent from the preceding week's measurement of 1.4 percent. Irrigation continued sporadically after that time, and differences in soil moisture content between the two plots were not marked during August and September. Both levels then climbed simultaneously in October, when a total of 119.6 mm of rain was recorded.

The results obtained from our soil moisture measurements appeared more erratic during the three years than anticipated. This may have been due in part to our small soil sample size and to the non-homogeneity of the soil. We routinely collected only 20 to 30 g of soil, whereas Israelson et al. (1944) used 200 g samples from the 11 farms they studied in Utah County. Obviously, samples of that size cannot be re-

moved repeatedly from small plots such as we had available.

Of interest was the fact that the soil moisture showed an immediate decline within one to two days after each irrigation. This is undoubtedly due to evapotranspiration from the short grass cover on pasture lands as well as good soil permeability. Leonard et al. (1971) found that irrigation of soils once every 15 days under a red-pine forest in New York kept the soil moisture level near that measured shortly after snow melt in the spring. Crops grown on soils characteristic of Utah County, however, are commonly irrigated every 8 to 10 days maximum.

Andersen, Levine, and Boatman (1970) found that the actual soil moisture 2.5 cm below soil surface on pasture grasses at Illinois did not reach the permanent wilting point during 1965, when 1,069.9 mm of precipitation, somewhat evenly distributed throughout the year, were recorded; but that soil moisture did reach that level 27 consecutive days during 1966 when a total of 944.5 mm was recorded. During the second year, however, a five-week period in August and September received only a total of 12.2 mm rain at which time the moisture deficit occurred. Thus, we see that the distribution of precipitation during summer months is more influential in determining the micro-environmental conditions than is the total amount accumulated during any one month. In our study, the longest period of time without measureable precipitation during the summer months was 22 days during June and July in 1970, 35 days during June and July in 1971, and 23 days during May and June in 1972. Irrigation, if done routinely on well-managed pastures, compensates for these longer dry spells in arid regions such as central Utah and will effectively keep the soil moisture above levels detrimental to vegetative cover during the summer season.

Wind patterns measured at 1 m above the ground during the year were very erratic but usually totaled between 1,000 and 2,500 km per month over the three-year study period. The totals and the daily averages for each year were 19,315 and 52 km, 22,691 and 61 km, and 22,255 and 60 km, respectively (Tables 1, 4, and 7). The highest monthly total of 2,756 km was recorded during April 1972 and the lowest monthly total of 1,183 km during November 1972. Total wind movements during May through October for our station compared to that at Utah Lake Station near Lehi, Utah (Table 13), were 9,737 and 17,209 km for 1970, 11,604 and 17,304 km for 1971, and 10,716 and 15,950 km for 1972. Since the anemometer

at the Utah Lake station was only one-half the approximate height above ground level as was ours, one would expect an even greater difference in wind totals had both measurements been recorded at the same level. The reduced wind at our station, situated on the east bench of Utah Valley near the mountains, is undoubtedly due to topological features and the location of numerous buildings nearby. As discussed above, since the Utah Lake station had considerably more wind than was measured at our plots, one would expect correspondingly more potential evaporation at that site. The fact that this did not occur, however, is probably explained in part by the two dissimilar gauges used.

Andersen, Levine, and Boatman (1970) found that total wind movement at soil surface on pasture lands was only 14 percent of that measured 1 m above ground at the same location. The impact of this phenomenon on pasture microenvironments would be that of reduced evaporation therefrom compared to that actually measured by standard evaporation pans located above the microclimatic zone of the pasture vegetation.

DeVries and Birch (1961) found that wind velocities at 2 m were generally greater at stations located in irrigated pastures in Australia than on a non-irrigated plot 6 km distant from irrigated lands, but they felt that the difference was due largely to different topography in the two areas and to the roughness of the irrigated pastures. They pointed out that the effect of irrigated lands on meteorologic conditions of adjacent drylands would become negligible at a distance equal to the length covered by the wind over the irrigated area.

Temperature extremes measured in the standard weather shelter showed that the annual averages for the monthly maximum, minimum, and mean temperatures were 16.5, 1.9, and 9.2°C; 16.3, 1.3, and 8.8°C; and 17.3, 1.5, and 9.4°C for the three years, respectively (Tables 2, 5, and 8). The average monthly means agreed very closely with the corresponding figures of 9.6, 9.1, and 10.0°C recorded for the same years at the official KOVO weather station (Table 11).

As discussed above, data from weather shelters are a poor indication of conditions at or near soil surface level; however, such data do offer the advantage of having been taken under similar physical conditions as prescribed by the U.S. Weather Bureau. Presumably geographical areas with similar macroclimates would have similar microclimates if measured under comparable vegetative cover, topography, soil texture, and soil moisture. Slight differences in temperatures measured with the maximum

and minimum thermometers within the weather shelter in this project compared to those recorded with the hygrothermograph located at the same site can be explained in part by the difference in time lag before response of the different instruments. Mercury- or alcohol-filled thermometers have a time lag of approximately 3 minutes, whereas hygrothermographs require up to 30 minutes (Landsberg, 1941). Because of this, temperature trends recorded by the hygrothermograph would tend to level out sooner and would generally yield lower maximum and higher minimum temperatures.

Considerably more pertinent to the present study is the comparison of temperatures recorded at or near the soil surface on the irrigated part of the station with those on the non-irrigated plot. Since all leads for the 3-lead distance thermographs were not positioned until April 1970, comparative annual statistics for that year cannot be given. For 1971, the yearly averages for maximum, minimum, and mean temperatures recorded 5 cm beneath soil surface under grass cover were 11.3, 5.4, and 8.4°C in irrigated plots and 12.1, 5.9, and 9.0°C in non-irrigated plots (Table 5). Comparable figures for 1972 were 11.4, 5.0, and 8.2°C and 13.9, 6.8, and 10.4°C, respectively (Table 8). The yearly averages for maximum, minimum, and mean temperatures recorded at soil surface under grass cover were 13.8, 5.6, and 9.7°C in irrigated plots and 16.5, 4.6, and 10.6°C in non-irrigated plots for 1971 (Table 6). Comparable figures for 1972 were 15.8, 5.9, and 10.9°C and 20.7, 4.9, and 12.8°C, respectively (Table 9). The yearly averages for maximum, minimum, and mean temperatures recorded at soil surface on bare ground were 24.6, 1.2, and 12.9°C in irrigated plots and 31.8, 1.2, and 16.5°C in non-irrigated plots for 1971 (Table 6). Comparable figures for 1972 were 30.0, -0.2, and 14.9°C and 32.8, -2.7, and 15.0°C, respectively (Table 9). The annual maximum and annual minimum extremes for those years for each site where temperatures were measured were: weather shelter: 36.1 and -25.6°C for 1971 and 36.7 and -25.6°C for 1972; 5 cm beneath soil surface under grass cover: 29.0 and -4.0 (1971) and 28.0 and -7.0°C (1972) for the irrigated plot and 30.0 and -5.0 (1971) and 37.0 and -6.0°C (1972) for the non-irrigated plot; at soil surface under grass cover: 34.0 and -4.0 (1971) and 41.0 and -6.0°C (1972) for the irrigated plot and 43.0 and -6.0 (1971) and 54.0 and -8.0°C (1972) for the non-irrigated plot; and at soil surface on bare ground: 62.0 and -11.0 (1971) and 63.0 and -15.0°C (1972) for the irrigated

plot and 72.0 and -12.0 (1971) and 68.0 and -16.0°C (1972) for the non-irrigated plot.

In the study at Illinois, where comparable measurements on pasture lands were taken during 1966 (Andersen, Levine, and Boatman, 1970), the annual maximum, annual minimum, and average monthly mean for temperatures recorded in the weather shelter were 35.6, -24.4, and 8.0°C, respectively; beneath soil surface under 10 cm grass cover: 36.0, -10.0, and 12.9°C; at soil surface under 10 cm grass cover: 46.0, -10.0, and 14.1°C; and at soil surface on bare ground: 64.0, -21.5, and 15.3°C. From this comparison, it is evident that the annual extremes and yearly means are similar at both geographical locations, especially if temperatures recorded from the non-irrigated plot are compared with those on the pasture plot at Illinois with no irrigation. The difference in the yearly means for each site monitored for the last year reported for each project (1966 for Illinois and 1972 for Utah) were: 1.4°C in the weather shelter, 2.5°C at 5 cm beneath soil surface under grass cover, 1.3°C at soil surface under grass cover, and 0.3°C at soil surface on bare ground.

The only temperatures routinely measured at or near soil surface in Utah of which we are aware are those recorded 10 cm beneath barren soil at Salt Lake City (Climatological Data, Utah, 1970, 1971, 1972). The annual maximum, annual minimum, and average mean at that site for 1970 were 27.8, -1.7, and 10.7°C, respectively; 33.9, -2.8, and 11.2°C for 1971; and 30.0, -1.7, and 12.4°C for 1972 (Table 14). Average annual means at that station compared to the average annual mean of the temperature 5 cm beneath soil surface under grass cover at our non-irrigated plot for the two years, where comparisons could be made, thus differed by 2.2°C for 1971 and 2.0°C for 1972. If compared, however, to means tabulated from measurements made at soil surface under grass cover, the difference was only 0.6°C for 1971 and 0.4°C for 1972.

DeVries and Birch (1961) noted that temperatures 5 cm beneath the surface in irrigated stations in Australia were approximately 10°C cooler in summer than at their non-irrigated plot. They attributed this partly to the cooling effect of evaporation and partly to the shading from the more dense vegetation on the irrigated stations. Watts (1973) noted that temperatures 5 cm beneath soil surface on bare ground in England reached a maximum earlier in the day and then decreased more quickly at night than did those temperatures measured at comparable depths under black polythene or glass cover. Also, the bare ground had to be irrigated six

times as often as the covered plots. Of particular interest was the fact that he was able to closely correlate growth measurements in plant cover with mean daily temperatures at 5 cm depth. This suggests that this level would be a good one to monitor for all meteorologic projects directly or indirectly related to research on plant or animal productivity.

Leonard et al. (1971) noted that the impact of irrigation on soil temperatures was influenced considerably by the temperature of the irrigating water. In their study in New York with pine forest cover, temperatures of irrigation water ranging from 0 to 5.5°C above that of the soil surface brought about a subsequent corresponding increase in the soil temperatures. In our study, the temperature of the irrigation water was invariably lower than that of the soil surface. The reflection of this finding upon the soil temperature profile can readily be seen in Fig. 51, which shows a gradual drop of about 5°C in the temperature recorded 5 cm beneath soil surface under grass cover, an immediate drop of about 10°C in the temperature at soil surface under grass cover, and a corresponding decrease of about 30°C at soil surface on bare ground.

When the temperature data for this project are examined on a daily basis (Fig. 33-51), the effect of irrigation on these temperatures can readily be seen. Almost without exception, the maximum daily temperatures on the irrigated plots during the pasture season were cooler than on the non-irrigated plots. This difference was least demonstrable with the measurements taken 5 cm beneath soil surface under grass cover (Fig. 33, 34, and 35), next most noticeable on the soil surface measurements under grass cover (Figs. 39, 40, and 41) and most noticeable with the recording of the maximum levels on the bare soil surface plot (Fig. 45, 46, and 47). The difference in minimum daily temperatures was not nearly so obvious, however, as noted from the same figures referred to above. Because of these similarities in minimum temperatures, the compared means of the daily temperatures on the irrigated and non-irrigated plots for each of the three sites and for each of the three years (Fig. 36, 42, and 48 for 1970; Fig. 37, 43, and 49 for 1971; and Fig. 38, 44, and 50 for 1972) are nearly the same. Although mean comparisons may be helpful for general

conclusions, the fact that they automatically eliminate extremes and ranges makes them difficult to interpret or use meaningfully. They are included herein only to show how similar these means were on the irrigated compared to the non-irrigated plot. Compared means of the three different sites or compared means for the three different years were not graphed, although the monthly averages of these data can be found in the annual summaries.

Even though daily observations were made on the presence or absence of dew or frost each morning in the present study, such measurements were somewhat subjective, especially during summer rainy periods or when snow covered the ground in the winter. Because of these facts, and since observations were made only for the irrigated section of the station, the data are neither graphed nor recorded herein. However, the mornings with detectable dew or frost are noted on the daily computer printouts which are available if desired. Under most circumstances dew was present on the pasture grass whenever the temperature at soil surface under grass cover was above freezing and when the relative humidity measured in the weather shelter reached 98 to 100 percent during the night. Frost naturally occurred with temperatures in the microclimate below freezing and when relative humidity was at maximum.

Andersen, Levine, and Boatman (1970) found that moisture from dew remained on pasture grass in Illinois for a daily average of 5.1 to 11.8 hours for months between May and October, when such measurements were recorded in their study. Daily totals were high even during warm summer days with relatively infrequent precipitation.

Even though the presence of dew on the pasture grasses would be an additional source of moisture for all biological organisms in that microenvironment, such moisture alone cannot prevent the ultimate drying of the vegetation later on during the day. Thus, as Andersen, Levine, and Boatman (1970) pointed out, the alternate hydration and dehydration of such organisms as nematode larvae may be more detrimental to their survival in microhabitats than that of continual desiccation. Additional studies are needed on the impact of moisture deficits upon biological organisms in microenvironments.

CONCLUSIONS

Meteorologic measurements obtained during the three-year study showed a marked impact of irrigation on the moisture and temperature

profiles of experimental pasture plots. Irrigation not only lowers the soil temperature (due to evaporation and to the fact that the irrigating

water used was invariably cooler than the soil on the plots) but also cools the air immediately above the soil surface. It also brings about a more dense vegetative cover with a resultant increase of shade, thereby contributing to increased evaporation and transpiration (evapotranspiration) from the additional surface area of the cover.

The overall moisture balance in the microclimate is thus dependent upon the accumulated precipitation and irrigation, contrasted with that lost to the macroclimate through evapotranspiration. This loss is influenced by the combined effects of the type and amount of vegetative cover, wind movements within or immediately above the grass, moisture content of the air, and the temperature at or near the soil surface zone. The temperature of the microclimate is dependent upon the solar energy reaching the surface, the albedo or reflective power of the soil and vegetative cover, the soil texture, and amount of soil moisture. It is therefore evident that irrigation influences directly or indirectly nearly all factors in the pasture microclimate. These interact in a complex manner to bring about favorable environments for increased plant productivity and optimum conditions for development and survival of biological organisms which inhabit that zone.

Irrigation was extremely sporadic in our study, but, as mentioned above, the timing of this was not under our control. A much better method would have been to use sprinkling irrigation, so that not only the timing but also the amount of water added could have been controlled. At the time the project was started, however, only flood irrigation was available and was therefore used throughout the study. Nevertheless, flood irrigation is considerably more common than sprinkling in this area, and irrigation intervals under natural conditions are also frequently sporadic.

Additional conclusions of this study relate to each of the meteorologic measurements taken. The precipitation patterns differed markedly during each year, which is typical of any semi-arid region, but nevertheless showed the general dryness associated with the pasture season in Utah. The fact that the long-term averages of precipitation for Provo (Table 10) are less than 25 mm of rainfall during June, July, August, and September illustrates the necessity for irrigation of all cultivated croplands in this area. Other forms of precipitation, such as snow or dew, also have an impact upon the pasture microenvironment; but with respect to plant productivity or creation of optimum environ-

ments for living organisms, they are not nearly as important as rain or irrigation of cultivated croplands or pastures in Utah. Snow cover moderates temperatures considerably at ground level in the winter, and dew adds additional moisture during the pasture season which could provide the film of water necessary for vertical migratory movements on the vegetation by such organisms as nematode larvae. Even though dew may represent a helpful addition of moisture during the pasture season for increased plant productivity, its impact on living organisms in the microclimatic zone is not clear, since alternating hydration and dehydration of organisms in that environment have been shown to be more detrimental to development of organisms in that microhabitat than that of sustained desiccation. Additional research is needed on the effect of moisture deficits on organisms inhabiting pasture microenvironments.

Relative humidity measurements were generally near maximum at least once during each 24-hour period even in warm weather and periods of infrequent rains. Since the small non-irrigated plot was established in the center of the irrigated part of the station, no measurements of relative humidity over non-irrigated areas were obtained. Such comparison would only be possible if measurements could be taken from large fields, and then one would have difficulty locating two separate areas with similar topography, yet far enough removed where wind movements would not influence the readings. Also, no measurements were obtained on relative humidity from the pasture microclimate per se, since, to our knowledge, the only devices capable of measuring relative humidity from such an environment cannot withstand saturation and thus cannot be used in extended field trials such as this one.

Potential evaporation was recorded only from the irrigated part of our station, since, as discussed above, the non-irrigated plot was within the irrigated area and was too small to permit a valid measurement from that section only. The level naturally inclined during the early part of the pasture season, reached its peak during the warmest months, and declined gradually thereafter. Temperature and wind were the most influential factors on this measurement. Burying the recording part of the evaporimeter into the ground so that the top of the evaporating pan would be level with the top of the grass cover would yield a measurement of potential evaporation more indicative of that occurring in the microenvironment. Such an arrangement could be used with sprinkling, but with the irrigation system we had available, the instrument

would likely have been flooded each time irrigation occurred.

The percent of cloud cover each morning was undoubtedly the most subjective of all data collected but nevertheless indicated trends during the year. The main drawback of this procedure was that it did not reflect subsequent changes during the day. Even though a rough indication of daily cloud cover was noticeable on the temperature curve recorded for one week on bare ground (Fig. 51), all other daily tracings of that measurement are not available to the reader. A recording pyrliometer would be advisable for such studies in the future.

Soil moisture samples gave extremely erratic results, probably relating in part to the small sample size taken. However, the compared moisture percentages on the irrigated and non-irrigated plots gave a good indication of the importance of irrigation to this geographical region. Gravimetric measurements for determination of soil moisture are inferior to those available with more costly equipment but nevertheless give a simplified indication of the moisture present. Larger or duplicate samples would have helped considerably, as would have conversion to volumetric water content values to help smooth out soil non-homogeneity.

Wind measurements were recorded only at 1 m height and gave only a general indication of air movements in grass. We were unable to follow the method used by Andersen, Levine, and Boatman (1970) with an anemometer placed at soil surface level as well, since with flood irrigation the totalizing mechanism of the anemometer would have been flooded each time irrigation occurred. Such a measurement could be included, however, with a comparable project done with sprinkling irrigation.

Temperatures recorded in the present project were the most complete of all measurements included herein. Weather shelter temperatures were included only for comparison of the macroclimate with the pasture microclimate and for

standardization of this project with such temperatures recorded in other geographical areas. Since temperatures in weather shelters are taken in a consistent manner as described by the U.S. Weather Bureau, measurements taken of macro- and microclimates at one site should provide a fairly accurate indication of the microclimate at a second comparable macroclimatic site, providing similar conditions of soil and vegetative cover existed. The average monthly maximum temperatures recorded in the weather shelter were generally higher and the average monthly minimum temperatures generally lower than those recorded on the irrigated plot 5 cm beneath soil surface or at soil surface under grass cover. However, the grand means of the monthly means for those measurements were quite comparable. Measurements on bare irrigated ground showed greater temperature extremes than those under grass cover or those recorded from the weather shelter. Also, those temperatures recorded on non-irrigated plots on bare ground showed extremes greater than those on irrigated plots. This was due in part to the fact that dry bare soil on non-irrigated surfaces loses more heat by outgoing radiation at night than those where the soil is darker due to the additional moisture from irrigation. Moist soils also have a higher heat capacity. Temperatures recorded 5 cm under grass cover were dampened in all effects and were influenced least by those factors which contribute to the overall heat and moisture balance of the pasture microenvironment.

The computer programs designed for this project proved to be very helpful in assembling and tabulating all data collected. Work is now in progress to develop additional programs for computerized construction and plotting of graphs of all daily observations after they are once columnized and keypunched on IBM cards. The successful completion of such programs will greatly facilitate the complete assimilation of all meteorologic data measured in future years.

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**A TAXONOMIC STUDY OF THE
WESTERN COLLARED LIZARDS,
CROTAPHYTUS COLLARIS AND
CROTAPHYTUS INSULARIS**

by

Nathan M. Smith
and
Wilmer W. Tanner



**BIOLOGICAL SERIES — VOLUME XIX, NUMBER 4
APRIL 1974/ISSN 0068-1024**

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A Taxonomic Study of the Western Collared Lizards, *Crotaphytus collaris* and *Crotaphytus insularis*

by

Nathan M. Smith¹ and Wilmer W. Tanner²

INTRODUCTION

The range of the Western Collared Lizard *Crotaphytus collaris baileyi* Stejneger (1890) as formerly construed included northern Mexico, the Baja California Peninsula, the Islands Angel de la Guarda and Tiburon in the Gulf of California, and parts of the seven western states of Arizona, California, Colorado, Idaho, Nevada, New Mexico, and Utah (Stejneger and Barbour, 1917). Within this vast area the geophysical features vary considerably and may serve as population barriers.

Although geophysical variation is broad throughout the range, niche requirements are narrow. The collared lizards require boulders for basking, lookouts, and shelter, and occupy mountain slopes, canyons, rocky gullies and boulder-strewn alluvial fans where vegetation is sparse (Stebbins, 1966). The many mountain ranges oriented on north-south axes have provided favorable conditions for extensive distribution of the collared lizard in the Great Basin, Arizona-Sonoran Desert, and Baja California Peninsula. Narrow niche requirements cause collared lizards to form demes with valleys between the mountain ranges acting as isolating barriers. The Imperial Valley, Gran Desierto of southern California and northwestern Mexico, is an important potential barrier between populations of the Great Basin and the Baja California Peninsula. The island populations in the Gulf of California were probably members of the mainland population in late Miocene or early Pliocene (Anderson, 1950), with Isla Tiburon still part of the mainland as recently as 10,000 years ago (Lawlor, 1971). This possible geophysical arrangement has been discussed by Tanner (1966) to explain the distribution of the night snakes in and around the Gulf of California. Portions of the Great Basin, which, according to Wells and Jorgensen (1964) were significantly cooler (and perhaps moister) 8,000 to 40,000 years ago, have only become suitable

habitat for the collared lizard since the Wisconsinian.

Systematists recognizing the potential isolating factors within the range originally attributed to *C. c. baileyi* have described *C. c. auriceps* Fitch and Tanner (1951) from the Upper Colorado River Basin, and *C. c. fuscus* Ingram and Tanner (1971) from the Chihuahuan Desert. Also, two insular forms, *C. insularis* Van Denburgh and Slevin (1921) and *C. dickersonae* Schmidt (1922), although given species rank, have long been recognized as closely related to *C. collaris* Say (Burt, 1928; Fitch and Tanner, 1951; Ingram and Tanner, 1971). Allen (1933) referred to the collared lizards from Tiburon Island as *C. c. dickersonae*.

Collecting trips were made to determine the geographic limits of the several populations and to gather live specimens for electrophoretic analysis of blood proteins. As a result, two new subspecies of *Crotaphytus* were named (Smith and Tanner, 1972). The present paper brings together the basic techniques and data used with an analysis of the characteristics of each population of *C. collaris* and *C. insularis*.

In this comparative taxonomic study multivariate analysis techniques are utilized (Ingram and Tanner, 1971) to study general external morphology and comparative cranial morphology. Disc gel electrophoresis, which was used to compare populations of *C. c. baileyi*, *C. c. auriceps*, and *C. c. bicinctores* is not included in this report because of the limited scope of the material available, but the data are available from the authors upon request. An analysis is made of the western-*collaris* complex and its relationship to *C. c. auriceps*, *C. c. baileyi*, and *C. c. fuscus*. The Great Plains population, *C. c. collaris*, is not included, however; a cursory analysis indicates that it also may be a heterogeneous group, and a study of its relationship is planned.

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REVIEW OF LITERATURE

An adequate review of the literature up to 1971 which is pertinent to this study was presented by Ingram and Tanner (1971:1-2) and will not be repeated here.

In 1971, Ingram and Tanner reaffirmed *C. c. auriceps* and defined the following distinguishing characteristics of *C. c. baileyi*: (1) the body is dark green; (2) yellow, if present on the head, does not extend posteriorly beyond the supraorbital semicircles or ventrally to the throat; (3) it has fewer fused interorbitals and a greater number of supralabials and loreal-lorilabials series than *C. c. collaris*. Ingram and Tanner then defined *C. c. fuscus* as the population found in the Chihuahuan Desert. They indicated *C. c. fuscus* most closely resembles *C. c. baileyi* and is distinguished from it by a combination of external morphological characters, the sum of which gives good distinction. In addition, *C. c. fuscus* has a brown body dorsum with no trace of green and the head is a light to cream color, with no trace of yellow.

Smith and Tanner (1972) designated the Great Basin collared lizard as *C. c. bicinctores*. It can be distinguished from *C. c. baileyi* and other members of the *collaris* complex by (1) fewer scales and fewer spots in the dorsal separation of the first collar, (2) greater number of enlarged median internasals, (3) second collar not extending onto the forearm, (4) greater number of scales from interparietal eye to the anterior edge of first collar, and (5) more extensive black pigmentation of the ventral groin. *C. c. bicinctores* is easily distinguished from the Baja California population (*C. i. vestigium*) by its collars and dorsal pattern. It is distinguished from *C. c. dickersonae* by its brown body and dorsal pattern (Fig. 1).

In addition, Smith and Tanner (1972) indicated a close relationship for the populations from Angel de la Guarda Island, Gulf of California, Mexico, and the Baja California Peninsula. The Angel Island population was designated *C. i. insularis*, and the population inhabiting the area north and west of Palm Springs, Riverside County, California, and south from there along the eastern slopes of the mountains into Baja California Sur, Mexico, was designated as *C. i. vestigium*. Characteristics of *C. i. vestigium* which distinguish it from *C. i. insularis* are fewer subdigital toe lamellae on the second and fourth toes, a larger second collar/svl index, and a smaller dorsal separation of both the first and second collars.

Axtell (1972), after indicating intergradation

between *C. c. bicinctores* and *C. c. baileyi*, chose to designate *bicinctores* as *C. insularis bicinctores*. Axtell's choice of designation is predicated on the basis his evidence indicates little genetic introgression. He lists similarities for *bicinctores* and *c. insularis* as a complete dark ventral collar, similar gular markings, compressed tail, extensive dark abdomino-groin pigmentation, small dorsal granules, and no greenish coloration.

A brief taxonomic history of *C. c. baileyi* and the insular collared lizard populations from Angel de la Guarda and Tiburon islands are listed with their synonymies as follows:

Crotaphytus collaris baileyi Stejneger

Crotaphytus baileyi Stejneger, 1890, N. Amer. Fauna, 3:103 (Type locality: Painted Desert, Desert of the Little Colorado R., Arizona; U.S. Nat. Mus.).

Crotaphytus collaris baileyi: Stone and Rehn, 1903, Proc. Acad. Nat. Sci. Phila., 55:30.

Crotaphytus collaris dickersonae Schmidt

Crotaphytus dickersonae Schmidt, 1922, Bull. Amer. Mus. Nat. Hist., 46:638 (Type locality: Tiburon Island, Sonora, Mexico; U.S. Nat. Mus.); Smith and Taylor, 1950, Bull. U.S. Nat. Mus., 199:93.

Crotaphytus collaris dickersonae: Allen, 1933, Occ. Pap. Mus. Zool. Univ. Mich., 259:7; Smith and Tanner, 1972, Great Basin Nat., 32:26.

Crotaphytus collaris baileyi: Stone and Rehn, 1903, Proc. Acad. Nat. Sci. Phila., 55:30.

Crotaphytus collaris auriceps Fitch and Tanner

Crotaphytus collaris auriceps Fitch and Tanner, 1951, Trans. Kans. Acad. Sci., 54(4):553 (Type locality: three and one-half miles north-northeast of Dewey Bridge, Grand Co., Utah; Kans. Mus. Nat. Hist.).

Crotaphytus collaris baileyi: Stone and Rehn, 1903, Proc. Acad. Nat. Sci. Phila., 55:30.

Crotaphytus collaris fuscus Ingram and Tanner

Crotaphytus collaris fuscus Ingram and Tanner, 1971, Brigham Young Univ. Sci. Bull. Biol. Ser., 13(2):23-24 (Type locality: six and one-half miles north and one and one-half miles west of Chihuahua City, Chihuahua, Mexico; Brigham Young Univ. Herpet. Mus.).

Crotaphytus collaris baileyi: Stone and Rehn, 1903, Proc. Acad. Nat. Sci. Phila., 55:30.

Crotaphytus collaris bicinctores
Smith and Tanner

Crotaphytus collaris bicinctores Smith and Tanner, 1972, Great Basin Nat., 32:27-29 (Type locality: Mercury Pass, Nevada Test Site, Nye Co., Nevada; Brigham Young Univ. Herpet. Mus.).

Crotaphytus collaris baileyi: Stone and Rehn, 1903, Proc. Acad. Nat. Sci. Phila., 55:30.

Crotaphytus insularis bicinctores: Axtell, 1972, Copeia, No. 4:721.

Crotaphytus insularis insularis
Van Denburgh and Slevin

Crotaphytus insularis Van Denburgh and Slevin,

1921, Proc. Calif. Acad. Sci., ser. 4, vol. 11:96 (Type locality: Angel de la Guarda Island, Baja California, Mexico; Calif. Acad. Sci.).

Crotaphytus insularis insularis: Smith and Tanner, 1972, Great Basin Nat., 32:27.

Crotaphytus collaris baileyi: Stone and Rehn, 1903, Proc. Acad. Nat. Sci. Phila., 55:30.

Crotaphytus insularis vestigium
Smith and Tanner

Crotaphytus insularis vestigium Smith and Tanner, 1972, Great Basin Nat., 32:27 (Type locality: Guadalupe Canyon, Juarez Mountains, Baja California, Mexico; Brigham Young Univ. Herpet. Mus.).

Crotaphytus collaris baileyi: Stone and Rehn, 1903, Proc. Acad. Nat. Sci. Phila., 55:30.

MATERIALS AND METHODS

External Morphology

Selection and Gathering of Material

Materials examined are from four principle sources: (1) the collection at the Brigham Young University Herpetological Museum; (2) materials examined at the California Academy of Sciences, Los Angeles County Museum, San Diego Society of Natural History, California State College at Long Beach, University of California at Berkeley, and the University of Arizona; (3) materials loaned from the institutions listed in the acknowledgments; and (4) live specimens collected and color photographed in the field with 35mm Agfachrome.

Several collecting trips, supported by an NDEA Educational Allowance, were made between 1969-1971. The first trip, in June 1969, was an extensive one, covering two weeks and 4,000 miles. During this period, specimens were collected from southwestern Colorado, western New Mexico to the Mexican border, most of Arizona, southeastern California, and southwestern Utah. During the last three weeks in May 1970, an extensive collecting trip was made to southern Nevada, southern California to the Mexican border, and most of Arizona. Specimens were taken from the Oatman-Kingman, Arizona, area, which is near an area of confirmed intergradation for *C. c. bicinctores* and *C. c. baileyi* (Axtell, 1972). In July 1970, specimens were collected through central and southeastern Utah. Specimens were taken from both

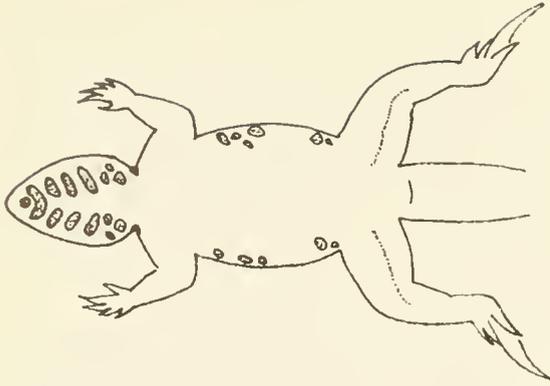
the east and west sides of the Colorado River in the area of Moab, Utah.

The fourth and final collecting trip was to Tiburon Island, Gulf of California, Mexico, during the first week in April 1971. A number of collared lizards (14) were caught and photographed on the island and three were caught on the mainland opposite the island. All specimens collected during these four trips are deposited in the Brigham Young University Herpetological Museum. A series from the Nevada Test Site (Research Grant Number AT(11-1) 1496, between the U.S. Atomic Energy Commission and Brigham Young University) and from Pyramid Lake, Nevada, were obtained by the junior author. Also, two trips were made by him to the Palm Springs area, and specimens were taken in Chino Canyon and east of Thousand Palms, Riverside County, California.

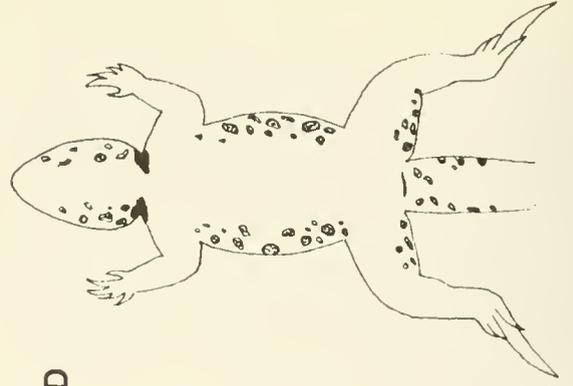
Following the procedure used by Ingram and Tanner (1971), collared lizards with a snout-vent length less than 80 mm or that were damaged were not included in the computer analysis portion of this study.

The collared lizards examined in this study are as follows:

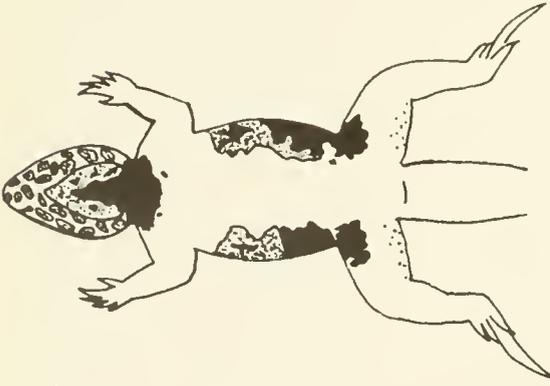
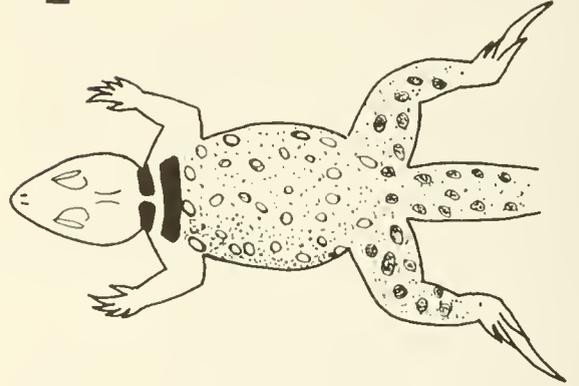
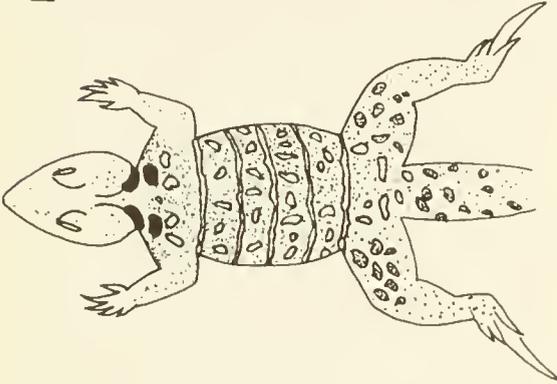
ARIZONA: Apache Co., BYU 497; LACM 16895; UIMNH 7524; USNM 38056. Coconino Co., CU 30081; SDSNH 12772-76; UIMNH 62445, 74789-92, 6543; USNM 45025-26, 60111, 60113, 60115, 60117-20, 86942; UU 217, 3006-08. Gila Co., UIMNH 74797-98. Graham Co., UIMNH 82348-50. Mohave Co., BYU 32104;



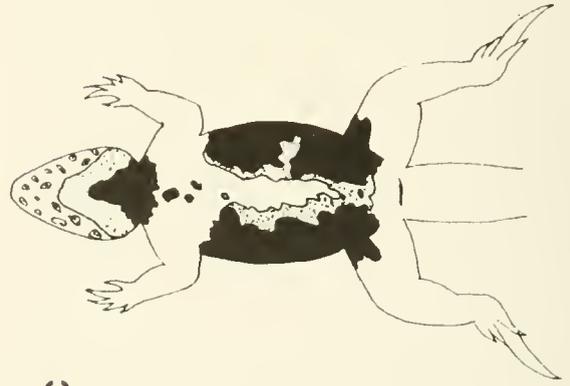
B



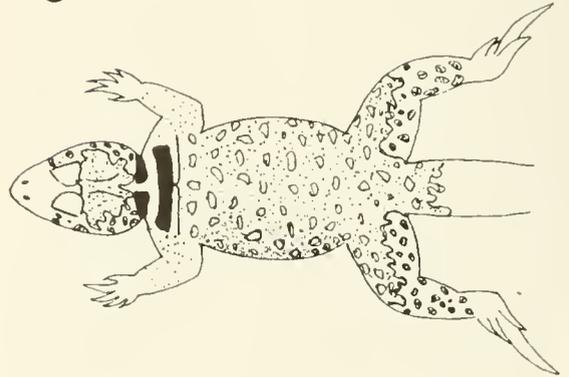
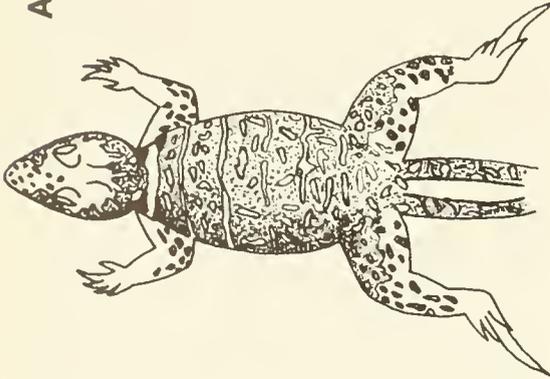
D



A



C



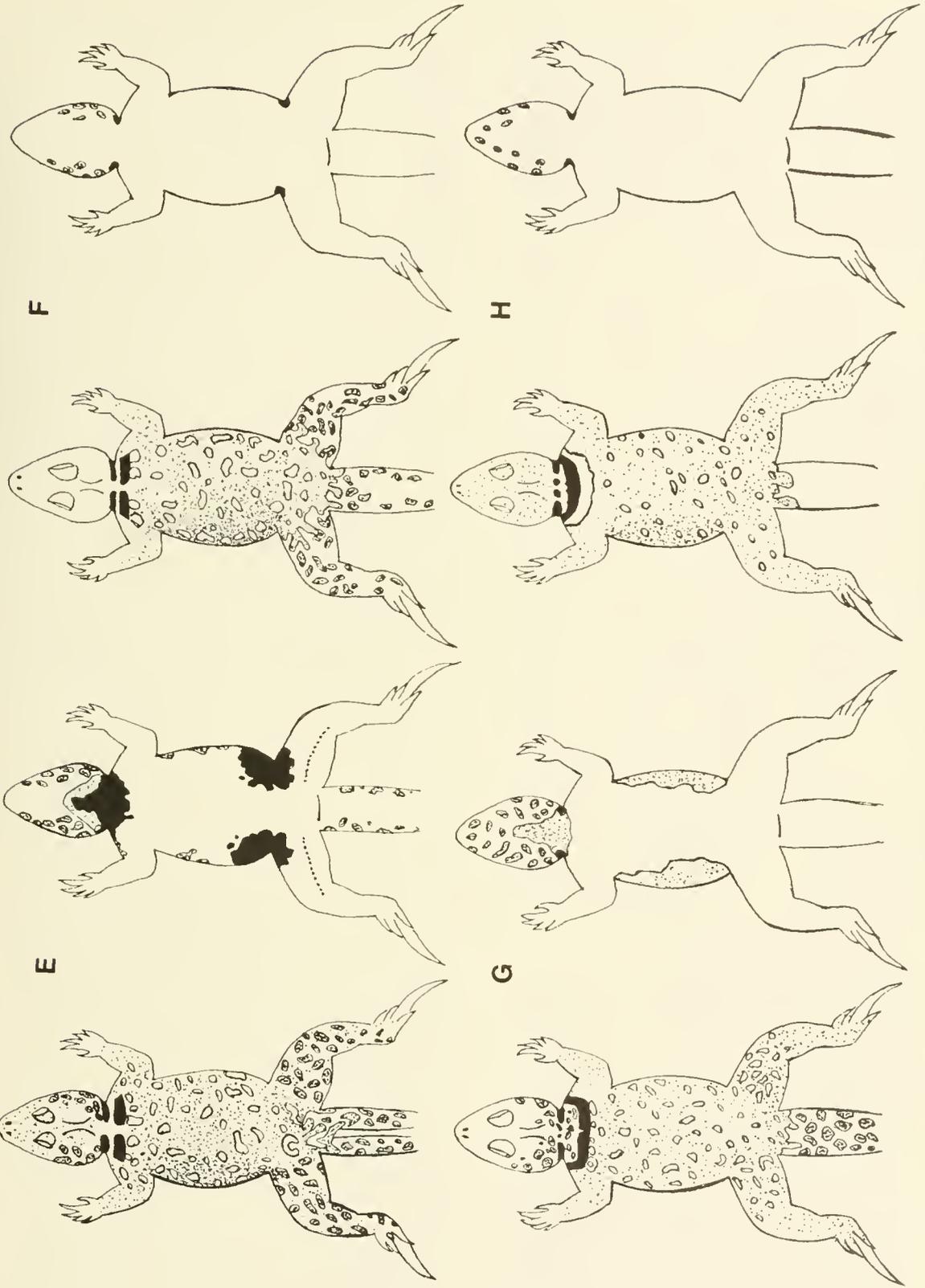


Fig. 1. Pattern characteristics: (A and B) male and female Baja types which are similar to specimens from Angel Island, (C and D) male and female Great Basin types, (E and F) male and female *dickersonae* types, (G and H) male and female *collaris*-complex types.

UIMNH 62446, 74785; USNM 86941, 115675-76; SDSNH 5291, 17302, 31769, 31937, LMK 31768. Navajo Co., UU 1603. Pima Co., CAS 81420; LACM 3983, 5899; UAZ 636, 666, 669-670, 672, 1509, 1511, 19986, 28625, 34364, 35539, 35715; Santa Cruz Co., UAZ 11241; Yavapai Co., BYU 2423; USNM 11860, 15689-90, 15992; UIMNH 74776. Yuma Co., BYU 2437, 32097-98, 32100-03; CAS-SU 15873, 18299; LACM 16892-93; SDSNH 16731, 17602, 33301; UAZ 623-27, 643-44, 680-81, 35673, 35676, 35714; UIMNH 74793, 74847.

CALIFORNIA: Imperial Co., BYU 33321; CAS-SU 13843; LACM 16898, 37783; SDSNH 11791, 12244-45, 13908-09, 29697-98, 38310. Inyo Co., BYU 40934-35; CAS 22153-54, 65216, 65221-22, 65224, 65481-82, 65515-17, 65581, 65585, 65636, 65662, 65681, 84241, 89621, 89626-30, 89633-34; CAS-SU 22072-73; LACM 26824, 36667, 36670; SDSNH 15878-79. Kern Co., BYU 31948; CAS 111006. Los Angeles Co., CSCLB 2747-51; LACM 16870, 26811, 26814, 63187-90; SDSNH 2834-36, 19481-82. Mono Co., CAS 84962. Riverside Co., BYU 2422, 2429-30, 2432, 2435, 2438, 31983, 32099; CAS-SU 22711; CSCLB 2744, RDK 600430-1, RDK 600611-1, RBL 600327-2, JAN 700510-2, VAP 660513-4; LACM 16873, 16875-76, 16885-89, 26821-22, 52889-90; SDSNH 20698-99, 39751; UCMVZ 1, 210-11, 231, 243, 74609-11, 76737, 41089, 51850-51, 71723. San Bernardino Co., BYU 33320; CAS 5245, 36268, 42185, 42785-91; CSCLB 2720-21, 2735-36, 2738-39, RBL 600529-5, RCS 700412-12; LACM 63179-80, 63182-83, 63188; SDSNH 2490, 5874, 11087, LMK 20888, 29664, 35703, 39874; UCMVZ 5368, 31634, 52486. San Diego Co., BYU 3994; CAS 62875, 64368; CAS-SU 7930; SDSNH 1687, 4701, 11088, 11958, 12551, 13250, 18591-92, 22327.

COLORADO: Los Animas Co., CU 1292, 2939. Mesa Co., BYU 1134. San Miguel Co., CU 4448, 4451, 4453, 4456, 4458.

IDAHO: Ada Co., BYU 507; CAS 64173. Butte Co., BYU 30772. Owyhee Co., BYU 2834; CAS 55247-48, 55253, 64163-64; NNC 7, 28; SDSNH 1444-45.

KANSAS: Montgomery Co., BYU 22167. Wilson Co., KU 41, 48-50, 54.

MEXICO: Isla Angel de la Guarda, CAS 49151, 50873-76, 50878-79, 86754-55, 86783-84; CAS-SU 21948, 22712; LACM 4001-02, 9854-55; SDSNH 46001; UCMVZ 96635-37. Baja California, CAS 11545-46, 14000-01, 17048, 18822, 19124-26; CSCLB LVR 670619-1, LVR670619-2, KAW 700324-6; CU 45855-61; LACM 16994, 16996-99, 63167-73, 63175-78; SDSNH 17052, 19788-92, 24392, 30107-11, 37815, 41612, 52950-

51, 52999; UCMVZ 9590, 51140, 73568. Chihuahua, BYU 13383-86, 13410-11, 13736, 14211, 15184, 16969-76, 17010, 17014; UCMVZ 70704. Sonora, BYU 2425, 39993, 39995, 40930-31; CAS 12768-70, 12770, 12772-77, 104467; CU 44201-03; CSCLB 2730, 2752-55, 2757, 2759-61, 2763-64, 2959; LACM 52882, 52886, 88798; SDSNH CRM117, 35917-19, 43254, 44063; UAZ 694, 697-710, 1513-14, 4634, 9625-26, 10248, 10597, 12114, 16578, 20144, 20255, 28072, 28662, 30226, 31391, 31482, 33781; UCMVZ 10163; USNM 2694. Isla del Tiburon, BYU 2426, 2433, 2443, 3163-65, 3167-69, 3172; CAS 14002-12, 53263-64; SDSNH 46003-06, 50665. Zacatecas, CAS 95961.

NEVADA: Clark Co., BYU 461, 40932-33; CAS-SU 20083-85. Churchill Co., LACM 26839-43. Lincoln Co., CAS 37025-36, 37029-31, 37033, 37035-36, 37038-39, 37041-42, 37044, 37046, 37058-59. Lyon Co., CAS 20576-80, 20583-85, 22660, 22662-64, 22690, 22705-06; LACM 26838. Nye Co., BYU 2418, 2424, 17275, 18815-16, 22189-96, 23629-30, 23882-83, 30088, 30587; CAS 37514, 37693-95, 37697, 37699-710, 37716, 37721; CAS-SU 20086-93, 20096. Washoe Co., BYU 2401, 2442, 3115; CAS 21487, 21489-90, 21492-94, 21496, 21498-500, 21505-06; SDSNH 38311, 38676-77.

NEW MEXICO: Chaves Co., LACM 3974-75. Dona Ana Co., USNM 22268, 25423. Lincoln Co., LACM 16990. Luna Co., BYU 31940, 31944, 32121. Quay Co., USNM 44940. Sierra Co., LACM 16992.

OKLAHOMA: Carter Co., BYU 500, 1574.

OREGON: Malheur Co., UAZ 21124.

TEXAS: El Paso Co., USNM 59351; UTEP 52, 55, 57. Garza Co., CU 32277. Jeff Davis Co., UAZ 35145. Randall Co., CU 13554-56. Roberts Co., USNM 32866. Stephens Co., BYU 13117.

UTAH: Beaver Co., BYU 12715. Emery Co., BYU 16496, 16774, 20089-90. Garfield Co., BYU 11740-41, 12699-701, 31882-83; UU 3329. Grand Co., BYU 2421, 2434, 3114, 12854-55. Kane Co., BYU 2732, 11331, 11384, 11386b, 14660, 14894-96, 14898-902, 18921, 21259-60, 21262-63, 40936-39; UU 1449. Millard Co., BYU 445, 447-48, 8753, 8755, 8883, 12946, 21000-02, 21703; UU 2802. San Juan Co., BYU 2419, 18335, 31945-46, 31951, 31981, 32088. Tooele Co., BYU 4305-06, 14818, 14820-21. Utah Co., BYU 552, 1455, 1630-31, 2844, 3116, 13041, 14689, 16602, 22129, 30382; UU 2038. Washington Co., BYU 446, 8754, 11324, 11386a, 12190, 12875.

SPECIMENS SEEN—NOT USED IN THE COMPUTER ANALYSIS: CAS 14002-03, 21608, 39114-15, 64966; CAS-SU 19125; LACM 8798-99, 16993, 36666, 52885-86, 63184; SDSNH

40074, 40139; UIMNH 74801; UU 122, 124, 33597.

Statistical Methods

After an initial examination of the museum specimens available at Brigham Young University and a review of the literature with its descriptions of the collared lizards from Tiburon and Angel de la Guardia Islands, it was hypothesized that there are eight distinct collared lizard populations in the Great Basin, the Baja California Peninsula, Tiburon and Angel islands, the Upper Colorado River Basin, Central Arizona, Chihuahua, Mexico, and the Great Plains.

The methods of analyses employed in this study, with minor exceptions, are those of Ingram and Tanner (1971:4). In step 2, we were limited to 17 and 13 specimens, respectively, for Angel and Tiburon islands which made a total sample of 150 individuals. In step 4, eight clusters were formed. Also we omitted step 5 and the color and pattern analysis.

The terminology for taxonomic characters is that used by Ingram and Tanner (1971:5).

The characters used in the evaluation, with their numbers, are as follows: (1) tail length/hind-leg length; (2) tail length/snout-vent length; (3) snout-vent length; (4) internasal scales; (5) number of fused interorbital scales; (6) fronto-parietal scales; (7) scales from the union of the posterior canthal and subocular to the supralabial; (8) supralabial scales; (9) infralabial contacts postmental; (10) gular scale rows; (11) number of enlarged internasals; (12) scales from rostral to interparietal; (13) dorsal scales from interparietal to anterior edge of first collar; (14) dorsal scales from the anterior edge of first collar to posterior edge of second collar; (15) total dorsal scales; (16) total ventral scales; (17) dorsal separation of the first collar; (18) dorsal separation of the second collar; (19) number of spots within the dorsal separation of first collar; (20) second collar length/snout-vent length; (21) subdigital lamellae of right hind foot, second toe; (22) fourth toe subdigital lamellae; (23) fifth toe subdigital lamellae; (24) femoral pores, right side; (25) second collar extends onto the upper arm; (26) dorsal light elongate spots present; (27) the pregroin brown black; (28) the coloration of the pregroin forms spot on the thigh; (29) dorsal ground color is blue green; (30) small spots on side of head; (31) large spots on side of head; and (32) reticulation on side of head forms patternal bars. Characters 25-32 are binary (0 = characteristic is absent, 1 = it is present).

Cranial Morphology

Stejneger (1890:103) distinguished *C. baileyi* from *C. collaris* stating that in the former the "head [is] narrower, and the snout [is] longer." In 1921, Van Denburgh and Slevin established *C. insularis* on the basis of a narrower head and longer snout than *baileyi*. Unfortunately, neither Stejneger nor Van Denburgh and Slevin listed the data upon which these statements were based. If their data contained measurements from juveniles, then it is possible these characters are not significant. To test this possibility, a section on cranial morphology is included in this study.

Selection of Material

A total of 126 specimens was selected from the seven areas used: the Great Basin group (N=20) from western Arizona, eastern California, Idaho, Nevada, and western Utah; the Baja group (N=20) from Baja and southern California; *C. i. insularis* (N=16) from Angel Island; *C. c. dickersonae* (N=20) from Tiburon Island; *C. c. auriceps* (N=10) from the Upper Colorado River Basin; *C. c. baileyi* (N=20) from central Arizona; and *C. c. fuscus* (N=20) from Chihuahua, Mexico. Only specimens known to represent these populations were used and all specimens had a snout-vent length greater than 80 mm. Approximately equal numbers of males and females were included in each sample.

The following collared lizards were examined in this portion of the study:

ARIZONA: Coconino Co., BYU 32116; LACM 28895; UIMNH 6453, 7525, 74786. Mohave Co., UIMNH 7524, 74781, 74787, 82349. Yavapai Co., UIMNH 74767-74, 74776-77, 82354.

CALIFORNIA: Inyo Co., LACM 36666, 36670. Los Angeles Co., LACM 63187. Riverside Co., LACM 16873, 16875. San Bernardino Co., LACM 63179.

MEXICO: Isla Angel de la Guarda, CAS-SU 21948, 22712; CAS 50873-76, 50878-79, 86755, 86783-84; LACM 4001-02, 9854-55; SDSNH 46001. Baja California, BYU 23337; CU 45855-58, 45860-65; LACM I6993-94, 16996-99, 63171. Chihuahua, BYU 13736, 14211, 15184, 15186-87, 16969, 16971-77, 17010, 17014; USNM 2725, 14242, 14307, 14307a. Isla del Tiburon, BYU 3163, 3167-68; CAS 14003-07, 14009, 14011-12, 53263-64; CU 26679-80, 35168; SDSNH 44063, 46005-06, 50665.

NEVADA: Clark Co., BYU 23629, 23883. Churchill Co., LACM 26843. Lincoln Co., CAS 37033, 37035. Lyon Co., CAS-SU 20576, 20585, 22690, 22705; LACM 26838. Washoe Co., CAS 21499.

TEXAS: El Paso Co., UU 493.

UTAH: Garfield Co., BYU 12700-01. Grand Co., BYU 551, 1625-26, 11737, 12854-55, 31949-50, 31981, 32111. Millard Co., BYU 21000-02.

Characters Used

A total of 16 characters were analyzed from six measurements taken from the intact, unskinned head. All measurements were made to the nearest 0.1 mm, using a Vernier Caliper. The measurements were as follows: (1) total skull length, distance from posterior of quadrate to anterior of rostral; (2) eye to snout, distance from the anterior corner of the eye to anterior of rostral; (3) head width at widest point, a point posterior to the eye, in the parietal region; (4) head width at eyes, distance from jaw to jaw at a point medial to each eye; (5) head width at nostrils, distance from each jaw at a point medial to each nostril; and (6) head depth at eyes, depth of head from a point medial to supraoculars.

The six measurements made for each skull were modified to form the following 16 characters which are listed with their character number: (1) total skull length; (2) eye-to-snout length; (3) head width at widest point; (4) head width at eyes; (5) eye-to-snout length/total skull length; (6) head width at widest point/total skull

length; (7) head width at eyes/total skull length; (8) head width at nostrils/total skull length; (9) head depth at eyes/total skull length; (10) head width at widest point/eye-to-snout length; (11) head width at eyes/eye-to-snout length; (12) head width at nostrils/eye-to-snout length; (13) head depth at eyes/eye-to-snout length; (14) head depth at eyes/head width at widest point; (15) head depth at eyes/head width at eyes; and (16) head depth at eyes/head width at nostrils.

Statistical Analysis

Dixon's BMD07M Computer Program (1968), the same stepwise discriminant analysis used in the external morphology portion of this study, was used at this point because the statistical verification of the seven populations was previously demonstrated.

The discriminant program calculates the mean, standard deviation, and the within-group correlation coefficient for each character. The U- and F- statistics which test the null hypothesis of no difference among populations are listed at each step. The number of correctly identified specimens is displayed at each step and the *a posteriori* probability for an individual's membership in each of the seven groups is given.

RESULTS

External Morphology

Cluster Analysis

Cluster analysis was used to form eight groups of closest morphological similarity (Fig. 2). To test for the independence of the eight groups formed by clustering from the eight groups postulated by geographical locality, a contingency table was formed (Table 1). The null hypothesis was tested by chi-square with forty-nine degrees of freedom. The test statistic is significant at the 0.001 level.

$$X^2(1-\alpha, 49) = \sum_{i=1}^m \sum_{j=1}^n (O_{ij} - E_{ij})^2 / E_{ij}$$

$$X^2(1-\alpha, 49) = 485.7$$

$$X^2(0.999, 49) = 85.4$$

Therefore, $X^2(1-\alpha, 49) \geq X^2(0.999, 49)$ and the null hypothesis is rejected.

Specimens from the various locations were labeled as follows: the Great Basin region of Idaho, western Utah, parts of western Arizona, Nevada, and California south and west to the

eastern edge of the Coachella Valley, Riverside County—the Great Basin group (*C. c. bicinctores*); Baja and southern California, west of Coachella Valley—the Baja group (*C. i. vestigium*); Angel Island—*C. i. insularis*; Tiburon Island—*C. c. dickersonae*; Upper Colorado River—*C. c. duriceps*; Central Arizona—*C. c. baileyi*; Chihuahuan Desert—*C. c. fuscus*; and other specimens from Colorado, New Mexico, Texas, Oklahoma—*C. c. collaris*.

Discriminant Analysis

Discriminant analysis, which predicts membership within a group on the basis of a set of continuously scaled attributes for the individual (Cooley and Lohnes, 1971), was used to define more accurately the relationships seen after cluster analysis. The BMD07M Computer Program of Dixon (1968) was used, with the output consisting of (1) character mean and standard deviation for each group (Table 2); (2) the coefficient of the discriminant function for each group (Table 3); (3) the F-statistic to show the difference between each group (Table

4); (4) the number of cases classified in each group after each new character enters the analysis (Table 5); (5) the U-statistic which tests the difference between groups (Table 6); and (6) the probability of each specimen's membership within a group (Table 7).

The output of the BMD07M lists both the U-statistic and approximate F-statistic. Each tests the null hypothesis of no difference between groups. The U-statistic is 0.00006 with 24,6164 degrees of freedom. The approximate F-statistic was used because of the availability of tables. The approximate F-value is 24.90764 with 144,831.93 degrees of freedom. The tabular F-value is $F(.999,120,120) = 1.76$ (Ostle, 1963). Therefore, $F(1-\alpha, 144,831.93) \geq F(.999,120, 120)$ and the null hypothesis of no difference between groups is rejected.

The F-statistics to test between each pair of groups are listed in Table 4. The tabular F-value is $F(.999,24,120) = 2.40$ (Ostle, 1963); therefore, the null hypothesis of no difference is rejected for each of the groups compared at the .001 level of significance.

Each postulated group contained lizards known to be from a given population. Individual lizards were compared to the discriminant functions (Table 3) and assigned to one of the seven possible populations each time a new character entered the program (Table 6 and 7). To test the program's ability to classify lizards from known populations, the percentage of correctly identified were divided by total number in the geographic sample (N_{corr}/N_{tot}). This was summed over all groups to get the total sample correctly identified (Table 8). Approximately

94 percent of the sample was identified correctly, which is well within the 75 percent taxonomic rule of Mayr (1969).

Cranial Morphology

Discriminant Analysis

The discriminant analysis of Dixon (1968) was used to test its ability to recognize, on the basis of cranial morphology, the seven previously postulated populations. The mean and standard deviation was calculated for each character (Table 9). Again the approximate F-value was used to test the null hypothesis of no difference between groups instead of the U-statistic because of the availability of F-tables. The approximate F-value is $F(1-\alpha, 54,570.59) = 4.7506$. The tabular F-value is $F(0.999,40,120) = 1.84$ (Ostle, 1963). Therefore, $F(1-\alpha, 54,570.59) \geq F(0.999,40,120)$ and the null hypothesis of no difference is rejected at the .001 level of significance.

An F-matrix of 9,111 degrees of freedom was calculated to determine if all groups differ significantly (Table 10). The tabular F-value is $F(0.999,9,60) = 3.69$ (Ostle, 1963). Therefore, not all groups are distinguishable at the .001 level of significance.

Table 11 lists the number of individuals classified into each group after nine characters have entered the analysis. From this information, the number of correctly identified specimens was calculated to see how many populations fit the 75 percent rule (Table 12). Only the Great Basin population was distinguishable with 75 percent accuracy using cranial morphology alone.

DISCUSSION

Ingram and Tanner (1972:6) indicated that the collared lizards of western Utah, Idaho, Nevada, California, and Baja California are very different from those east of the Colorado River.

The objective of this study has been to distinguish the collared lizard populations of these western states from those which are contiguous to the east (*C. c. baileyi*, *C. c. auriceps*, and

Table 1. A contingency table to test the independence of Ward's clustering method and the proposed groups.

Clusters	Proposed Groups							
	Great Basin	Baja Calif.	Angel Island	Tiburon Island	Upper Colorado	Central Arizona	Chihuahuan Desert	Great Plains
1	4	6	0	6	0	0	0	0
2	0	12	0	7	0	0	0	0
3	16	0	0	0	0	0	0	0
4	0	2	17	0	0	0	0	0
5	0	0	0	0	9	9	2	4
6	0	0	0	0	9	5	4	4
7	0	0	0	0	1	3	12	0
8	0	0	0	0	1	3	2	12

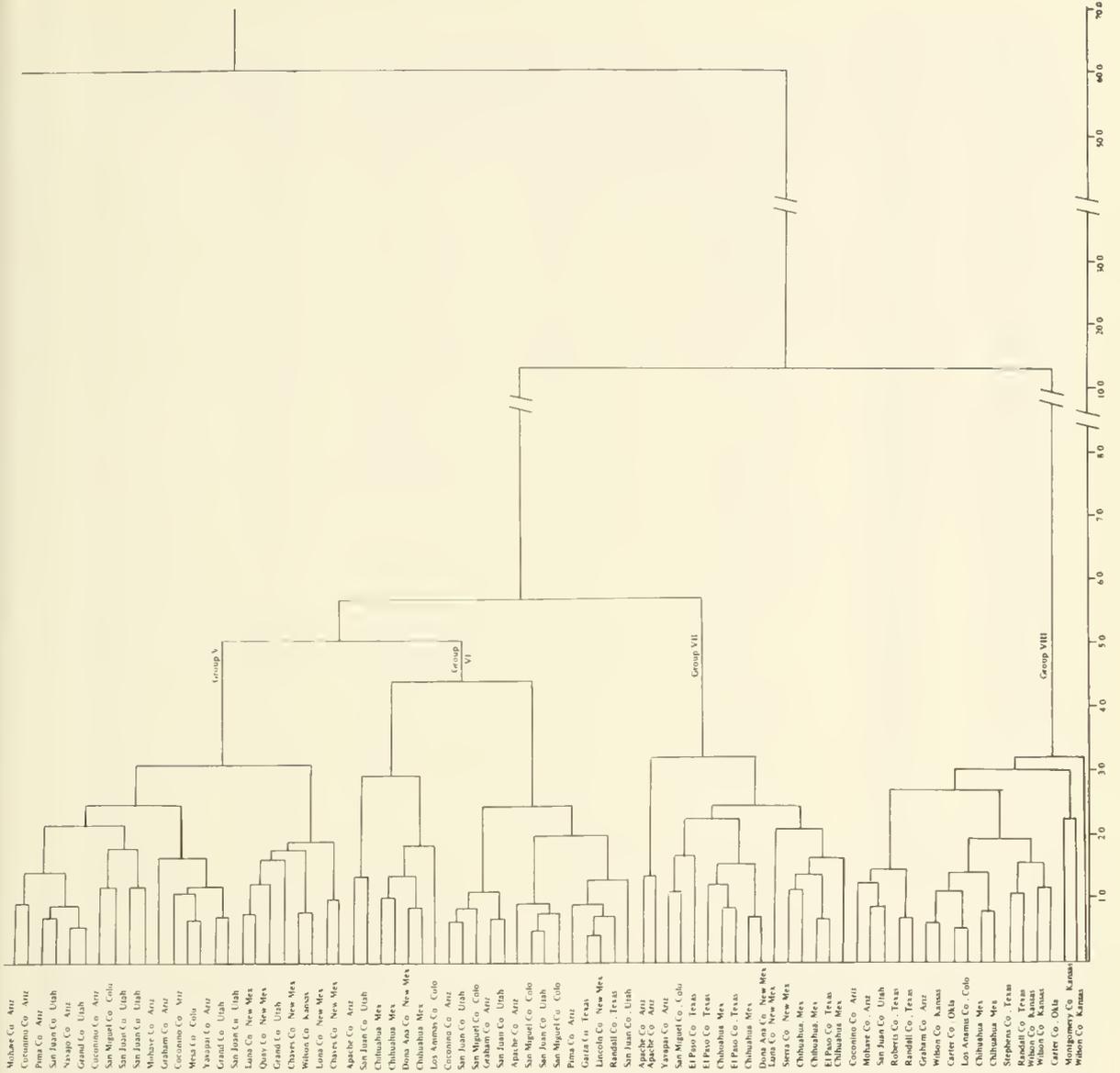


Table 2. A listing of the means and standard deviations for the 32 characters measured on the individuals used

Character	Groups					
	<i>bicinctores</i> (N=50)		<i>vestigium</i> (N=30)		<i>insularis</i> (N=21)	
	Mean	Standard Deviation	Mean	Standard Deviation	Mean	Standard Deviation
1	2.2	0.1	2.3	0.5	2.3	0.1
2	1.9	0.1	2.1	0.4	2.1	0.1
3	91.2	7.1	95.0	15.0	97.4	10.5
4	5.9	0.6	5.0	0.5	5.3	0.6
5	0.0	0.2	0.0	0.0	0.2	0.4
6	3.0	0.8	3.3	0.8	3.0	0.6
7	8.3	0.9	7.2	1.2	8.8	0.8
8	14.7	1.2	15.0	1.6	16.0	1.2
9	0.1	0.3	0.6	0.5	0.1	0.4
10	59.2	4.7	63.1	7.2	67.4	5.4
11	1.3	0.9	2.5	1.3	3.0	1.0
12	15.9	1.3	16.1	1.6	17.3	1.5
13	34.8	3.6	36.9	4.4	41.3	3.7
14	29.1	4.5	25.5	3.9	25.1	0.7
15	174.2	11.2	177.6	12.9	188.6	9.7
16	206.3	11.1	216.2	18.4	227.0	11.4
17	5.1	4.1	19.7	4.0	35.4	12.3
18	2.5	3.4	26.6	9.3	44.1	4.1
19	0.0	0.0	0.1	0.4	0.0	0.0
20	0.1	0.0	0.1	0.0	0.0	0.0
21	19.7	1.2	19.2	1.7	22.0	1.0
22	37.6	2.0	36.1	3.0	41.7	2.0
23	20.1	1.7	27.1	37.1	24.7	1.7
24	17.8	1.3	19.5	2.0	20.2	1.3
25	0.0	0.0	0.0	0.0	0.0	0.0
26	0.0	0.2	1.0	0.2	0.9	0.4
27	0.5	0.5	0.6	0.5	0.4	0.5
28	0.5	0.5	0.6	0.5	0.3	0.5
29	0.3	0.4	0.0	0.0	0.0	0.0
30	0.2	0.4	0.3	0.5	0.6	0.5
31	0.3	0.5	0.6	0.5	0.3	0.5
32	0.9	0.3	0.7	0.5	0.7	0.5

C. c. fuscus) and to determine their relationships to the previously established species, *C. insularis* and *C. dickersonae*. To delimit their characteristics, an investigation was made of their external morphology. Because cranial morphology has been used as a prominent character to distinguish collared lizard populations (Stejneger, 1890; Van Denburgh and Slevin, 1921), we have investigated, by discriminant analysis, its ability to define unilaterally the seven populations within this study (Table 9).

External Morphology

Initially, eight collared lizard populations were postulated (Table 1). The clustan program of Wishart (1968) was used to partition individuals into clusters of closest morphological similarity. The program was discontinued after eight clusters had been formed and a contingency table constructed to test for the independence of the postulated groups with those

formed by cluster analysis. The chi-square test indicated that the groups formed by the two methods are significantly related.

Once the above populations were established, the stepwise discriminant analysis program of Dixon (1968) was used to compile discriminant functions to define more precisely the characteristics of each population. The discriminant program forms a new character, Z, which is the value of the set of discriminant functions formed from linear combinations of the original characters. Characters are added in a linear stepwise manner to maximize the difference between each population. Using this procedure, it is possible with 24 variables to identify correctly 90 percent of each group in this study (Table 7).

Within the discriminant analysis, five of the first seven characters listed dealt with collar pattern (Table 7). When the mean and one standard deviation are plotted for the four non-binary variables of these five collar characteristics (Fig. 3), several population groupings are

in forming the discriminant functions.

<i>dickersonae</i> (N=20)		<i>baileyi</i> (N=20)		<i>fuscus</i> (N=20)		<i>auriceps</i> (N=10)	
Mean	Standard Deviation	Mean	Standard Deviation	Mean	Standard Deviation	Mean	Standard Deviation
2.2	0.1	2.2	0.1	2.1	0.2	2.2	0.3
2.0	0.3	1.9	0.1	1.9	0.2	1.8	0.2
92.6	24.1	92.2	6.0	93.2	7.8	94.3	7.3
5.3	0.5	6.1	0.4	5.8	0.8	5.8	0.8
0.0	0.0	0.2	0.4	0.5	0.8	0.1	0.3
3.6	0.6	2.0	0.6	1.7	0.8	2.3	0.8
7.6	1.1	7.4	1.0	6.5	0.8	8.6	1.5
13.6	0.6	13.0	1.8	14.5	1.3	12.5	0.7
0.2	0.4	1.0	0.2	0.9	0.2	0.9	0.3
60.3	5.3	61.2	6.0	62.4	6.2	66.1	4.5
1.6	0.5	0.5	0.7	0.5	0.6	0.1	0.3
16.5	1.2	14.6	1.6	14.3	1.7	15.7	1.2
40.4	3.0	24.3	6.9	27.6	3.5	24.5	6.1
25.7	1.9	33.5	5.1	27.8	3.3	33.7	6.5
173.0	13.0	161.0	10.0	152.1	9.2	158.1	7.9
208.6	9.4	189.7	10.1	184.3	9.4	195.4	9.8
6.7	2.6	24.1	7.0	23.4	5.7	28.9	4.7
2.6	1.1	4.5	7.0	5.9	5.9	1.4	1.8
0.0	0.0	1.9	0.5	1.9	0.2	1.9	0.3
0.2	0.0	0.2	0.0	0.2	0.0	0.2	0.0
19.3	0.6	19.3	1.6	18.7	1.6	17.3	1.3
34.6	1.3	34.6	2.0	34.6	3.0	33.0	3.9
18.8	1.5	15.5	1.6	15.3	1.7	15.0	1.7
18.6	0.9	17.7	1.6	18.1	1.5	18.6	1.6
0.2	0.4	1.0	0.0	1.0	0.0	0.9	0.3
1.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0
0.7	0.4	0.0	0.0	0.0	0.0	0.0	0.0
0.9	0.3	0.0	0.0	0.0	0.0	0.0	0.0
1.0	0.0	0.9	0.4	0.0	0.0	0.8	0.6
0.8	0.4	0.4	0.5	0.9	0.4	0.1	0.3
0.2	0.4	0.4	0.5	0.0	0.0	0.5	0.5
0.5	0.5	0.2	0.4	0.3	0.5	0.5	0.5

possible. Comparison of the number of unique spots within the dorsal separation of the first collar (Fig. 3IV) shows the existence of a distinct eastern (*auriceps*, *baileyi*, *fuscus*) and western complex (*dickersonae*, *bicinctores*, *vestigiun*, *insularis*). When the dorsal separation of the second collar is compared (Fig. 3III), *C. insularis* and *C. i. vestigium* are sharply defined while *C. c. bicinctores* and *C. c. dickersonae* are allied with the *collaris* complex. We note from our data that *C. c. dickersonae* is allied with both the eastern and western complexes depending upon the variable studied, thus supporting its possible intermediary position. The blue to green color pattern of *C. c. dickersonae*, as well as its oral pigmentation (Axtell, 1972), link it with the eastern complex, but the discriminant analysis program, BMDO7M, confuses it more often with *C. c. bicinctores* than with any of the eastern populations. Moreover, using the clustan program (Fig. 2), we had difficulty distinguishing *C. c.*

dickersonae and *C. i. vestigium*. Therefore, a strong relationship of *C. c. dickersonae* to the western populations is indicated.

The *a posteriori* technique used by Ingram and Tanner (1971) was used in this study to determine areas of intergradation within the western complex and between it and the *collaris* complex. To do this, a large number of collared lizards (369) from all areas of the western complex were inserted into the discriminant analysis program as unknowns, and the *a posteriori* probability for membership in each of the seven groups was calculated. Analysis of this portion of the BMDO7M program indicated most of the populations apparently exhibit little intergradation (Fig. 4), however, exceptions to this will be discussed in the succeeding section on population characteristics.

Although we were unable to locate in the field distinct hybrid zones for *C. c. bicinctores* and members of the *collaris* complex, we strongly believed they existed, and this has since

Table 3. A listing of the coefficients of the discriminant functions after 24 characters have been entered into the discriminant analysis.

Character	Groups						
	<i>bicinctores</i>	<i>vestigium</i>	<i>insularis</i>	<i>dickersonae</i>	<i>baileyi</i>	<i>fuscus</i>	<i>auriceps</i>
3	0.36226	0.44728	0.42848	0.45130	0.43575	0.50236	0.42086
4	14.63895	10.93610	12.74734	12.18521	15.86134	14.90975	13.40478
5	11.35417	12.24668	15.48502	12.77270	14.02354	16.45863	13.60895
6	-2.54088	-0.94370	-2.33630	-0.26514	-5.53481	-5.14219	-5.64448
7	3.23171	1.82818	4.22291	1.55059	4.06717	3.76096	5.55091
8	3.85278	3.45407	3.26712	3.24393	3.52133	3.97844	2.81999
9	18.72758	24.49905	24.25928	17.58437	23.31706	21.23149	23.47716
11	0.23926	2.55489	3.48512	0.17327	0.30980	-0.25982	-0.14585
12	4.85020	5.77467	6.38672	5.32886	5.51403	5.72580	6.58892
13	0.19337	0.19038	0.04178	0.60606	-0.49817	0.03978	-0.39207
15	0.72727	0.62564	0.68925	0.54926	0.82512	0.66800	0.73172
16	0.74275	0.84646	0.73013	0.79176	0.62601	0.66604	0.72710
17	-0.17721	0.13376	0.61486	-0.18022	0.28508	0.20895	0.38181
18	0.52595	1.49761	1.88647	0.82280	0.80442	0.91227	0.67961
19	8.27618	8.79661	4.42210	9.42294	37.53778	39.39021	39.79042
20	464.44434	484.50488	327.03882	581.21729	553.91357	610.33252	525.34448
21	6.43277	5.13985	7.11056	5.47452	5.72452	5.30954	3.84222
23	-0.21490	-0.18263	-0.27868	-0.17966	-0.22353	-0.20750	-0.19154
24	2.39604	3.14634	2.47195	3.44348	3.56539	3.53492	3.99242
25	-11.70876	-12.66015	-7.65450	-3.18096	40.52048	36.31189	38.14626
26	-10.62225	16.41115	10.58251	17.64139	-9.40444	-8.44764	-9.30175
29	-8.40836	-8.49082	-8.37933	-0.25997	4.76858	-5.80569	3.35294
30	18.44745	16.25493	20.84308	18.84085	17.67749	20.89793	15.69166
32	0.50571	-1.09726	0.24414	-2.22648	-5.08565	-5.09013	-1.87483
constant	-395.93677	-418.50757	-472.26001	-416.04150	-476.39014	-478.31909	-458.56494

Table 4. A summary of the F-statistics which show the differences between individual groups $F(.999, 24, 120) = 2.40$, at the .001 level of significance (Ostle, 1963).

Groups	Groups					
	<i>bicinctores</i>	<i>vestigium</i>	<i>insularis</i>	<i>dickersonae</i>	<i>baileyi</i>	<i>fuscus</i>
<i>vestigium</i>	45.05					
<i>insularis</i>	66.55	17.89				
<i>dickersonae</i>	24.81	19.79	47.47			
<i>baileyi</i>	75.37	82.96	93.10	56.11		
<i>fuscus</i>	72.24	76.71	89.32	54.13	5.76	
<i>auriceps</i>	45.20	51.57	62.22	38.66	3.01	6.55

Table 5. Number of cases classified into each group after 24 characters entered into the stepwise discriminant analysis program.

Groups	Groups						
	<i>bicinctores</i>	<i>vestigium</i>	<i>insularis</i>	<i>dickersonae</i>	<i>baileyi</i>	<i>fuscus</i>	<i>auriceps</i>
<i>bicinctores</i>	49	0	0	1	0	0	0
<i>vestigium</i>	0	29	1	0	0	0	0
<i>insularis</i>	0	1	20	0	0	0	0
<i>dickersonae</i>	0	0	0	20	0	0	0
<i>baileyi</i>	0	0	0	0	18	1	1
<i>fuscus</i>	0	0	0	0	0	20	0
<i>auriceps</i>	0	0	0	0	1	0	9

Table 6. Summary table of the sequential entry of characters into the BMD07M discriminant analysis program with their F-value to enter or remove along with the U-statistic at each step.

Step	Variable		F-value Enter or Remove	U-statistic
	Entered	Removed		
1	19		334.6821	0.0755
2	18		178.9013	0.0100
3	26		74.8575	0.0026
4	29		26.4363	0.0013
5	25		23.6078	0.0007
6	17		13.0184	0.0005
7	20		9.4747	0.0003
8	21		7.8510	0.0003
9	30		7.1107	0.0002
10	13		5.8263	0.0002
11	7		5.1555	0.0001
12	5		2.4926	0.0001
13	4		2.3347	0.0001
14	9		2.2488	0.0001
15	11		2.2193	0.0001
16	24		2.1778	0.0001
17	6		1.9843	0.0001
18	15		2.1924	0.0001
19	32		1.6604	0.0001
20	16		1.2632	0.0001
21	12		1.2978	0.0001
22	8		1.1968	0.0001
23	23		1.0629	0.0001
24	3		1.0144	0.0001

Table 7. A percentage comparison of correctly identified individuals within groups as new variables were added to the discriminant functions.

Step	Variable Added	Groups						
		<i>bicinctores</i>	<i>vestigium</i>	<i>insularis</i>	<i>dickersonae</i>	<i>baileyi</i>	<i>fuscus</i>	<i>auriceps</i>
1	19	0	0	0	100	5	95	0
2	18	62	77	95	65	5	60	70
3	26	96	73	95	100	5	65	70
4	29	96	83	95	100	35	100	30
5	25	96	87	95	100	85	100	10
6	17	96	90	95	100	60	100	30
7	20	96	93	90	100	65	100	60
8	21	96	93	90	100	65	100	60
9	30	96	93	95	100	60	100	80
10	13	96	93	95	100	70	100	90
11	7	96	97	95	100	75	100	90
12	5	96	97	95	100	75	100	90
13	4	96	97	95	100	70	100	80
14	9	96	97	95	100	70	100	80
15	11	96	97	95	100	70	100	80
16	24	96	97	95	100	75	100	90
17	6	96	97	95	100	75	100	90
20	16	98	97	95	100	85	100	90
24	3	98	97	95	100	90	100	90

Table 8. Percentage of sample identified correctly using the discriminant analysis.

Group	Sample Size	Ncorr./Ntot.	Percentage
<i>bicinctores</i>	50	49/50	98.00
<i>vestigium</i>	30	29/30	96.67
<i>insularis</i>	21	20/21	95.25
<i>dickersonae</i>	20	20/20	100.00
<i>baileyi</i>	20	18/20	90.00
<i>fuscus</i>	20	20/20	100.00
<i>auriceps</i>	10	9/10	90.00
Total	171	165/171	94.15

been verified by Axtell (1972) in an area north of Kingman, Arizona. Axtell further cites specimens from Coconino and Maricopa counties, Arizona, as possible hybrids. Banta (1960) described a greenish collared lizard taken west of Davis Dam, Clark County, Nevada, but indicated it was a color trait seldom seen in western populations of collared lizards. A preserved specimen, LACM 26824, from Inyo County, California, well within the range of *C. c. bicinctores*, appears to be green and has a very

Table 9. A listing of the means and standard deviations of the 16 cranial morphology characters.

Character	Groups					
	<i>bicinctores</i>		<i>vestigium</i>		<i>insularis</i>	
	Mean	Standard Deviation	Mean	Standard Deviation	Mean	Standard Deviation
1	25.61	1.87	27.57	3.32	27.39	3.25
2	11.63	0.77	12.54	1.14	12.88	1.50
3	16.31	1.48	17.37	2.33	16.31	1.90
4	14.06	0.77	15.11	1.90	14.92	1.52
5	0.45	0.02	0.46	0.02	0.47	0.01
6	0.64	0.03	0.63	0.03	0.60	0.02
7	0.55	0.03	0.55	0.02	0.55	0.02
8	0.02	0.00	0.02	0.00	0.02	0.00
9	0.02	0.00	0.02	0.00	0.02	0.00
10	1.40	0.09	1.38	0.10	1.27	0.05
11	1.21	0.07	1.20	0.07	1.16	0.05
12	0.04	0.00	0.04	0.00	0.04	0.00
13	0.05	0.00	0.05	0.00	0.05	0.01
14	0.04	0.00	0.04	0.00	0.04	0.00
15	0.05	0.00	0.04	0.01	0.04	0.00
16	1.40	0.09	1.38	0.10	1.27	0.05

Table 10. A summary of the F-statistics which show the differences between individual groups in the cranial morphology study. $F(.999,9,60) = 3.69$, at the .001 level of significance (Ostle, 1963).

Groups	Groups					
	<i>bicinctores</i>	<i>vestigium</i>	<i>insularis</i>	<i>dickersonae</i>	<i>baileyi</i>	<i>fuscus</i>
<i>vestigium</i>	1.43030					
<i>insularis</i>	6.97606	4.87994				
<i>dickersonae</i>	2.46489	1.71034	7.09683			
<i>baileyi</i>	2.78564	4.65735	13.80026	5.94830		
<i>fuscus</i>	6.63592	9.44739	18.35388	9.77859	1.86056	
<i>auriceps</i>	3.67191	3.90008	11.17101	5.49404	1.46455	3.15051

Table 11. Number of cases classified into each group after nine characters entered into the stepwise discriminant analysis program for cranial morphology.

Groups	Groups						
	<i>bicinctores</i>	<i>vestigium</i>	<i>insularis</i>	<i>dickersonae</i>	<i>baileyi</i>	<i>fuscus</i>	<i>auriceps</i>
<i>bicinctores</i>	15	1	2	0	2	0	0
<i>vestigium</i>	2	9	4	3	2	0	0
<i>insularis</i>	1	4	11	0	0	0	0
<i>dickersonae</i>	5	5	1	7	1	0	1
<i>baileyi</i>	4	2	0	0	9	3	2
<i>fuscus</i>	1	0	0	1	6	9	3
<i>auriceps</i>	0	2	0	0	3	1	4

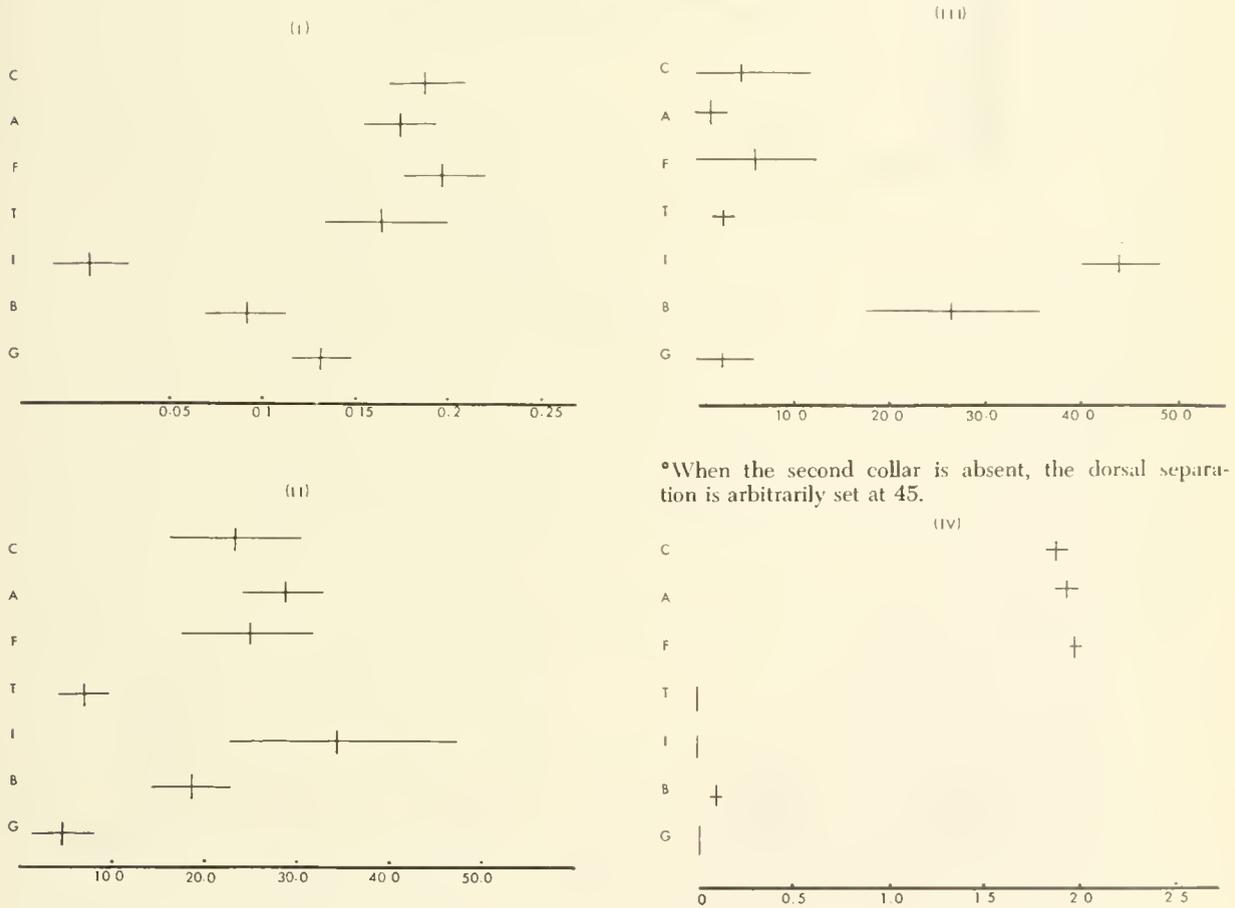
Table 12. Percentage of sample identified correctly from discriminant analysis of the head characters after nine characters considered.

Group	Sample Size	Ncorr./ Ntot.	Percentage
<i>bicinctores</i>	20	15/20	75.00
<i>vestigium</i>	20	9/20	45.00
<i>insularis</i>	16	11/16	68.75
<i>dickersonae</i>	20	7/20	35.00
<i>baileyi</i>	20	9/20	45.00
<i>fuscus</i>	20	9/20	45.00
<i>auriceps</i>	10	4/10	40.00
Total	126	64/126	50.79

unusual dorsal recticulation. Future investigation could reveal hybrids in the Moab area of Grand County, Utah. It is difficult to locate contact zones because collared lizards seldom cross the valleys which separate them from their preferred mountain slopes. Hence they are demic even within the range of unquestionably similar populations.

Following the technique of Rao (1952), a graph of the first two canonical variables was plotted which represents in two-dimensional space the relationships of the seven populations studied (Fig. 5). The overlapping populations

Groups							
<i>dickersonae</i>		<i>baileyi</i>		<i>fuscus</i>		<i>auriceps</i>	
Mean	Standard Deviation	Mean	Standard Deviation	Mean	Standard Deviation	Mean	Standard Deviation
29.16	5.25	26.55	3.01	25.64	3.60	25.37	2.36
12.92	1.82	11.82	1.31	11.37	1.43	11.27	0.86
18.32	3.45	18.07	2.62	17.79	2.82	17.13	2.11
15.43	2.11	15.02	1.66	14.87	1.76	14.78	1.78
0.45	0.02	0.45	0.02	0.44	0.02	0.45	0.03
0.63	0.02	0.68	0.03	0.69	0.03	0.67	0.03
0.53	0.04	0.57	0.03	0.58	0.02	0.58	0.03
0.02	0.00	0.02	0.00	0.02	0.00	0.02	0.00
0.02	0.00	0.03	0.00	0.03	0.00	0.03	0.00
1.41	0.10	1.53	0.10	1.56	0.10	1.52	0.14
1.20	0.07	1.27	0.10	1.31	0.05	1.31	0.13
0.04	0.01	0.04	0.00	0.04	0.00	0.04	0.00
0.05	0.01	0.06	0.00	0.06	0.00	0.06	0.00
0.04	0.01	0.04	0.00	0.04	0.00	0.04	0.00
0.04	0.01	0.05	0.00	0.05	0.00	0.05	0.00
1.41	0.10	1.53	0.10	1.56	0.10	1.52	0.14

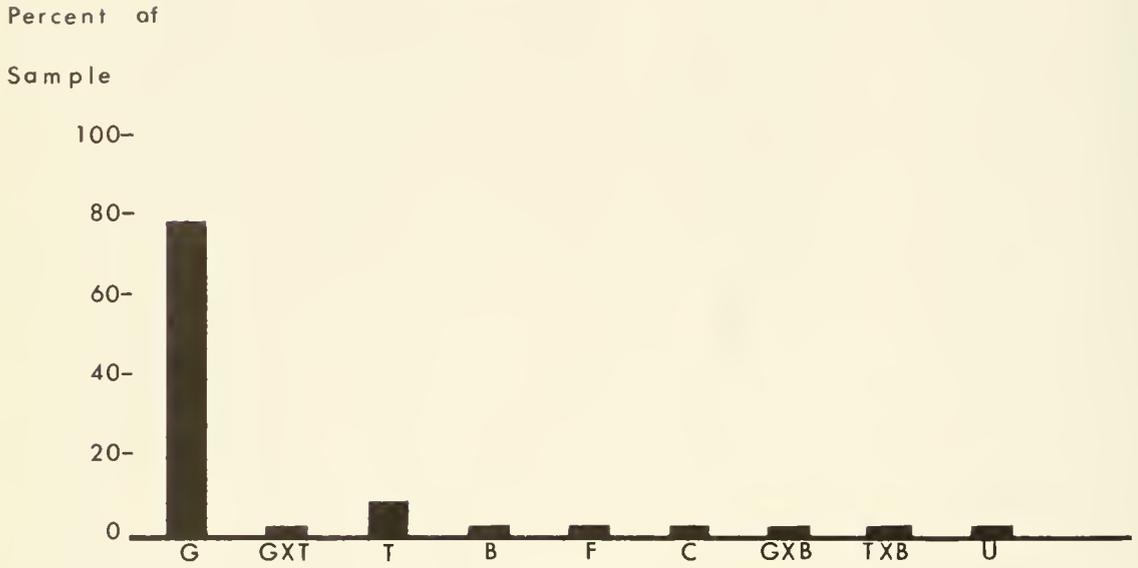


*When the second collar is absent, the dorsal separation is arbitrarily set at 45.

Fig. 3. Means and standard deviations plotted for the four nonbinary characters that contribute most to the distinction of the four western-complex populations from *C. e. baileyi*, *C. c. auriceps*, and *C. c. fuscus*: (I) second collar length/snout-vent length, (II) number of scales within dorsal separation of first collar, (III) number of scales within dorsal

separation of second collar, (IV) number of spots within dorsal separation of first collar. (C) central Arizona, (A) upper Colorado River Basin, (F) Chihuahuan Desert, (T) Tiburon Island, (I) Angel Island, (B) Baja California-southern California, and (G) Great Basin populations.

Great Basin
(Idaho, Nevada, western Utah, southwestern Arizona,
eastern California)



Sonora, Mexico
(West of Highway 15, Organ Pipe National Monument
area and southern end Tinajas Altas Mountains exclusive
of Tiburon Island)

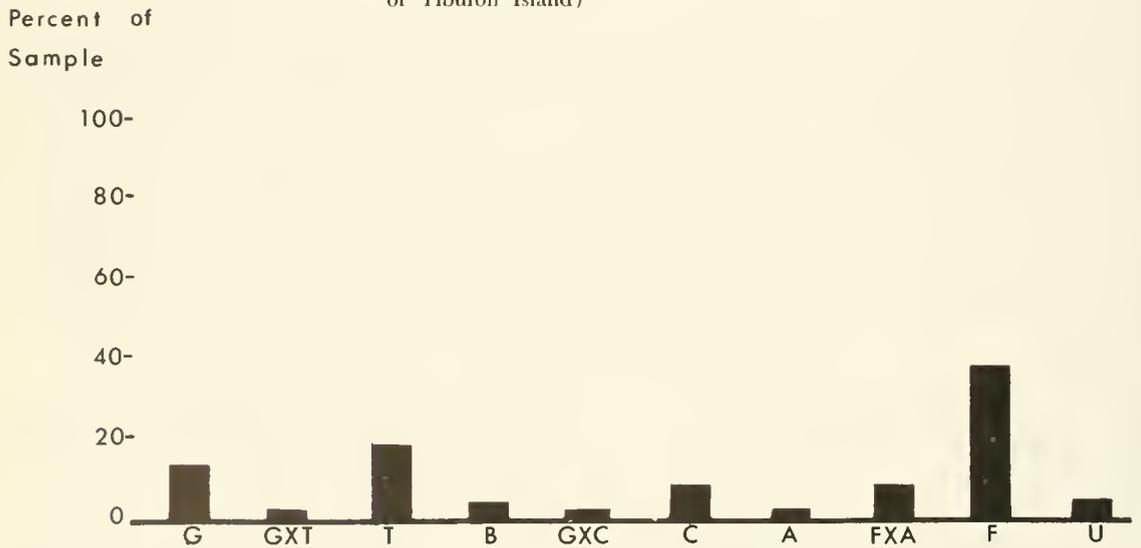


Fig. 4. Continued on next page.

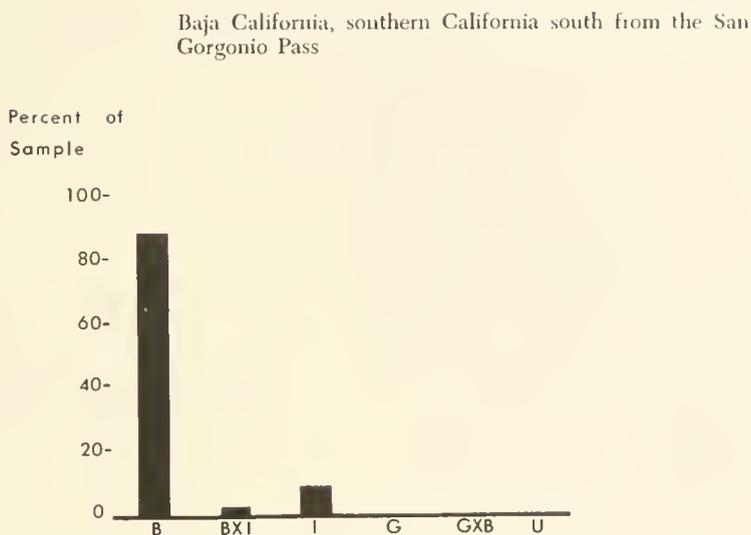


Fig. 4. A comparison of collared lizard populations from the Great Basin, northwest Sonora, Mexico, and Baja California-southern California.

A key to the abbreviations used in Fig. 4.

- A—*auriceps* population from the Upper Colorado River Basin.
- B—*vestigium* from the Baja California, southern California population.
- C—*baileyi* population from Central Arizona.
- F—*fuscus* population from Chihuahuan Desert.
- G—*bicinctores* population from Idaho, Nevada, western Utah and Arizona, and eastern California.
- I—*insularis* population from Angel Island.
- T—*dickersonae* population from Tiburon Island.
- GXT—intergrade population of *bicinctores* and *dickersonae*.
- CXG—intergrade population of *baileyi* and *bicinctores*.
- AXG—intergrade population of *auriceps* and *bicinctores*.
- FXG—intergrade population of *fuscus* and *bicinctores*.
- CXF—intergrade population of *baileyi* and *fuscus*.
- BXI—intergrade population of *vestigium* and *insularis*.
- GXB—intergrade population of *vestigium* and *bicinctores*.
- U—Individuals not assignable to any of the above groups.

are Great Basin and Tiburon, with a few members of the Tiburon group shifting toward the *collaris* complex. This is expected, since we consider the Tiburon-Sonoran populations to have been derived from those populations evolving to the east and now designated as *C. c. fuscus*. The Baja California group is more closely related to the Tiburon group in the characters studied than it is to the Great Basin population. This is in agreement with the results of the cluster analysis. There are two valid reasons members of the *collaris* complex did not separate as well in this plot as the one shown by Ingram and Tanner (1971:23): (1) a more reduced scale was used to plot this graph, and (2) not all the same characters used by Ingram and Tanner were used in this study. These two points should be kept in mind along with the

fact that our statistical tests supported these eastern populations (Table 4).

Cranial Morphology

The skull has been shown to be significant in the definition of subspecific taxa (Avery and Tanner, 1964, 1971; Presch, 1969; Robison and Tanner, 1962). Van Denburgh and Slevin (1921) declared *C. insularis* to have a longer, narrower head than *C. c. baileyi*. In comparing the cranial morphology of the seven populations of this study, only the Great Basin group reached 75 percent distinction (Table 12). The character which best separates the western and *collaris* complexes is head width at widest point/total skull length (Fig. 6). Within these complexes, the distinctions, except for the Great Basin group, are not significant.

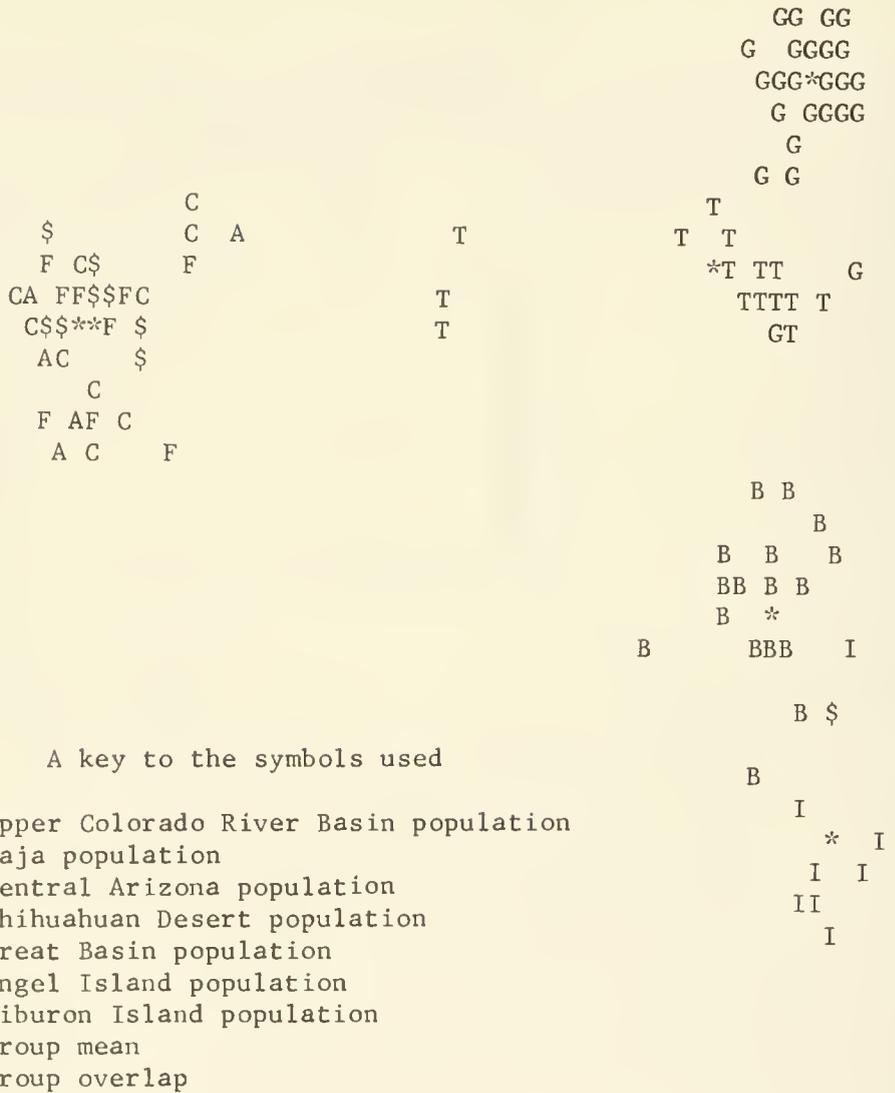


Fig. 5. A two-dimensional representation of the external morphological interpopulation relationships formed from canonical varieties.

Although Van Denburgh's data were apparently linear rather than proportional (1922:116), his assumption that *C. insularis* is distinguishable from *C. c. baileyi*, as defined by us, by cranial characteristics is correct (Table 11). Additional research is needed to determine if osseous elements are responsible for the differences in cranial proportions.

On the basis of cranial measurements, members of the western complex show a closer relationship to one another than to members of the *collaris* complex. This is the same relationship which evolved in the cluster analysis portion of this study. Using the *a posteriori* probabilities

generated by the BMD07M program, it is not possible to determine distinct areas of intergradation for the Great Basin group and the *collaris* complex.

Population Characteristics and Systematics

The characteristics which distinguish members of the *collaris* complex have been summarized by Ingram and Tanner (1971:21-24). The characters which separate them from the western complex are: (1) one or more spots present in the dorsum of the first collar; (2) absence of a prominent ventral black groin patch on the males; (3) fewer scales occurring

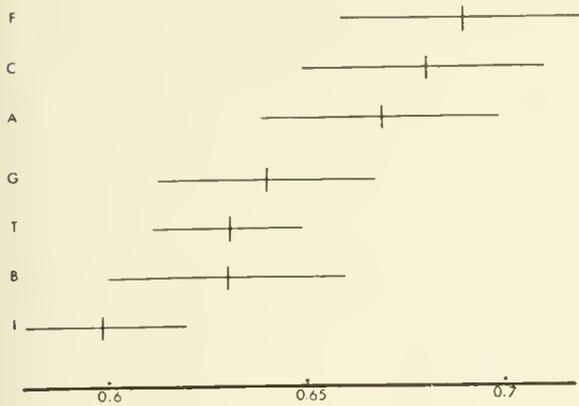


Fig. 6. The mean and standard deviation for head width at widest point/total skull length: (F) *C. c. fuscus*, (C) *C. c. baileyi*, (A) *C. c. auriceps*, (G) *C. c. bicinctores*, (T) *C. c. dickersonae*, (B) *C. i. vestigium*, (I) *C. i. insularis*.

from the interparietal to the anterior border of the first collar, and (4) the second collar usually extending onto the upper arm. Additionally, Axtell (1972) suggests a rounded tail and dark oral pigmentation as characteristic of the *collaris* complex.

The four populations of the western complex are believed to represent two species of *Crotaphytus*. The Great Basin and Tiburon Island-Western Sonoran populations are considered *C. collaris*. The southern California, Baja California, and Angel Island populations are considered *C. insularis*. The Great Basin population, which we consider *C. c. bicinctores* (although similar to *C. insularis* with its brownish dorsal coloration, ventral collar, gular, and abdomino-lateral pigmentation), is distinctly different in dorsal pattern and collar characteristics. Upon visual inspection, there is no confusion between a *C. c. bicinctores* and *C. insularis*; this is true even between females (Smith and Tanner, 1972: Fig. 1). Such is not the case when comparing females of two closely related subspecies such as *C. c. fuscus* and *C. c. baileyi*. Cluster analysis (Fig. 2) and canonical analysis (Fig. 5) sharply distinguish *C. c. bicinctores* from *C. insularis*; however, the distinction between Baja California and Angel Island populations, two populations we consider to be subspecifically related, is not so apparent.

In our earlier paper (Smith and Tanner, 1972), we indicated an area of sympatry for *C. c. bicinctores* and *C. i. vestigium* in the vicinity of the San Gorgonio Pass, Riverside County, California. This assumption was based upon a female *bicinctores*, CSCLB VAP 660513-4, said to have been taken from the side of the road

leading from Palm Springs to the aerial tramway in an area which is occupied by *vestigium*. This specimen, when reconsidered, may represent the results of human intervention in collared lizard distribution. Dr. Ernest Tinkum and James Davis of Indio, Riverside County, California (pers. comm.), indicate they have not observed *bicinctores* from this area. Until a thorough ecological study can be completed within the vicinity of the San Gorgonio Pass, we now prefer to believe *bicinctores* and *vestigium* represent allopatric species (Fig. 7). Additional specimens of interest from this area are LACM 16889, a female *bicinctores* from Cabazon, Riverside County, California; and UCMVZ I, a female *vestigium* from Hallgrade, near Cabazon. The latter specimen was taken by W. P. Taylor in 1908. Stephen B. Ruth, from the USMVZ, has examined the field notes and reports that Taylor's base camp was 1½ miles south of Cabazon and that on May 9 Taylor walked up to Hurley Flat (which was south of his camp) via the Hallgrade. In this case, the specimen was seemingly taken on the low foothills at the base of the San Jacinto Mountains.

Axtell (1972) has taken the position that *bicinctores* should be placed in the *Crotaphytus insularis* species complex. His arrangement is based on some morphological similarities between these species, and we readily agree that there are similarities. However, if one is to accept his hypothesis that *bicinctores* is specifically distinct from *C. collaris* because introgression is very narrow in the Cerbat Mountains where he has pinpointed intergradation, then by that reasoning—and on the basis of the information presented above—we would suggest that *bicinctores* is also specifically distinct from *insularis*. In the information to follow, we will give indications of additional intergradation between *bicinctores* and other *collaris* subspecies in northern Sonora, Mexico. These data seem to relate *bicinctores* more closely to *baileyi*, *fuscus*, and *dickersonae*, and we, therefore, prefer to group *bicinctores* with *collaris* at present.

The possibility that *bicinctores*, which has been found as far north in the upper Colorado River Basin as the Potash Road (BYU 3114), Grand County, Utah, intergrades with *C. c. auriceps* has not yet been demonstrated. However, Axtell (1972) has demonstrated that *bicinctores* does intergrade in Arizona with *C. c. baileyi*, which is a close relative of *auriceps*.

In the southern portion of its range, *bicinctores* has not been shown to contact or intergrade directly with *C. c. dickersonae*; but it does intergrade with *C. c. fuscus*, and *C. c.*

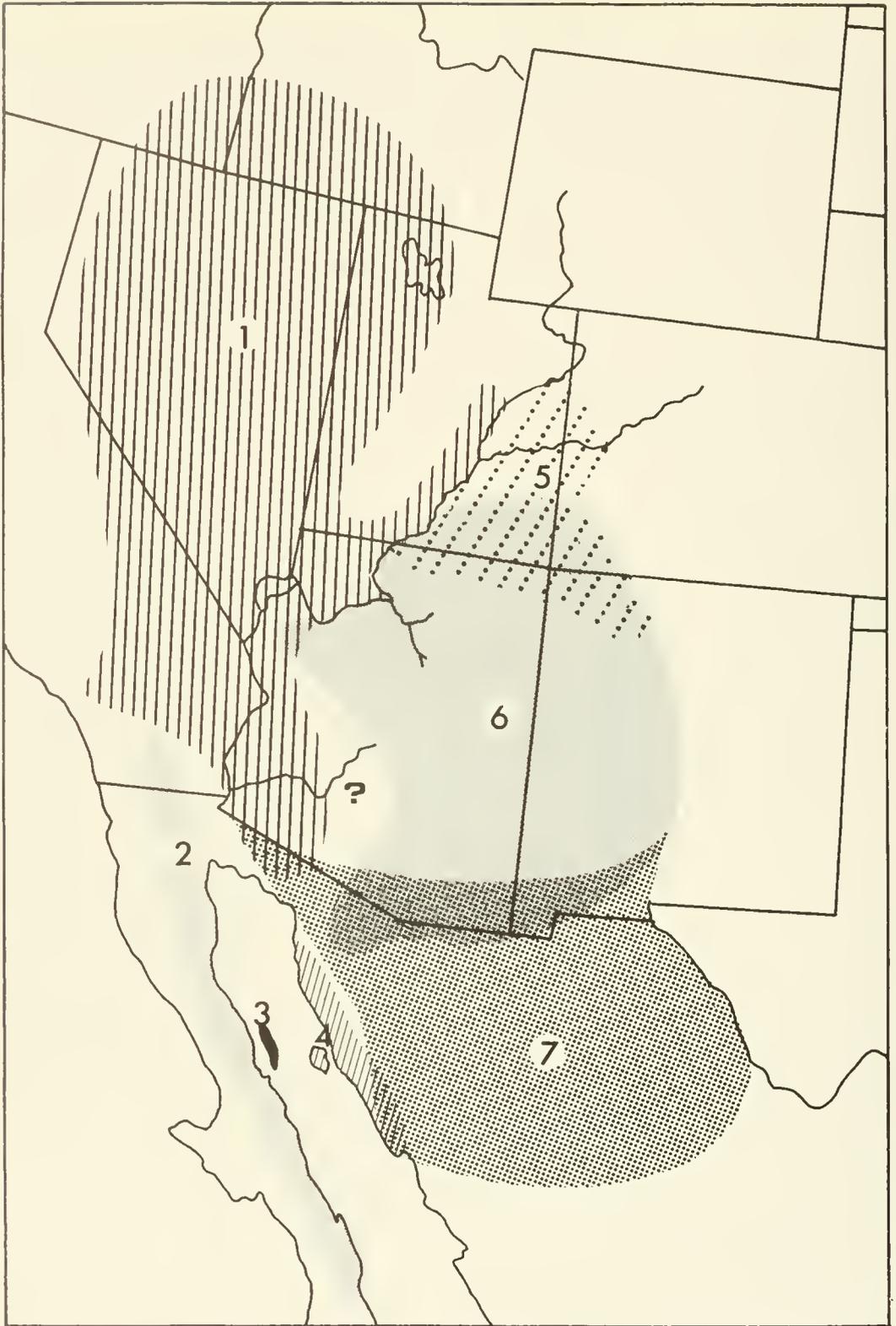


Fig. 7. Range map for *Crotophytus collaris* and *Crotophytus insularis*: (1) *C. c. bicinctores*, (2) *C. i. vestigium*, (3) *C. i. insularis*, (4) *C. c. dickersonae*, (5) *C. c. auriceps*, (6) *C. c. baileyi*, (7) *C. c. fuscus*.

fuscus intergrades with *C. c. dickersonae* (See the following discussion of population characteristics for *dickersonae*).

Specimen UAZ 12114 from an area midway between MacDougal and Sykes Crater in northwestern Sonora, Mexico, is considered by us to be an intergrade between *C. c. bicinctores* and *C. c. fuscus*. Its appearance is very much like *bicinctores*. The *a posteriori* probability was 1.000 for *bicinctores*. It has, however, *fuscus* characteristics such as its second collar extending on to the forearm, the first collar having an anterior extension that could be interpreted as the incomplete formation of spots, a rounded tail (a *collaris* character suggested by Axtell, 1972), a very reduced ventral groin patch, minor pigmentation of the dewlap, postmentals contacting the infralabials, and 34 subdigital lamellae on the fourth toe.

Similarly, UAZ 10248 from 36.7 miles west of Sonoita has *a posteriori* probabilities of 0.687 for *C. c. auriceps* and 0.307 for *C. c. fuscus*. Visual inspection of the color and dorsal pattern reminds one of *bicinctores*. Additional *bicinctores* characteristics include: 3 frontoparietals, 3 scutae in dorsal separation of first collar, no scutae in dorsal separation of second collar, and 21 subdigital lamellae on the fifth toe. It is seemingly an intergrade of *fuscus* and *bicinctores*.

Specimens which we have observed from Organ Pipe National Monument, Pima County, Arizona (UAZ 636, 1511; LACM 3983, 5899), have appeared to be *fuscus*; but visual inspection of the first collar pattern suggests it is not nearly so characteristic as those from the type locality in Chihuahua, Mexico. When the dorsal collar pattern is masked and only the pattern on the back is visible, it is often difficult to distinguish these *fuscus* specimens from *bicinctores*.

Several specimens from the area of Caborca and San Luis, Sonora, are especially interesting because of the *a posteriori* probability listed for them by the BMD07M program. On the basis of this information, one would suspect this to be an area of intergradation or at least an area which represents the remnants of genes representing *bicinctores*, *dickersonae*, *fuscus*, and other members of the eastern complex, which may now be geographically or ecologically isolated. The specimens, with their localities and probabilities, are UCMVZ 10163, ♂, 30 miles W Caborca, .406 *fuscus*, .353 *bicinctores*, .241 *dickersonae*; CAS 104467, ♀, 9 miles E Caborca, .529 *bicinctores*, .435 *baileyi*, .024 *fuscus*. Additional field studies in this area are needed before complete relationships and distributions can be

ascertained. However, present data indicates considerable intergradation.

The members of *C. c. dickersonae* are similar to *C. c. bicinctores* in many respects, including collar pattern, but are distinguished from them by their blue or green dorsal ground color and dorsal light elongate spots. These two populations are so closely related that many of their morphological characteristics, although different, show considerable overlap (Table 2). The dorsal light elongate spots of *dickersonae* are suggestive of those found in *C. insularis*. The ventral pigmentation of male *dickersonae* is not as pronounced as that seen in *bicinctores* or *insularis*. The range of *dickersonae* can now be extended north from near Kino Bay to Puerto Libertad (UAZ 20144) and to El Desomboque, Sonora, Mexico (UAZ 704, 705, and 30226). Its range south from Kino Bay is not completely known, but two specimens (BYU 40930-31) from the hills north of Guaymas show intergrading characters between *dickersonae* and *fuscus*.

Both of the above specimens have *a posteriori* probabilities of 1.000 for *dickersonae*. Visual inspection reveals the male (BYU 40931) to have dorsal light elongate spots, a blue green cast, 3 frontoparietals, no fused interorbitals, 9 loreal-lorilabials and 2 enlarged internasals—all of which characterize *dickersonae*. Conversely, the second collar extends boldly onto the upper forearm, the postmentals contact the infralabials, there are 5 scutae within the dorsal separation of the first collar, and the tail is round—all of which characterize *fuscus*. In addition, the first collar unites ventrally and there is bold abdomino-lateral pigmentation, which is not characteristic of either population. Axtell (1972) noted this exaggerated effect on the variables found in his intergrades of *bicinctores* and *baileyi*. Such intergrade variables cause one to wonder if *bicinctores* has not arisen as a result of hybridization between several of the subspecies and established its range in the lower Colorado River Basin with its major extension into the Great Basin. The female of this pair (BYU 40930) has *dickersonae* characteristics of 3 frontoparietals, 8 loreal-lorilabials, 7 scutae in the dorsal separation of the first collar, and dorsal light elongate spots. Her *fuscus* characteristics include 1 fused interorbital, 21 scutae from the interparietal to anterior edge of first collar, 5 scutae in the dorsal separation of the second collar, and the extension of the second collar onto the arm. We consider both of these specimens to be intergrades between *fuscus* and *dickersonae*.

The following additional specimens from the Guaymas area are listed with their museum number and their BMDO7M *a posteriori* probabilities. The probabilities are not consistently in favor of any given population indicating a gene pool that has traits for *dickersonae*, *fuscus*, *bicinctores*, *baileyi*, and *auriceps*. We have not been able to collect collared lizards in the area near Guaymas and suggest that this will be essential to understand better the complete relationship of *dickersonae* and *fuscus*. The specimens, with their identification and *a posteriori* probabilities, are: LACM 52886, ♂, 9 miles NW Guaymas, .005 *dickersonae*, .004 *fuscus*, .991 *bicinctores*; LACM 52882, ♀, 9 miles NW Guaymas, 1.000 *fuscus*; UAZ 10597, ♀, 29.3 miles S Los Pocitos, .795 *fuscus*, .205 *baileyi*; SDSNH 35918, ♂, between Guaymas and Empalme, .669 *auriceps*, .268 *fuscus*, .058 *baileyi*, .006 *bicinctores*; SDSNH 35919, ♂, between Guaymas and Empalme, .404 *baileyi*, .339 *fuscus*, .214 *bicinctores*, .043 *auriceps*; and SDSNH CRM 117, ♂, Playa Miramar SW of Guaymas, 1.000 *fuscus*.

Specimen CAS-SU 14002, reported collected from Tiburon Island, is a perfect example of *C. i. insularis* and presents an anomalistic situation. The specimen was collected 7 May 1952. CAS-SU 14003-14012 taken by the same party two days earlier, 5 May 1952, from Tiburon Island, are typical *dickersonae*. To us it seems very possible the CAS-SU 14002 has been mislabeled.

The Baja California-southern California population, *C. insularis vestigium*, represents a distinct taxon. It differs from *C. c. baileyi* in those characters which distinguish it from *C. c. bicinctores*. *Crotaphytus i. vestigium* can be distinguished from the Great Basin population by its reduced first and second collar and the distinct dorsal transverse bands which separate light elongate spots (Smith and Tanner, 1972: Fig. 1).

Crotaphytus i. vestigium can be distinguished from *C. i. insularis* by fewer lamellae on the second and fourth toe, a larger second collar/s-v ratio, and a smaller dorsal separation of both the first and second collars (Table 2).

Phyletic Relationships

It is noteworthy that cluster analysis separated collared lizards into eastern and western groups, producing four clusters for the western complexes and four for the eastern. These, we believe, can be used as indicators of phyletic relationships (Fig. 2). Within the western group, the most distinct population is *C. i. insularis* from Angel Island, one of the older

islands in the Gulf of California (Anderson, 1950). Female collared lizards from Angel Island, according to Banta (1961), bear a similarity to the leopard lizard *Crotaphytus wislizenii silus*. It is probable that the collared lizards from Angel Island display some of the genetic variance which gave rise to *C. wislizenii* and are a relict population which was derived from a more widespread population, the remnants of which are now found on the island and Baja California Peninsula. Banta (1961) believes *C. collaris* is an older population than the leopard lizards. This we have not been able to demonstrate from our data; however, previous studies have shown that *Crotaphytus reticulatus* of eastern Mexico and southcentral Texas, a form which lacks the collar pattern of *C. collaris*, is probably an intermediate between *C. collaris* and *C. wislizenii* (Robison and Tanner, 1962; Montanucci, 1969). The two species in the genus which may be considered the more primitive members of the collared lizard complex are found on the extreme eastern edge (*reticulatus*) and the extreme western edge (*insularis*) of their distribution.

The historical distribution of the collared lizard in the Gulf of California region is a matter of speculation at present. Those found on Angel Island and the Baja California Peninsula are more closely related to each other than they are to *C. c. dickersonae* from Tiburon Island or *bicinctores* in the Great Basin (Fig. 5), indicating a long period of isolation in the western portion of the Gulf. The Baja California Peninsula is thought to have formed some four to ten million years ago in late Pliocene by crustal movement (Moore and Buffington, 1968). A peculiar feature in this hypothesis is the formation of the northern portion of the Gulf of California before the existence of a southern entrance (Larson, Menard, and Smith, 1968). It is possible, therefore, to hypothesize at least three modes of distribution of the collared lizard from mainland Mexico to the Baja California Peninsula: (1) the peninsular populations were isolated by the peninsular drift which formed the Gulf of California; (2) the collared lizard extended its range to the Baja California Peninsula by a migration south of the newly forming Gulf of California, later to be isolated as the peninsula was formed; (3) the collared lizard migrated around the northern end of the Gulf of California and later had its range restricted to the peninsula, isolating it from the more recent populations to the north and east.

The origin of the Angel Island population from the Baja California population is difficult

to assess because of the absence of a good fossil record. Angel Island is a deep-water island formed during the Pliocene (Anderson, 1950). A possible land bridge between the island and the peninsula might have permitted unrestricted distribution of the collared lizard. Later, when the land bridge was inundated, the insular population became a relict. It is also possible that the collared lizard was rafted to the island before the channel became extensive.

Tiburon, a shallow-water island, was undoubtedly separated from Sonora, Mexico, when the level of the seas rose during the recession of the last glacial period of 10,000 to 15,000 years ago (Lawlor, 1971). Even today, the channel between the island and the mainland is very narrow (ca. 5 miles) and shallow at low tide. *Crotaphytus c. dickersonae* was described from Tiburon Island (Schmidt, 1922), but this study has shown that it is not restricted to the island and occurs at least along the nearby Sonoran coast. Morphology indicates that *dickersonae* has not diverged to any great extent from the original stock which gave rise to it and *bicinctores* of the Great Basin. The canonical analysis (Fig. 5) indicates that *dickersonae* diverged from the *collaris* complex from which all members of the western complex of *collaris* probably arose at a much later date than the *insularis* stock.

The Great Basin, formed in late Tertiary (Banta, 1961), did not present a favorable environment for the modern collared lizard until late Pliocene or early Pleistocene, when many north-south oriented mountains were formed (Axlerod, 1948). The northern range of the collared lizard population in the Great Basin ebbed and enlarged with changing Pleistocene climatic conditions (Banta, 1961) until the arid conditions beginning about 11,000 years ago (Antevs, 1955; Broecker, 1957) permitted its present northern extension. The modern collared lizard apparently did not invade the Great Basin or the Great Plains before Pleistocene (Brattstrom, 1954; Harris and Findley, 1964; and Gehlbach, 1965a), although Gilmore (1941) described the genus *Aciprion* Cope from the Oligocene deposits of Wyoming as similar to *Crotaphytus*.

The Great Basin collared lizard, *C. c. bicinctores*, is possibly a more xeric form than members of the eastern *collaris* complex. Miller and Stebbins (1964) report that collared lizards do not occur at elevations above 5700 feet in the mountains of Joshua Tree National Monument, San Bernardino County, California; whereas members of the *collaris* complex are found up to

7500 feet elevation in the Zuni Mountains of northwestern New Mexico (Gehlbach, 1965b). The preference of a more mesic environment by members of the *collaris* complex might be explained by natural selection for their green coloration; conversely, the brown coloration of the more xeric western form seemingly provides them an adaptive advantage in their arid environment.

Tiburon-Sonoran and Great Basin populations evidently had their genesis in northcentral Mexico, probably from the line of *C. c. fuscus*, spreading west to the Gulf Coast and the Colorado River and later invading and occupying the west side of the river as well as the extremely dry areas of western Arizona. In Utah, the Colorado River has served as an effective barrier, limiting the range of *C. c. bicinctores* to the west side of the river. A proposed phylogenetic relationship is shown in Fig. 8. Distribution and relationship is based primarily upon morphological characteristics.

The phylogeny of the genus *Crotaphytus* apparently had its beginnings in southcentral United States and northcentral Mexico before the Pleistocene (Robinson and Van Devender, 1973). Indications are that the genus, or its immediate ancestral stock, was well established and gave rise to a radiation, which resulted in a division of the genus into the primitive collared lizard and the leopard lizard branches, perhaps as early as late Pliocene. Although the fossil record does not support a Pliocene radiation for the crotaphytines, if *Aciprion* Cope is a member of this iguanid line, its origin may then be extended back into middle Tertiary. We surmise that the original stock of the *collaris* group may not have exhibited the collar so typical of the group as we recognize it today. We, therefore, suspect that *C. reticulatus* is a remnant of a much older and originally more widespread population than members of the presently extant collared lizard group. We further suspect that this primitive stock continued to evolve and gave rise to the *collaris* group which has been so successful in its invasion of the great plains, the Rio Grande Valley, the plateaus and mountains of Sonora, Arizona, New Mexico, Utah, and the Great Basin since the Pleistocene. We are not certain as to whether the *insularis* group represents a primitive *collaris* stock which has recently been replaced in most of the western distributional areas or if it represents a modification of the western *collaris* group which has, through isolation, become modified from the ancestral stock which also gave rise to the Sonoran and Great Basin populations. The re-

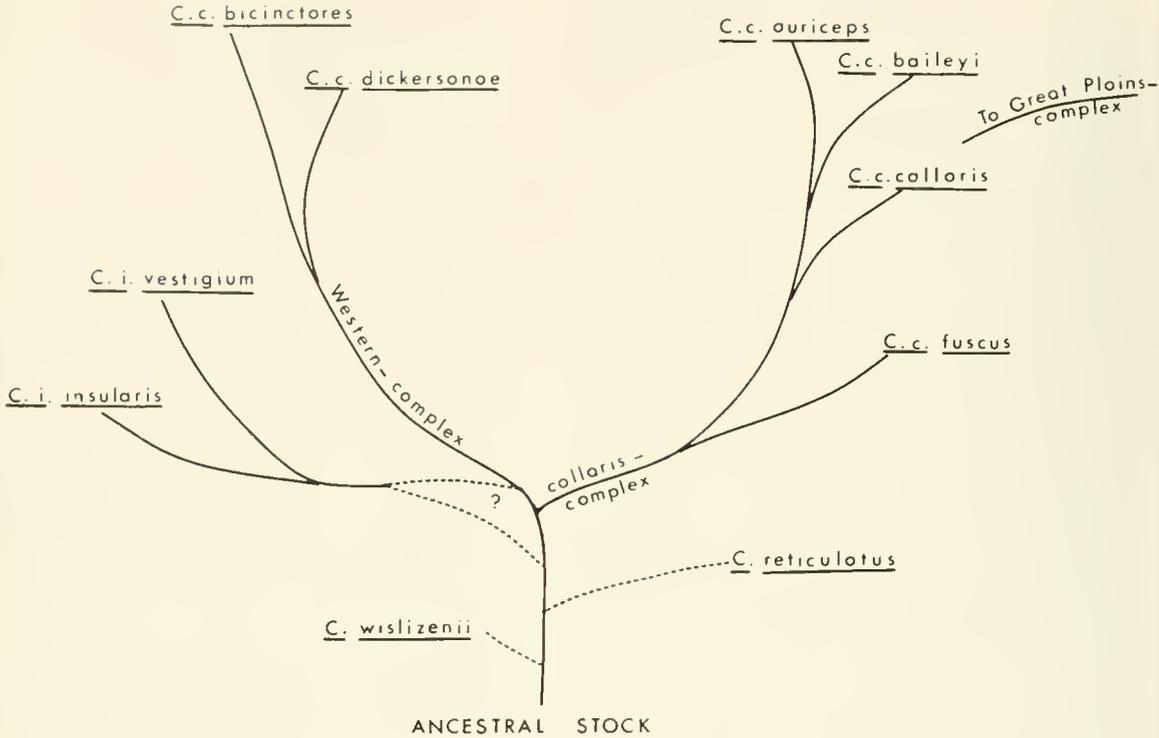


Fig. 8. Proposed phylogenetic relationship of *Crotaphytus*.

duced collar in the *insularis* populations is so distinct from the collar pattern found in the other western subspecies of *collaris* that we are inclined to believe the *insularis* group is more primitive than other collared lizards. The *insularis* group perhaps preceded the *collaris* groups into the western deserts and at present represents a relict which arose shortly after the *collaris* ancestral stock was established in the more central and southern part of their present distribution.

The ancestral stock of the *collaris* complex appears to have been derived from a stock similar to *C. c. fuscus*. There seems to be little reason to doubt its close relationship to those forms now occurring from the Great Plains westward to the Colorado River. Although these populations have been separated into a series of subspecies, they are all similar in many basic characteristics. Their distinction from the western *collaris* subspecies is undoubtedly a series of adaptive modifications resulting from the changing environment and perhaps isolation. The extensive development of the collars of *bicinctores* and *dickersonae*, plus the fact that they do not overlap the distribution of *insularis*,

is additional indication that they are more recent arrivals than *insularis*. These circumstances again suggest a relict distributional pattern. Assuming this to be the general trend in the past development of this branch of the genus *Crotaphytus*, we could readily assume that the ebbing of the Ice Age allowed the then established *collaris* stock to extend its distribution northward and to the west. It occupied extensive areas in central and western United States and at the same time was undergoing adaptive changes which led to the distinct subspecies populations now extant.

Perhaps the most extensive subspecific group is that of *bicinctores*. Even though this group extends from southern California and southwestern Arizona northward into Nevada, Utah, and southern Idaho, its distribution presumably is so recent or its genetical makeup so stable that subspeciation has not occurred. This is in contrast to the subspecies eline extending northward from Chihuahua into southeastern Utah. The Great Plains populations must still be carefully examined, and we expect that they may also show a similar evolutionary development to that observed in the *baileyi* branch.

SUMMARY AND CONCLUSIONS

The heterogeneous nature of the collared lizards west of the Colorado River prompted this study. Samples from known populations of *C. c. auriceps*, *C. c. baileyi*, and *C. c. fuscus* were used as a base for defining the western populations. External morphology and cranial morphology were compared by cluster, canonical, and discriminant analyses.

Results of these analyses show a western complex of four populations which are distinct from the three base populations of the *collaris* complex. Members within the western complex are distinguishable with at least 90 percent reliability by discriminant analysis. Because of intergradation patterns seen in western Sonora, Mexico, *Crotaphytus dickersonae* is considered to be *Crotaphytus collaris dickersonae*. The Great Basin population is retained as *Crotaphytus collaris bicinctores*. The population from southern California and Baja California, which is distinct and has no demonstrated intergrades

with *C. c. bicinctores*, is considered *Crotaphytus insularis vestigium*, and the population from Isla Angel de la Guarda is designated *Crotaphytus insularis insularis*.

The range of *C. c. dickersonae* is shown to extend from Isla Tiburon onto the Sonoran coast opposite the island and from Bahía Kino north to El Desemboque. *Crotaphytus c. bicinctores* extends from the Yuma, Arizona, area north through eastern California, western Arizona, Nevada, central Utah (west of the Colorado River), southern Idaho, and southeastern Oregon. The western range of *C. c. baileyi* is restricted to central Arizona. The range of *C. i. insularis* is restricted to Isla Angel de la Guarda and *C. i. vestigium* to a narrow strip extending along the eastern mountain slopes from central Baja California, Mexico, to the foothills south of the San Geronio Pass, near Palm Springs, California.

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APPENDIX I

Key to the species of *Crotaphytus*

- 1a. Collars on neck absent dorsally and ventrally 2
- 1b. Collar or collars present on neck dorsally and/or ventrally 3
- 2a. Supraorbital semicircles absent; body pattern with spots but not reticulated *wislizenii*
- 2b. Supraorbital semicircles present; occasionally with a vertical black bar on shoulder; body pattern boldly reticulated *reticulatus*
- 3a. Two collars present on dorsum of neck, first collar often incomplete dorsally and with spotting in the dorsum between the two lateral arms of collar *collaris*
- 3b. Collars present or absent; when present reduced, usually incomplete dorsally and without dorsal spots in the first collar; body pattern with distinct light cross bands, often with light elongate spots between the cross bands *insularis*

APPENDIX II

Key to subspecies of *Crotaphytus collaris* and *Crotaphytus insularis*

- 1a. One or more spots in dorsum of the first collar; adult males lack a dark pigmented gular and groin; first collar not united ventrally; second collar usually extends onto upper arm (Fig. 3G-H) 2
- 1b. Spots absent in dorsum of first collar; adult males have a dark pigmented gular and groin and first collar unites ventrally or nearly so; second collar not extended onto upper arm 5
- 2a. Interorbitals form two rows, usually without a fusion of the scales in these two rows; supralabials usually 11 or more; gular region of adult males boldly reticulated 3
- 2b. Interorbitals have one to four scales fused in the interorbital series; supralabials usually 10 or less; gular region of adult males not boldly reticulated *C. c. collaris*
- 3a. Body dorsum brown with no trace of green, head cream colored with no trace of yellow *C. c. fuscus*
- 3b. Body dorsum green or blue; head yellow or light 4
- 4a. Head yellow or white; if yellow, not extending under the chin or caudally past supraorbital semicircles *C. c. baileyi*
- 4b. Head yellow with yellow extending under the chin and caudally to or just past the second collar *C. c. auriceps*
- 5a. Body dorsum blue, green or gray, with large light dorsal elongate spots; second collar length/snout-vent averages from 0.13 to 0.19; number scales from interparietal to anterior border of first collar 37-43 *C. c. dickersonae*
- 5b. Body dorsum brown or tan, with transverse bands of yellow, orange, or white; second collar length/snout-vent length usually less than 0.14 6
- 6a. Second collar meets, or nearly meets dorsally, usually never more than 10 scales separate the two dorsal arms of the second collar; first collar separated by 1-9 scales (Fig. 3B) *C. c. bicinctores*
- 6b. Second collar reduced or absent, usually with distinct white transverse dorsal bands; first collar separated by 16 to 40 plus scales (Fig. 3A) 7
- 7a. Second collar very reduced or absent; fourth toe subdigital lamellae 39-45 *C. i. insularis*
- 7b. Second collar less reduced and usually a portion of it present; fourth toe subdigital lamellae 33-37 *C. i. vestigium*

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**LIFE HISTORY AND ECOLOGY OF THE
GREAT BASIN SAGEBRUSH SWIFT,
SCELOPORUS GRACIOSUS GRACIOSUS
BAIRD AND GIRARD, 1852**

by

Gary L. Burkholder
and
Wilmer W. Tanner



BIOLOGICAL SERIES—VOLUME XIX, NUMBER 5

DECEMBER 1974/ISSN 0068-1024

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by

Gary L. Burkholder¹ and Wilmer W. Tanner²

INTRODUCTION

The sagebrush swift, *Sceloporus graciosus graciosus*, is the most abundant reptile in the transitional zone of the Great Basin. In this habitat, being preyed upon by larger vertebrates and, in turn, preying upon arthropods, it serves as an intermediate link in the food chain. Previous ecological studies have dealt only with isolated aspects of the sagebrush swift's natural history. This study was undertaken to consolidate and to add to our knowledge of this species.

The sagebrush swift is found in western North America, from northeastern Washington and west central Montana south to northern Arizona, New Mexico, and southern California and from eastern Wyoming to the coast of northern California. Populations are also found in southern California, Baja California, western Texas, and southeastern New Mexico (Stebbins, 1966). One specimen was among those collected by the Stansbury Expedition to the Valley of the Great Salt Lake in 1849; this specimen was sent to the U.S. National Museum, where it was described by Baird and Girard in 1852.

Stejneger (1893) reported *S. g. graciosus* to occupy sagebrush areas at 2,450 m elevation in the White and Inyo mountains on the border of California and Nevada. In 1912 Taylor observed that Nevada populations were mainly ground-dwellers occupying sagebrush and pinyon-juniper plant associations. He also noted predation of sagebrush swifts by *Crotaphytus wislizenii*. Richardson (1915) made a survey of reptiles of northwestern Nevada and adjacent territory and found considerable morphological variation between populations. He noted that sagebrush swifts were abundant on low, sparsely forested moraines among *Artemisia tridentata*, *Arctostaphylos* sp., and *Ceanothus* sp.

More recently, Woodbury and Woodbury (1945) observed courtship behavior and gonadal

cycle. Stebbins (1944 and 1948) and Stebbins and Robinson (1946) studied territoriality and longevity in northern California populations of *S. g. gracilis*.

The stomach contents of *graciosus* in Utah were analyzed in studies by Paek (1921), Gertsch and Woodbury (1930), Knowlton and Janes (1932), Knowlton and Thomas (1936), and Knowlton, Maddock, and Wood (1946).

Studies on body temperature have been carried out by Licht (1965). Mueller (1969) recorded the mean body temperature of *graciosus* from Yellowstone National Park. Other studies on thermo-regulation in species of *Sceloporus* have been carried out by Cole (1943), Cowles and Bogert (1944), Bogert (1949), Larson (1961), and Brattstrom (1965).

Growth studies on *S. g. graciosus* at Yellowstone National Park were done by Mueller and Moore (1969); however, the results were based on few individuals. Stebbins (1944) studied the growth dynamics of California populations of *S. g. gracilis*. Tinkle (1973) has provided an extensive population analysis of the sagebrush swift in southern Utah.

There have been a number of ecological studies of other species of *Sceloporus*. A study by Blair (1960) on *S. olivaceus* in Texas includes reproductive cycles, population dynamics, predation, and home range. Mayhew (1962, 1963a, and 1963b) studied the size of home range, reproductive cycles, and growth of *S. orcutti* in California. Fitch (1940) studied the growth and behavior of *S. occidentalis*; Wilhoft and Quay (1961) reported its testicular histology and seasonal changes. Other studies on the western fence lizard have been made by Johnson (1965—food habits), Davis (1967—growth dynamics), and Tanner and Hopkin (1972)—reproduction, growth, and home range). Crenshaw

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(1955) studied the reproductive cycle, habitat, and growth of *S. undulatus*; Carpenter (1959) studied population dynamics. Crisp (1964a and 1964b) examined the female and male reproductive cycles in *S. cyanogenys*. Zweifel (1949), Carpenter (1960), and Goldberg (1970a,

1970b, and 1971) studied ovoviviparity, parturition and behavior, and histology of the reproductive cycle, respectively, in *S. jarrovi*. Methodology and understanding of *S. g. graciosus* have been enhanced by these studies.

MATERIALS AND METHODS

Field work was started in the spring of 1970 on a study plot at the eastern edge of the Brigham Young University farm, southeast of Spanish Fork, Utah. The plot is 1.2 hectares set with rows of stakes at right angles, each stake being 12.2 m from other stakes. At the base of each stake a can trap was buried flush with the ground level as explained by Tanner and Hopkin (1972).

The elevation of the study plot lies between 1,493 and 1,554 m. The slope is approximately 40 degrees, facing west and containing a dry wash (Fig. 1 and 2A-B). The wash creates

north- and south-facing slopes within the plot. The substratum on the south-facing slope was developed from a large talus slope which is light in color and of a fine gravelly nature. Small rocky outcroppings and large solitary boulders occur on both slopes of the wash. The area south of the wash (north-facing slope and southern end of plot) has a more humus soil but is still rocky and has a surface covering of small gravel in some areas.

Two days of each week were devoted to checking traps and two to noosing and returning lizards to the place of capture. Each lizard

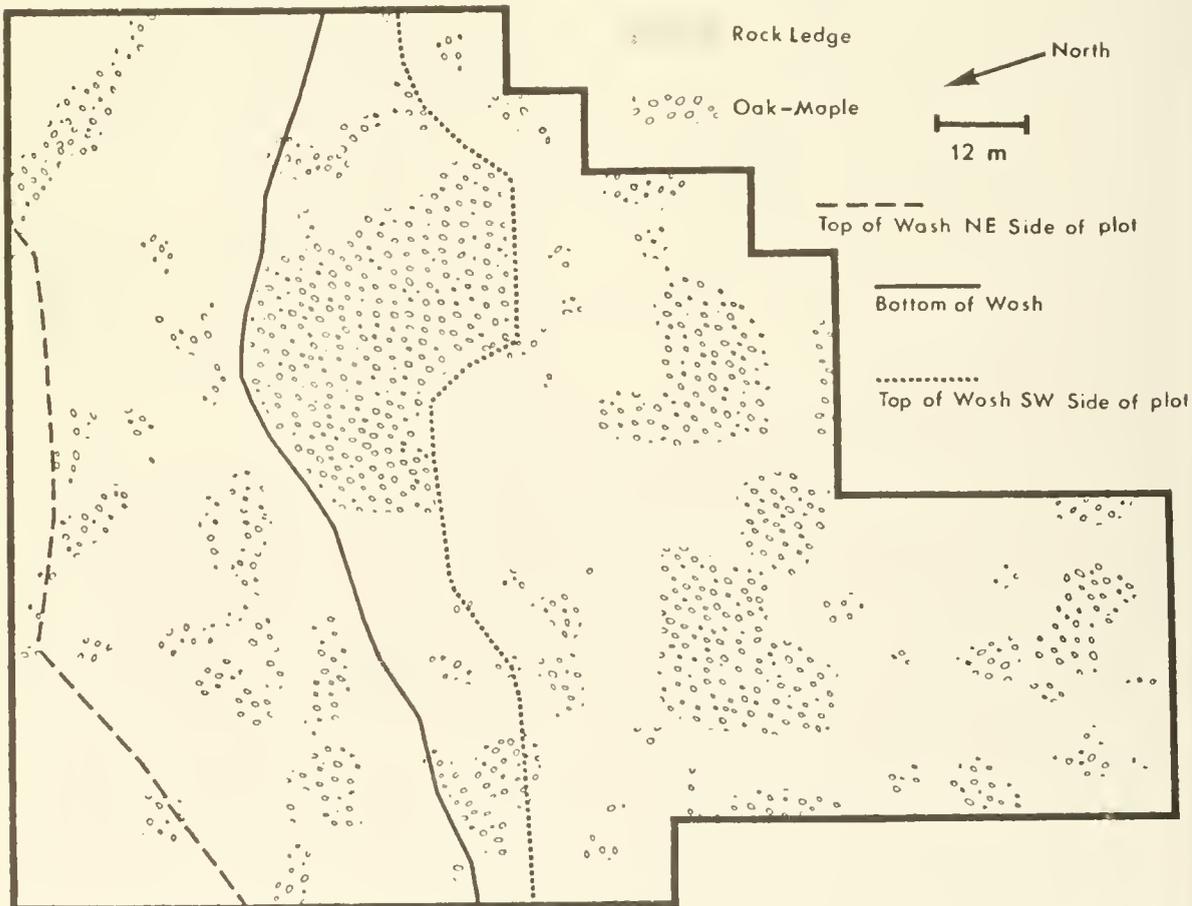


Fig. 1. Outline of study plot with dominant vegetation and topography indicated. BYU Farm, Spanish Fork, Utah.



Fig. 2A-B. Study plot habitat features. A depicts the south-facing slope and B the north-facing slope.

was marked by toe clipping and its weight, size, sex, and external appearance were recorded, as well as body temperature at the time of capture. Air temperatures at approximately 3 mm and 1 m above the substrate were taken soon after noting the lizard's temperature. Notes on behavior, activity, and feeding were also recorded while working in the study area. A hydrothermograph was used to record weather data on the study plot, and United States climatological data were obtained from a station located 2.5 km north of the study area. A vegetation analysis of all plant species occurring on the plot was made in 1971, while flowering species were collected throughout the year.

Lizards were collected throughout Utah County and parts of Salt Lake and Wasatch counties. These lizards were autopsied in the laboratory to analyze reproductive stages, weight of gonads, stomach contents, and fat body weights; these data were compared with external measurements taken from study plot lizards. Observations of behavior in the laboratory were made by keeping lizards in two boxes partly filled with sand, rocks, and pieces of wood, creating a suitable habitat. Eggs laid in captivity were incubated in the laboratory at approximately 28 C.

Male testicular cycles and meiosis in female ovaries were analyzed by histological sections. Stomach contents were analyzed with a stereoscopic microscope, and arthropod volumes were measured by water displacement in a 10-cc graduated cylinder. All statistical tests of results were at the 5 percent level of confidence. The statistical tests used were chi-square, analysis of variance, and the paired *t*-test.

Description of the Study Area and General Observations of the Research

Habitat

Study plot vegetation included annual and perennial herbs, shrubs, and trees. The dominant plant association consisted of bigtooth maple, *Acer grandidentatum*; Gambel oak, *Quercus gambelii*; and sagebrush, *Artemisia tridentata*. Distribution of the oak and maple is depicted in Fig. 1. Subdominants, abundant in some areas of the study plot, include snake-weed, *Gutierrezia sarothrae*; *Petrodora pumila*; blue bunch wheatgrass, *Agropyron spicatum*; nuttongrass, *Poa longiligula*; needle grass, *Stipa comata*; and junegrass, *Koeleria cristata*. Some perennial and annual herbs were balsam root, *Balsamorhiza sagittata*; and two species of brome grass, *Bromus* spp. The dominant and

subdominant plant types grew in clusters, with ample open spaces (Fig. 2A-B). This type of spatial arrangement appears to be necessary for *S. g. graciosus* to occupy an area.

Collection sites throughout Utah County where lizards were taken usually had the same general environmental features as the study plot. Most had Gambel oak, bigtooth maple, and sagebrush as associated dominants. Some collection sites supported *Juniperus osteosperma* or sagebrush only. Elevation of collection sites ranged from 1,371 to 1,981 m. South-facing slopes usually provided the best sites for collecting, primarily because these habitats were more often chosen by *graciosus* (Fig. 2A-B).

Summers are hot, with few overcast days from mid-May to mid-September and with average daily maximum temperatures ranging from 30 to 37 C for July. There are approximately 180 or more frost-free days from April through September. However, irregular cold fronts may periodically reduce activity in March through the first of May and in late September and October. Precipitation and temperature on the study plot are summarized in Fig. 3. The average seasonal temperatures were similar during the years of this study and the precipitation averaged about 10 inches (25.4 cm) during the activity season, 1 inch (2.54 cm) per month. The least precipitation occurred in late June, July, and the first half of August. The precipitation total was lowest in 1972 and highest in 1970 (March through August).

Emergence

In 1970, 1971, and 1972 the first lizards emerged when average daily temperatures reached 10 to 13 C (Fig. 3). These early animals were juveniles of both sexes and adult males. The first adult male emerged 19 days before adult females in 1970 (22 March/10 April), nine days earlier in 1971 (21 March/29 March), and 21 days earlier in 1972 (5 March/25 March)—an average of 16.3 days between male and female emergence. Males were caught soon after emergence (indicated by the moist mud on the body).

Seasonal and Daily Lizard Temperatures

Mean preferred body temperature for study plot adults taken for the season, June to September, was 32.6 (19.0-38.8) C, juveniles 33.1 (21.0-38.4) C, and hatchlings 31.2 (26.0-35.4) C. Hatchlings did not tolerate temperatures much above 36 C. Temperature observations from the field for hatchlings during August and September ranged from 26.0 to 35.5 C. Periods of

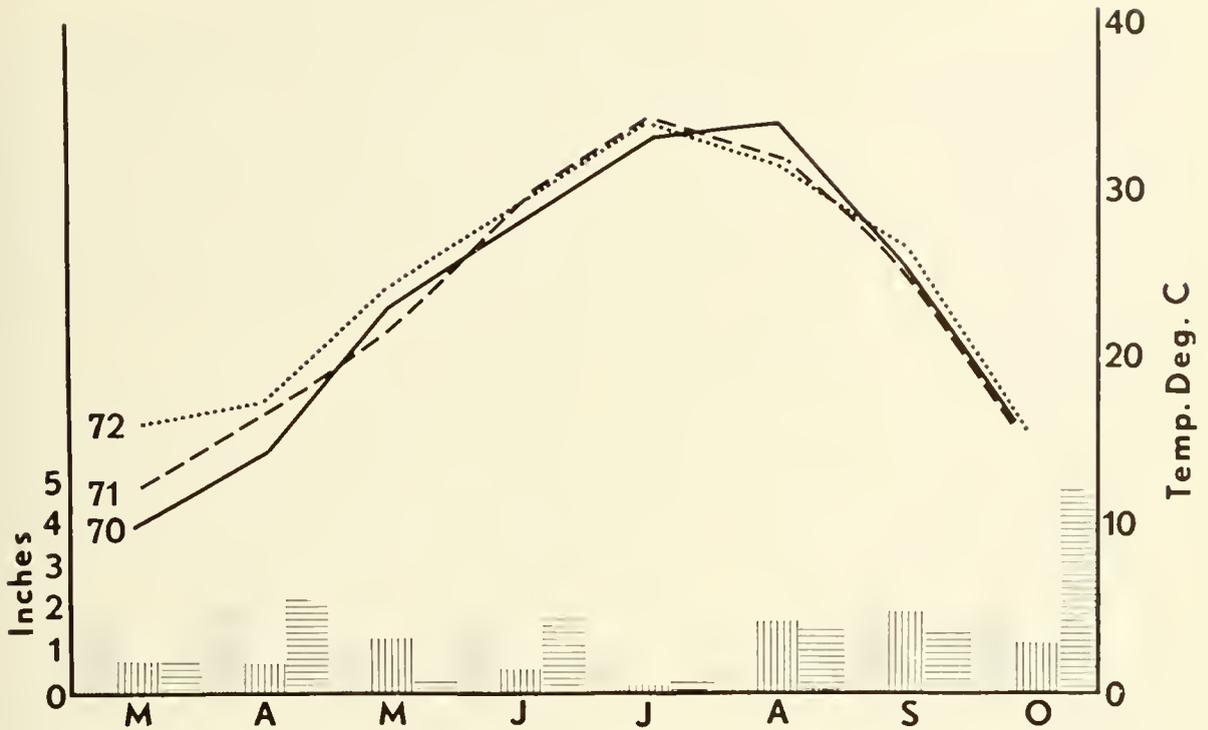


Fig. 3. Precipitation (columns) and temperature (lines) by month for study plot for 1970 through 1972. Shaded columns represent 1970, vertical lines 1971, and horizontal lines 1972.

20 to 30 minutes in a paper bag at temperatures near or above 38 C proved fatal, suggesting a lower critical thermal maximum for hatchlings than for adults.

Lizards emerged from overnight retreats with body temperatures of 16 to 21 C. Basking range was 21 to 28 C and normal activity range was 28 to 37 C. Adult and juvenile lizards were able to tolerate temperatures of 38 to 40 C. The critical thermal maximum in the laboratory was 43 C for an adult male and 44 C for an adult female. They were captured in March and April and kept in captivity at temperatures of 24 to 27 C.

In Fig. 4, the average temperatures of males and females are compared to temperatures of air 3 mm and 1 m above the substrate. During periods of intense heat in July and August, lizards could be found only in the oak-maple thickets and under sagebrush, rocks (crevices and overhangs), and other forms of cover. Some remained under cover until the heat of the day passed, while others in the oak-maple thickets were more active. The contrast between periods of low and high activity between 1000 and 1200 hours in July and August is represented in Fig. 5. Some lizards were at the basking areas before sun up during June, July, and August. This activity was seemingly

caused by early morning light and high temperatures (15-17 C).

Daily and Seasonal Activity

A summary of the daily activity for study plot lizards during the 1971 activity season is diagrammed in Fig. 5. High temperatures for

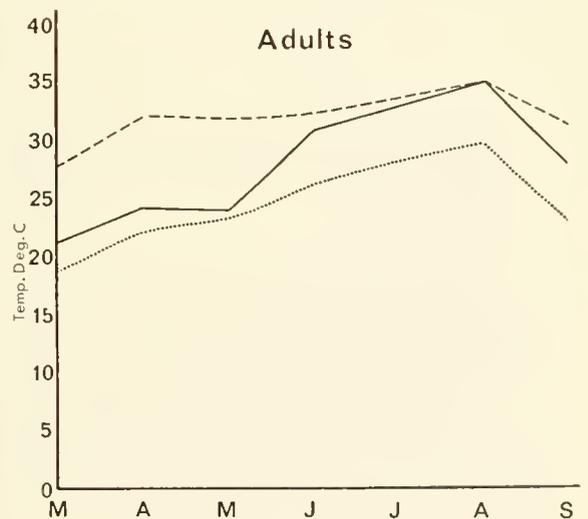


Fig. 4. Mean temperatures of adult lizards and of air (3 mm and 1 m) above substrate. Dashed line represents lizards; solid line, air (3 mm); dotted line, air (1 m). 1971.

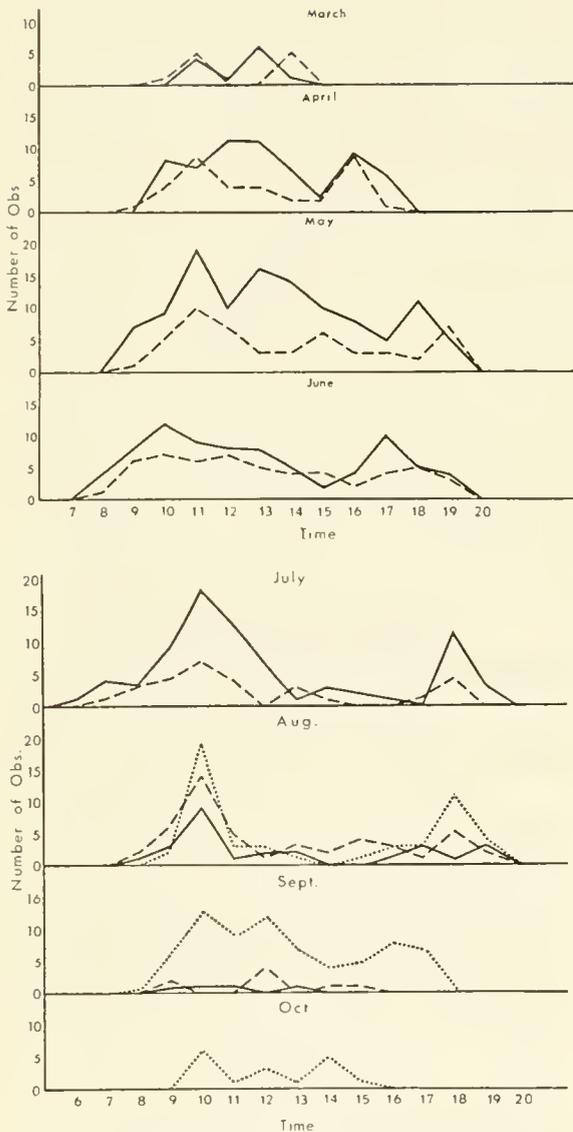


Fig. 5. Number and age of lizards observed, plotted against time of day, throughout the activity season of 1971 and March 1972. Solid line represents adults; dashed line, juveniles; dotted line, hatchlings.

air at 1 m and 3 m above the substrate in late June, July, and August ranged from 34 to 40 C and from 43.2 to 45.0 C. Temperatures above 50 C for actual substrate surface were noted frequently during the afternoons of the warmer months. Our data indicate that adults and juveniles have the same daily activity throughout the year, with the activity of juveniles extending into September.

Local Weather Conditions

Periodic cold fronts in March, April, and early May, if severe enough and over a period

of several days, stopped all activity in the field. One or two days of warming were required before full activity resumed. Heavy thunderstorms during June, July, and August stopped activity periodically. Lizards reappeared as soon as the sky was clear. They basked for 10 to 20 minutes, or until body temperatures rose sufficiently. If a storm came late in the afternoon, they did not reappear until the next day. Cold fronts in September and October interrupted activity in much the same manner as earlier in the year.

Slope Preference

The number of lizards observed per hectare on each slope of the plot is summarized in Table I. Adults and juveniles preferred the south-facing slope throughout the activity season. Hatchlings, after emergence, followed the same trend. Little activity occurred on the north- and west-facing slopes.

Hibernation

Hibernation of adults began in late August or early September and was recognized when individuals were no longer seen at their basking stations. Juveniles remained active until mid- or late September and hatchlings remained active until mid-October. One place of hibernation was found when an adult male was sighted on 10 March at the opening to a rodent burrow. He was completely covered with mud, indicating a recent emergence.

Feeding Behavior

On 28 April 1971 an adult female was observed climbing on sagebrush and feeding among the foliage. On 13 July 1971 an adult male ran a few feet from the cover of a small oak bush, grasped a large grasshopper, ate it, and then returned to the oak bush. The lizard shook the prey by lateral movements of the head before swallowing it. On 25 May 1971 an adult male was observed moving up the trunk of an oak tree and feeding on small insects. Though specimens ate both large and small prey while in captivity, they rubbed the sides of their heads on the substrate while eating the large prey.

Aggressive Behavior

Aggression in the field and captivity was observed in many forms in all age classes and in both sexes. An example of such aggression between territorial males follows. Chased into the territory of another by the observer, the intruder was immediately challenged by the resident and a melee of biting and rolling en-

Table 1. Preference of adults, juveniles, and hatchlings for north-, south-, and west-facing slopes of the study plot. These values are ratios (number of observations) by month, which are based on the total number of observations on each slope divided by the area of each slope.

	Adults			Juveniles			Hatchlings		
	N	S	W	N	S	W	N	S	W
March	..	6.2			8.9	.007	..		
April	4.3	15.7	1.7		5.5				
May	16.4	25.3	3.7	3.2	8.9	2.9			
June	17.4	38.4	9.6	15.3	46.6	13.3			
July	22.0	26.7	5.0	18.6	19.9	14.0			
August	4.3	15.7	3.3	6.5	22.6	13.9	17.5	43.2	40.7
September		2.1	.035	1.0	2.7	7.0	12.0	101.4	40.0
October							4.3	55.5	14.0

sued, followed by a breakaway and standoff of about five centimeters. Bodies were compressed laterally to show the blue sides. Each stood high on all limbs with the back slightly arched and the dewlap lowered. Laboratory observations of territorial males revealed that the resident was always able to vanquish the intruder.

The following description covers all major actions observed in captive interactions. The intruder was placed in the box of the resident, whereupon he immediately stood high. The resident moved toward him from the side, moving his head to either side as he approached, as the intruder moved away sideways. Then the resident positioned himself parallel to the intruder, facing the opposite direction, and stood high on both limbs, compressing his sides to show the blue and lowering his dewlap. He then made a quick strike at the intruder, who ran, followed closely by the resident. When they stopped, the intruder assumed a position of passiveness with his head and tail lowered and with his body pressed low to the ground. The resident repeated the parallel body stance and then moved at the intruder, who again ran. This was repeated three times (Fig. 6A-B). Field observations in which a biting melee occurred often resulted in a temporary standoff until one was vanquished. Juvenile intruders were not tolerated by adult males and were immediately chased from the territory.

Females also reacted aggressively toward males after they had copulated. Such females, when approached by a male, flattened the body laterally, lowered the dewlap, pointed the tail upward and arched the body (Fig. 6C-D). Sometimes a female would move toward the male in a challenging posture and he would move away. Other times the female assumed this pose at the mere approach of the male and hopped on stiff legs toward him.

Basking and Panting

All age classes were observed basking on the substrate, rocks, boulders, and branches of sagebrush, under bushes, and along the main branches of oak and maple trees. Basking usually began in the morning just after the rays of the sun had spread over the study plot. The lizard's ventral surface was in direct contact with the substrate. In captivity, basking behavior under sun lamps was essentially the same. On several occasions lizards were observed panting, opening the mouth and going through the motions of breathing rapidly. In captivity, panting occurred at room temperatures of 37 to 40 C; field observations were similar.

Pushups

Sceloporus graciosus was not included in the behavioral studies of Purdue and Carpenter (1972a and b). Because of the specialized nature of their study, we have not attempted to duplicate it for *graciosus*. Our data are general and provide only field observations. Pushups were observed in all age classes and in both sexes. They appear to be most important in courtship and territoriality behavior. Males often climbed on a rock or some other object and then engaged in one low pushup and stopped; this was sometimes followed by a second (high) and a third (low) one. Other pushup sequences are possible, but the above is the most normal and may be repeated several times. During the breeding season, males did pushups as they moved through their territories. When a female was encountered, he performed while slowly approaching her. At this time of the activity season, or while in the presence of females or other males, pushups were performed very high on the forelimbs. As he approached to about 7 to 10 cm from the female, the sequence was one low and one or two high pushups.



Fig. 6A-D. Aggressive behavior between males (A and B) and between females and males (C and D).



Fig. 6 A-D (Continued)

Reproductive Behavior

Mating behavior was observed eight times in the field and three times in captivity. On 4 June 1971 a female moved a distance of approximately two feet through a bush after being disturbed. It was then noticed that she carried a male with her. He had hold of her neck, was in a dominant position over her body, and was doing partial pushups while holding on to her. The posterior part of his body was then brought under the female, putting the vents into contact. The hemipenis was inserted into the cloaca as the vents came into contact. There was no movement of the posterior part of the male's body and the hemipenis was held inserted for approximately eight seconds, after which the female broke away, leaving the male stationary. He pursued her persistently for a few feet with the tail raised and the hemipenis still everted. It took approximately one minute for the hemipenis to be retracted. The male exhibited an erratic pursuit of the female in contrast to normal running and courting. As males approached females in the field, they did pushups and rapidly bobbed their heads. Females were grasped anywhere from midbody to just behind the ear, and males remained in a dominant position over the female for 8-10 seconds before attempting to copulate.

Captive reproductive behavior was similar, but with the following variations. When a male first noticed the female, he approached her with his head bobbing. The female was passive, not moving and remaining low to the ground. The male grasped the female twice before taking a firm grip on her shoulder, then assuming a dominant position over her. A few seconds elapsed without movement before copulation occurred. The hemipenis contracted rhythmically in waves of approximately two per second. After a short period of separation and reintroduction, the male no longer approached the female. The basic posture of the male and female during copulation is shown in Fig. 7A-C. One male rubbed the vent on the substrate after the hemipenis had been retracted. In a few instances the male did not perform pushups or head bobbing before he grasped the female. Actual times of copulation (contact of genital organs) in captivity ranged from 5 to 10 seconds. The tail of the female in each case thrashed during copulation.

A complete sequence of egg laying was not observed; however, laboratory observation revealed that females dig into the substrate 15 to 20 cm, lay eggs, and then fill in these holes as they return to the surface.

Food Habits

The contents of 393 stomachs were examined in 1971 and 1972. All age groups throughout the activity season for both years were included. Data in Table 2 indicate the major families of arthropods that were preyed upon by *S. g. graciosus*.

Data indicate a seasonal fluctuation of prey items taken by two age groups in 1971 at the ordinal level. In both years lizards were opportunistic in their feeding habits, with monthly changes in diet following the changes in abundance of different orders of arthropods. In each age group, in both years, the priority of numbers and consistency of orders eaten in each month were essentially the same.

The number and size of prey items consumed each month by adult males were noticeably different from those consumed by females. For example, of 1,383 Hymenoptera, 991 (predominantly ants) were consumed by females; and of 284 Coleoptera, 149 were consumed by males. With regard to total numbers of all orders eaten by females, 1,494 of 2,157 were consumed, indicating that females consume a larger number of items than males. When considering volume, the order of priority for food items changed. For example, Hymenoptera were the most frequent stomach item; however, in adults they made up 5.47 cc, while Coleoptera made up 7.26 cc. Total volume was 14.00 cc for males and 15.70 cc for females. These volumes indicate that, while females eat more, they eat smaller prey; total volume consumed is not significantly different.

Ontogenetic Changes in Color and Color Pattern

According to Stebbins (1966), hatchlings (24-27 mm SVL) have the characteristic color pattern of adults. In the central Utah population we find that males at 24.5 to 32.0 mm SVL begin to show faint blue green ventral belly patches. By the time they average 34 mm SVL in mid-September, the ventral patches are edged with black. The blue is still blended with the green and is not yet as dark as in adults. Males reaching 36 to 39 mm SVL show traces of throat barring. Females may show a faint outline of ventral patches between 32 and 35 mm SVL.

Juvenile males continue to develop darker blue patches ventrally, and by late April and May (at approximately 40-45 mm SVL), they have essentially the same color pattern as adult males of 55 to 60 mm SVL. Juvenile males that are over 47 mm SVL in mid-May are essentially of the same brilliance as adults.

TABLE 2. Analysis of the stomach contents of 183 *S. g. graciosus* collected in 1970 and 1971 listed by order and family from highest to lowest in number of each.

Taxon	1970	Total	Taxon	1971	Total
<i>Hymenoptera</i>			<i>Hymenoptera</i>		
Formicidae		2806	Formicidae		1981
Andrenidae		86	Unclassified		39
Eulophidae		36	Andrenidae		20
Unclassified		28	Eulophidae		16
Halictidae		22	Halictidae		10
Other		24	Other		41
Total		3002	Total		2107
<i>Coleoptera</i>			<i>Coleoptera</i>		
Curculionidae		126	Curculionidae		131
Unclassified		64	Chrysomelidae		53
Carabidae		41	Coccinellidae		48
Chrysomelidae		35	Scarabaeidae		45
Elateridae		28	Unclassified		33
Coccinellidae		20	Elateridae		32
Tenebrionidae		15	Carabidae		27
Other		24	Tenebrionidae		12
Total		353	Other		18
			Total		399
<i>Arachnoidea</i>			<i>Isoptera</i>		
Araneida			Rhinotermitidae		237
Unclassified		53			
Lycosidae		40	<i>Hemiptera</i>		
Other		10	Unclassified		77
Total		103	Lygaeidae		57
			Other		23
<i>Hemiptera</i>			Total		157
Lygaeidae		39	<i>Arachnoidea</i>		
Unclassified		23	Araneida		
Other		16	Unclassified		84
Total		78	Lycosidae		17
			Acarina		28
<i>Homoptera</i>			Total		129
Cicadellidae		30	<i>Homoptera</i>		
Aphidae		15	Aphidae		59
Membraeidae		11	Cicadellidae		28
Fulgoridae		10	Unclassified		17
Unclassified		5	Other		7
Total		71	Total		111
<i>Orthoptera</i>			<i>Diptera</i>		
Locustidae		47	Unclassified		27
Gryllidae		2	Chironomidae		18
Total		49	Other		36
			Total		81
<i>Isoptera</i>			<i>Lepidoptera</i>		
Rhinotermitidae		43	Unclassified		56
			Geometridae		3
<i>Lepidoptera</i>			Total		59
Unclassified		34	<i>Orthoptera</i>		
Other		10	Locustidae		51
Total		44	Other		6
			Total		57
<i>Diptera</i>			<i>Microcoryphia</i>		
Unclassified		39	Machilidae		15
			Other Orders		6
<i>Isopoda</i>		15	Other Orders		6
			Grand Total (1971)		3367
<i>Trichoptera</i>		4			
Other Orders		7			
Grand Total (1970)		3807			



Fig. 7A-C. Copulation sequence of lizards in captivity indicating major posture of the male and female.



Fig. 7 A-C (Continued)

Juvenile females lose the outline of a ventral pattern as they grow and do not become orange laterally until they become breeding adults.

When adult females emerge (March or April), there is no nuptial color laterally. The venter is white and the normal dorsal and lateral color pattern is present (Stebbins, 1966). In April and May, while the female cycle is undergoing vitellogenesis and the ovarian eggs are approaching ovulation (6.5-7.0 mm diameter), they begin to take on the orange coloration laterally. This color may extend from the head to the groin region and even onto the tail. Females reached their most brilliant nuptial colors while carrying oviducal eggs, between 8 and 24 June 1971.

In females the ventral patches are usually lime yellow and extend to the throat and the anteroventral part of the tail. This lime yellow suffusion follows the same sequence as the lateral orange areas, although some females may have the lateral orange, but with the ventral yellow greatly reduced. After mid-July the nuptial colors are lost. Two exceptions to this were a pair of females captured on 27 August 1970 and 20 August 1971 which were very orange, but palpation revealed no oviducal eggs.

Adult males emerging in March have the characteristic color and pattern described by Stebbins (1966). The most brilliant period for the lateroventral blue and black is April through July, though some males may still be brilliantly colored in August. There is also considerable blue green in the lateral scales of the shoulder region and posteriorly onto the base of the tail. There is no blue green on the tail where regeneration has occurred.

Parasitism and Predation

Stomachs were removed approximately 3 to 5 mm below the pyloric sphincter. While removing stomachs from 690 specimens, one tapeworm was found in an adult male and one in an adult female. These were identified as *Oochoristica scelopori*; no nematodes were found. External parasites were either ticks or mites (Acarina) and were found on specimens from West Canyon, Utah County.

Examination of 690 preserved specimens from Utah County and parts of Wasatch and Salt Lake counties, revealed only two cases where the cardrum of the lizard was discolored and a heavy growth had replaced the thin transparent structure. Abnormalities were not ob-

served internally on autopsied specimens. Animals from the study plot were checked externally only and no infections other than an occasional swollen toe from identification clipping or natural loss were observed. Infection or swelling at the point of tail breakage was not observed.

Predation was not witnessed in the field. Utah County records indicate the night snake *Hypsiglena torquata* as a predator. Possible predators in sympatric areas may include predaceous reptiles, hawks, and mammals.

Ontogenetic Changes in the Tail

Ten arbitrary size classes were chosen and the mean SVL and tail length were taken on 20 animals in each size class except for the smallest and largest sizes. The mean SVL of each size class was plotted against the mean tail length (Fig. 8), contrasting males and females throughout their growth from hatchlings to adults.

Tail Breakage of Study Plot Lizards

Hatchlings, juveniles, first-year (after second hibernation), and older adults were analyzed in 1970 and 1971 for tail breakage. Males and females were contrasted throughout the activity season. These data can be summarized as follows: adults, males 14 of 69 (21 percent), females 18 of 116 (15 percent); juveniles, males, 10 of 97 (10.3 percent), females 8 of 131 (6.1 percent); hatchlings, males, 5 of 247 (2 percent), females 10 of 231 (4.3 percent). There was an increase in breakage from hatchlings to adults (3 percent, 8 percent, 18 percent). One specimen from the field and one from the study plot had bifurcated tails.

The regenerated portion did not have the same color or color pattern as an intact tail. This was strikingly apparent in males with the blue green on some lateral scales which extended onto the proximal half of the tail.

Average Size of Females at Sexual Maturity

Sexual maturity in females was determined by noting the development of the gonads. The main criteria used were the presence of yolking follicles in the ovaries, oviducal eggs, or corpora lutea during the reproductive period. Most reproductive activity took place before 1 July; therefore, 1 July was used as the date females were considered mature for that particular year. All females 53 mm SVL or larger were considered mature. Study plot females found with eggs (based on palpation and color and weight of females) were in this range. Three females which were 47, 48, and 49 mm SVL, autopsied on 28 May 1970 and 7 June 1971, had small yolking ovarian eggs 2 or 3 mm in diameter. Egg development in these females was late in the season compared to other larger females. If these eggs were eventually laid, it would have been late compared to the average time taken to reach ovulatory size and egg laying. Such individuals made up only 1 percent of the breeding population.

Follicle Growth

As females grew from hatchlings to adults, the average number of unyolked follicles increased in number and enlarged. Ovaries were visible as small white tissue masses in the smallest hatchlings captured (25 mm SVL). The August hatchlings between 25 and 33 mm SVL may have none; however, 70 percent had one to four follicles (Table 4). September and October hatchlings, just prior to hibernation, showed an increase in size and number of follicles. During hibernation there appeared to be little growth in the ovaries, although we did not examine hibernating lizards. In the spring, follicles continued to increase in size and number until June, then decreased in July and increased again in August (Table 3).

Adult females underwent seasonal changes

TABLE 3. Number of unyolked follicles in hatchlings and juveniles by month, 1970-71. All measurements are

	HATCHLINGS								
	March-April			May			June		
	SVL	Dia.	Foll. No.	SVL	Dia.	Foll. No.	SVL	Dia.	Foll. No.
Mean									
Range									
Number ^o									
	JUVENILES								
Mean	34.8	.40	11.3	40.0	.70	16.4	43.2	.80	15.8
Range	30-37	.1-1.1	7-13	35-45	.1-1.7	9-23	40-50	.1-2.0	8-22
Number ^o	11			11			15		

^oNumber of specimens examined.

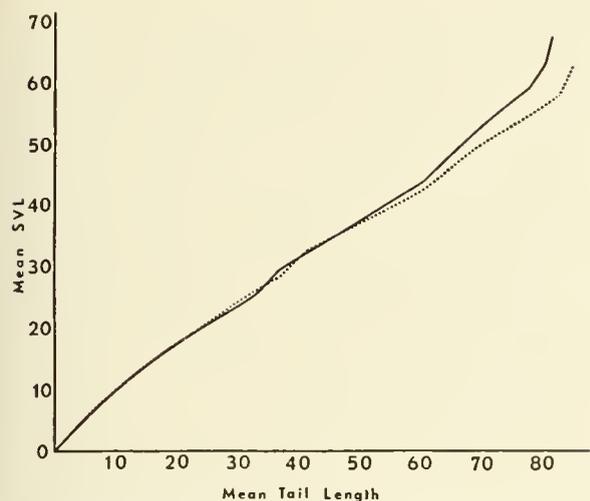


Fig. 8. Mean snout-vent length of sagebrush swifts plotted against mean tail length (mm) for 1970-71. Females are represented by solid line and males by dotted line.

in the number and size of unyolked follicles (Fig. 9). The total number of follicles may change seasonally, with the lowest number occurring in July after the eggs are laid (Table 4). Our data indicate that from March to June a decrease in size and number of unyolked follicles above 1.5 mm occurred. Between 1 July and 15 August only five follicles above 1.5 mm were seen in 1971 and only one in 1970 (Fig. 9). This indicates that follicles show a reduction in size in July and the first half of August. From mid-August until hibernation there was an increase in mean follicle number and size. In September follicles ranged between 1.9 and 2.0 mm, appeared to be yellowing, and perhaps were beginning vitellogenesis.

In Fig. 10 the total number of follicles in each of five lizard size classes are compared, indicating that unyolked follicles increased in number as females became larger and older.

in millimeters.

Meiosis

Serial histological sections revealed that follicles went through meiosis both in the fall (August-September) and spring (March-April). Eleven of the first 12 females collected from 29 March to 29 April 1971 were undergoing meiosis. Of the last 13 females captured 24 August to 23 September, 12 were undergoing meiosis. The size range (determined from slides) of follicles undergoing meiosis was .5 to 1.5 mm—average size in the fall being .96 and in the spring being 1.05.

Yolk Deposition

Females were not yolking follicles in August. In September follicles were slightly larger and from cream to light yellowish in color. All began soon after emergence in the spring. Yolking eggs continued to increase in size up to the

TABLE 4. Fluctuation in the number of unyolked follicles in the ovaries of adult females, 1970-71.

Month	Follicles	Number of		
		Lizards	Range	Mean
<i>March</i>				
1970				
1971	46	2	20-26	23.0
<i>April</i>				
1970	78	4	18-21	19.5
1971	323	15	7-31	21.5
<i>May</i>				
1970	134	6	10-30	22.3
1971	541	27	13-28	20.0
<i>June</i>				
1970	108	5	18-28	21.6
1971	1244	74	4-27	16.8
<i>July</i>				
1970	322	18	11-24	17.9
1971	584	37	9-24	15.8
<i>Aug.</i>				
1970	466	22	12-31	21.2
1971	354	20	12-35	17.7
<i>Sept.</i>				
1970	112	5	20-25	22.4
1971	219	10	15-33	21.9

HATCHLINGS

	July			August			Sept.-Oct.		
	SVL	Dia.	Foll. No.	SVL	Dia.	Foll. No.	SVL	Dia.	Foll. No.
Mean				27.8	.20	2.5	33.4	.34	7.8
Range				25-33	1-4	1-4	31-41	1-9	3-21
Number°				4			17		

JUVENILES

Mean	43.2	.70	13.7	52.1	.74	15.7
Range	40-53.5	1-1.5	7-24	50-53	1-1.6	12-21
Number°	23			7		

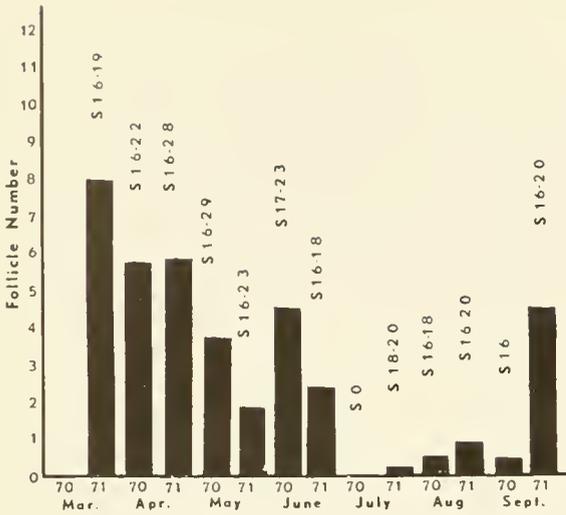


Fig. 9. Mean number of unyolked follicles greater than 1.5 mm in diameter in adult females plotted against 30-day intervals throughout the activity seasons of 1970 and 1971. The S represents the size range of follicles in mm.

time of ovulation. The smallest diameter for definite yolk deposition (by color) ranged from 1.5 to 2.0 mm (late March and early April), which is close to the approximate size of meiotic follicles (mean 1.30 mm). Yolking eggs increased from an average of 1.75 mm in late March to a peak of 7.09 mm in diameter in the first half of June, with a range of 6.5 to 8.5 mm just prior to ovulation. This was an increase of approximately .07 mm per day. Weight followed the same trend as size. Eggs less than 2.0 mm in diameter weighed less than 0.1 g. In June oviducal eggs averaged .21 g per egg (N-65) with a range of .14 to .28 g per egg. These were from clutches ranging from two to seven eggs. Yolk deposition occurred in the populations from 29 March to 3 July, a period of 97 days.

Ovulation

Eggs passed into the coelom and from there into the oviducts. Ova in the coelom were flaccid and the only structure holding the yolk was the vitelline membrane. One female (BYU 3338, 64 mm SVL) found on 10 June 1971 contained some eggs recently ovulated, two in the coelom, and others entering the oviducts—a total of seven eggs in the clutch. Judging from the delicate nature of ovulated eggs, it would seem that females might reduce their activity to prevent breakage; breakage was not observed. A female captured on 29 May 1970 had six eggs (three per ovary) and all were between 6 and 7 mm in diameter. In addition, there were two eggs (5 mm each) free in the coelom. They

were greyish and slightly crenated in appearance, yet pliable and with discolored yolk. Ovulation in *graciosus* took place approximately between 2 June and 3 July 1971, the 32-day period between the first and last oviducal eggs. The majority of females were undergoing ovulation from 2 June to 24 June (22 days), at which time oviducal eggs and the first corpora lutea appeared. In 1970 the development of eggs was approximately 15 days later than in 1971. The actual time required for each stage (yolk deposition, etc.) remained fairly constant in terms of active days.

Mating Time in the Field

Copulations were observed in the field between 21 May and 4 June 1971 and in captivity between 2 June and 9 June. At this time males and females were seen together in the field in contrast to the periods before and after the majority of copulations. Observations of field and captive individuals from 21 May to 9 June suggest that the majority copulate over a period of approximately 20 days. This time period may extend earlier into May but probably not later into June, except in years with unusually late springs.

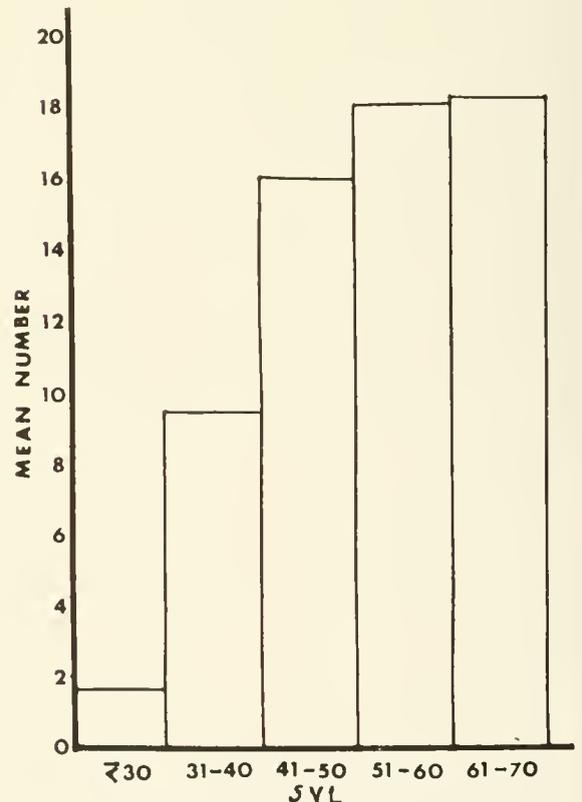


Fig. 10. Unyolked ovarian follicles plotted against snout-vent length. Hatchlings to adults.

Egg and Clutch Size and Weights Following Oviposition

Clutch size and SVL for females laying eggs in captivity are listed in Table 5. Twelve clutches (68 eggs) were weighed and measured within one to five days after oviposition. The mean size of recently oviposited eggs was 13.4 x 7.9 mm with a range of 12.0 x 6.5 to 15.5 x 9.0 mm. The mean weight was .48 g per egg with a range of .30 to .76 g per egg. Compared to the weights of oviducal eggs, these recently laid eggs averaged .20 g more. They were also larger in size, 13.4 x 7.9 mm as compared to 12.0 x 7.1 mm. A few clutches were in moist sand for a few days and undoubtedly increased in size and weight by water absorption.

Size and Weight Changes in Gravid and Nongravid Females

The size and weight changes in females before and after laying and the time that elapsed between the periods are listed in Table 6. Compared to the average weight of clutches, the average weight per egg was .48 g (Table 5). These data also indicate that females that have laid eggs with an intervening period of 10 days or less show no difference in size (SVL) but weigh 1.5 to 3.0 g less.

Clutch Size, Clutches per Year, and Comparisons of Left and Right Ovaries and Oviducts

Clutch size in *graciosus* was determined after the method used by Tinkle (1961). The number of ovarian eggs, oviducal eggs, and corpora lutea in both ovaries and oviducts are listed in Table 7. Clutch size was 6.03 eggs per female. There were slight but not significant differences in the number of ovarian eggs, ovi-

TABLE 5. Number and weight of ova 1 to 3 days after laying (1972) for 12 clutches laid in the laboratory.

Number of eggs in Clutch	SVL	Weight of Clutch	Average Weight per Egg
8	63	4.80	.600
5	62	2.28	.456
6	62	3.12	.520
6	65	2.05	.341
7	64	3.39	.481
5	62	2.72	.544
5	59	2.31	.462
4	59	2.26	.565
6	61	2.69	.448
5	58	2.11	.428
5	69	2.46	.410
6	63	2.47	.494
Mean 5.66	62.3	2.72	.479
Range 4-8	58-69	2.05-1.80	.341-.600

ducal eggs, and corpora lutea. The mean for either left or right side was 3.00 eggs each. The overall mean clutch size for each of the three methods mentioned above was 6.22, 5.85, and 5.90 eggs per female, respectively.

Corpora Lutea

Corpora lutea of BYU 3338, which had just ovulated, were used as a standard of appearance; they were red (vascular), and the tissue proper was thin and translucent in appearance. Recent corpora lutea were large (3-4 mm in diameter) and doughnut shaped, with an indented area on one side near the center. They regressed in size by one-third (2-3 mm) and became less vascular and greyish in appearance, while the eggs remained in the oviducts. Soon after the eggs were ovipositioned, the corpora lutea turned yellowish, beginning a rapid re-

TABLE 6. Size and weight differentials of female lizards before and after eggs are laid (1970-71)

Date	Date Gravid	Weight Gravid	SVL Gravid	Date not Gravid	Weight after Laying	Days Between	Weight Difference	SVL After
1970	6-26-70	9.32	58.0	7-11-70	7.56	16	1.76	59.0
	7- 7-70	7.24	59.0	7-14-70	4.83	7	2.76	59.0
	7-14-70	9.08	61.5	7-31-70	7.54	18	1.54	63.0
1971	6-18-71	9.11	64.0	7-16-71	7.31	29	1.80	65.0
	6-26-71	7.11	58.0	7- 9-71	5.70	14	1.41	59.0
	6- 4-71	9.56	64.0	7- 9-71	7.38	35	2.18	64.0
	6-15-71	8.24	62.0	6-24-71	5.20	10	3.04	60.0
	6- 8-71	10.65	66.0	6-21-71	8.03	14	2.62	66.0
	6-18-71	8.06	60.0	6-25-71	5.17	8	2.89	57.0
	6-21-71	9.06	65.0	7-15-71	6.24	25	2.82	61.0
	7- 7-71	8.14	64.0	7-16-71	5.14	9	2.00	
1972°	6-30-72	8.12	62.0	7- 2-72	5.37	3	2.75	61.0
	6-30-72	6.85	60.0	7- 4-72	4.96	5	1.89	58.0
	6-30-72	9.80	69.0	7-10-72	7.56	11	2.24	69.0
	6-30-72	7.55	64.0	7- 7-72	5.56	6	1.99	63.0
Average		8.53	62.4		6.24	14	2.24	61.7

°Captive.

TABLE 7. Clutch size in *S. g. graciosus* for 1970 through 1972.

	Yolked Ovarian Eggs		Oviducal Eggs		Corpora Lutea	
	Left	Right	Left	Right	Left	Right
Total	205	206	134	147	88	83
Number	68	64	48	48	29	29
Range	1-6	1-5	1-5	1-5	2-4	2-4
Mean	3.01	3.21	2.79	3.06	3.03	2.86
Combined mean	6.22		5.85		5.90	
863 Ovarian eggs, oviducal eggs, and corpora lutea						
143 Lizards						
2-10 Range						
6.03 Mean clutch size						

gression until they disappeared in approximately 10 to 12 days. Corpora lutea were found in the population from 2 June to 17 July 1970, a period of 45 days, and 15 June to 25 July 1971, a period of 40 days.

Atretic Follicles

Atretic follicles were of three types. First, yolking follicles were considered to be atretic if there were corpora lutea or oviducal eggs present. These follicles appeared to be the beginning of a second clutch; however, based on average time for vitellogenesis and oviducal development, they were late in the season for successful incubation. In addition, females were not found with oviducal eggs after the third week in July. Nuptial colors persisted beyond this date in only three individuals, but no eggs were found. Second, follicles that were few in number and appeared yolked in an ovary but were turning reddish yellow were considered atretic. These were apparently regressing in size. This condition was also observed before ovulation in a few females in which some yolked ova changed color and remained smaller in size. The third condition was that of crenulated ova in the oviduct. In all three types a total of about 13 percent of the females examined had atretic follicles.

Oviducal Egg Period in Oviducts, Size and Weight

In 1971 oviducal eggs were found from 2 June to 10 July, a period of 38 days. Two captive females copulated on 7 and 9 June and laid eggs on 28 June and 2 July. These were periods of 22, 24, and 27 days, an average of 24.3 days, which is the approximate time eggs are in the oviducts, assuming that ovulation occurs at or just after copulation. Both 1970 and 1971 oviducal eggs were used for calculating size and weight of eggs. Oviducal eggs were

weighed with the oviduct, which added a slight bias to the weight of the eggs. They averaged 12.0 x 7.1 mm with a range of 10 x 7.5, 11 x 6.5 mm to 14 x 8, and 15 x 7 mm. The average weight per oviducal clutch was .28 g with a range of .20 to .38 g. This was .07 g greater than ovarian eggs. In 1971 oviducts were vascularized from 10 May to 10 July. After oviposition the oviducts are no longer convoluted and lose their vascularization.

Ovamigration and Oviduct Anatomy

Transcolumic migration occurs frequently in *graciosus*. Of 48 females having oviducal eggs, 20 had eggs in the right or left oviducts that were of a different number than corpora lutea in the ovaries. Forty-two percent of these females had undergone transcolumic migration of ova. Therefore, ovamigration at the time of ovulation is essentially a 50:50 relationship in which any ovum has an equal chance of entering either oviduct. This has a limitation apparently in that no more than five eggs were ever found in one oviduct. The trend of migration follows several patterns. First, there is an even number of corpora lutea in the ovaries with a reduced number in one of the oviducts. Second, they are exactly reversed from ovary to oviduct—e.g., two corpora lutea in the right ovary, but three eggs in the right oviduct. Third, corpora lutea are of unequal numbers in the ovaries and there is a highly unequal number of eggs in the oviducts. For example, BYU 32616's right oviduct had three eggs and the right ovary had one corpora lutea. The fourth condition is an equal number of corpora lutea in the ovaries with an equal migration of ova to each oviduct.

The oviducts approaching ovulation appear convoluted and vascularized. At their anterior end they open into a slitlike ostium. The ovaries are attached dorsally to the body wall anterior to the oviduct. The oviduct is laterally displaced in relation to the ovary, with the expanded ostium lateral to the adjacent ovary and also at an angle to it.

Oviposition

Egg laying occurs after eggs in the oviducts have received the membranous shell. The period during which females are laying eggs, oviposition, was calculated from study plot and collection data (1970-71). At our study plot the egg-laying period lasted 29 days, (3 July-31 July) in 1970 and 31 days (19 June-20 July) in 1971. Clutch size increased as females grew in size (Fig. 11).

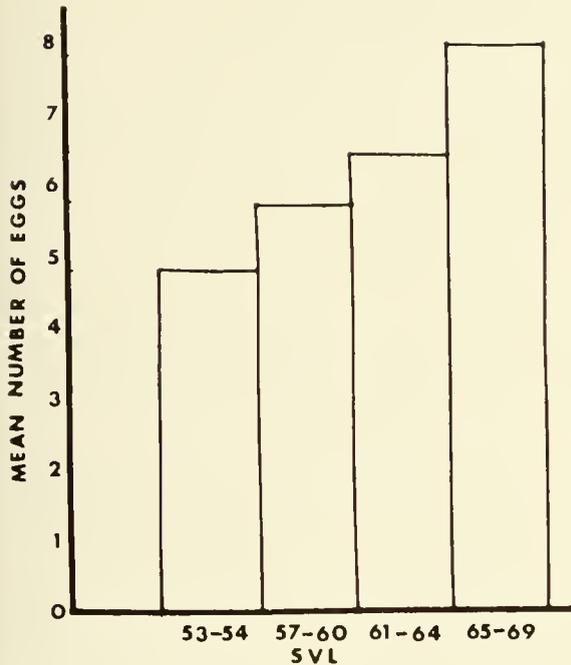


Fig. 11. Clutch size plotted against SVL in four size classes of female *S. g. graciosus*.

Incubation Period

The period from the first captured female with only corpora lutea to the first hatching extended from 3 July to 24 August 1970, 21 June to 6 August 1971, and 17 June to 10 August 1972, periods of 43, 48, and 55 days, respectively. The incubation periods from field data were as follows: 1970, 6 July to 17 August; 1971, 19 June to 1 August; 1972, 1 July to 10 August (periods of 43, 44, and 41 days, respectively, for a combined average of 43 days). The incubation period for eggs from the time of oviposition in 1970, combining the field and study plot data, was 48 days. In 1971 the period was 46 days, and in 1972, 48 days. The average period combined for three years was 47 days. The data also indicate that the incubation period of 1970 was approximately 15 days later than for 1971, with 1972 in between. In addition to this indirect data, nine clutches of eggs were incubated in the laboratory at 27 to 28 C in quart jars partly filled with moist sand. The overall average for these clutches was 49 days, a figure similar to the field and study plot data. The average period for clutches where the exact date of laying was known was 46 days, which closely approached the overall average. From these data was derived the average incubation period from the time the eggs were laid: 48 days, with a range of 44 to 52 days.

Oviducal eggs taken from field females and those captive females having recently oviposited each showed a distinct area where the embryo had probably been growing since the time of fertilization. Known measurements of captive females placed the eggs in the oviducts for a period of approximately 22 to 27 days. This was particularly true if eggs were ovulated shortly after copulation (1-5 days) and if they were fertilized at or about the time they entered the oviduct. Data concerning ovulation time and copulation period strongly suggest that fertilization occurred at or shortly after the eggs entered the oviducts. If this were the case, it would add approximately 25 days to the actual incubation period.

Sixty-eight eggs were laid and recovered from the pen where 13 females were kept. Eight eggs (11.7 percent) were infertile. Seven clutches did not contain infertile eggs, two had two each, and four had one each. Infertile eggs appeared softer and amber in color. They did not attain turgidness, were soon attacked by fungus, and, unless removed, began to contaminate the entire clutch. From the remaining 60 eggs, 11 died just before their clutch mates hatched. The embryos were between 20 and 23 mm SVL. The yolk sac was intact with a small amount of yolk still remaining. The 49 eggs remaining were reduced by fungus contamination and other causes, leaving only 34 eggs that hatched.

Average Size of Males at Sexual Maturity

Sexual maturity was determined by gonadal development, size, and glandular development. The main criterion used was the presence of spermatozoa in the testes and epididymis during the reproductive period. As in females, 1 July was used as a seasonal date when males, on the basis of size, were considered mature. Some juveniles may reach mature size by the second week in July and may be mistaken for adults even though they are not sexually mature. Based on the above criteria, males 52 mm SVL were considered sexually mature. There were three exceptions (1 percent of total mature males) in 1970 and 1971 field specimens. These three were 43, 46, and 50 mm SVL. In 1970 and 1971, none of the breeding population of plot males were below 52 mm SVL. This was based on external appearance of males (ventral color, discolored pre-anal area, and swollen tail base). While a few juvenile males in 1972 appeared as above in late June and early July, our autopsy data indicate that juveniles are not functional until after the second hibernation.

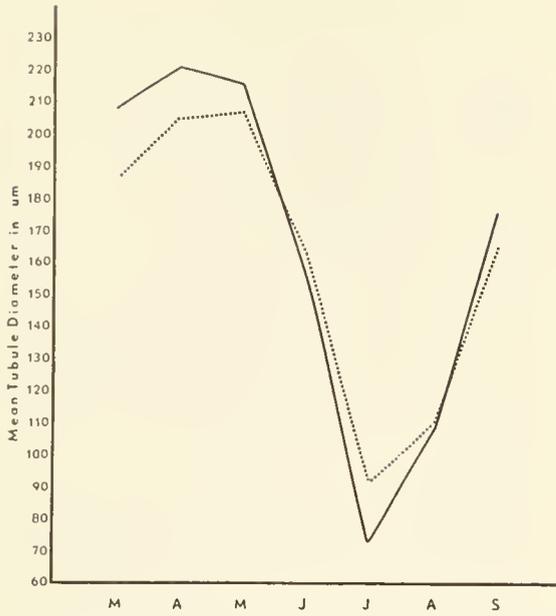


Fig. 12. Mean seminiferous tubule diameter (um) by month for 1970 and 1971. Solid line represents 1970, dotted line, 1971.

Spermatogenic Cycle

Histology of the testicular cycle in males was grouped into eight stages by Mayhew (1971). Stages of mature males during the 1971 activity season are listed in Table 8. This table and Fig. 12 to 14 depict mean seminiferous

TABLE 8. Observed spermatogenic stages in sexually mature *S. g. graciosus* for 1970-71, during the first and second half of each month of the activity season.*

Stage	March		April		May		June		July		Aug.		Sept.	
	1	2	1	2	1	2	1	2	1	2	1	2	1	2
1		3								2	18	18	11	3
2		2												
3		7	4											
4		1	4											
5			1	1										
6				5	9	9	5	4						
7					2	2	5	10	6	2				
8									5	8	8			
Total		13	9	6	11	11	10	14	11	12	26	24	11	3

*Stages of annual spermatogenic cycle of adult males are after Mayhew (1971).

tubule diameter, gonad weight, and epididymis epithelial height (thickness) by month and are used in constructing the spermatogenic cycle of 1970 and 1971 in the following sections.

In March 1970 male gonads were at stages 3 and 4. Seminiferous tubule diameter averaged

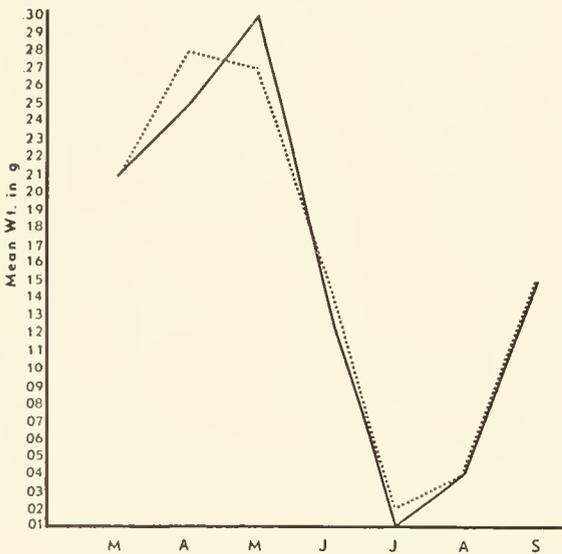


Fig. 13. Mean weight (g) of testis by month for 1970 and 1971. Solid line represents 1970, dotted line, 1971.

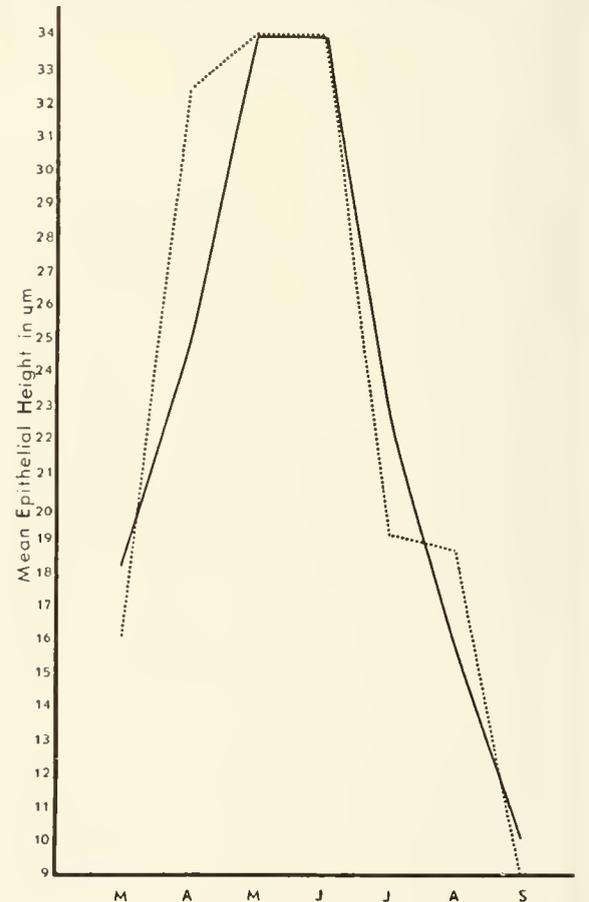


Fig. 14. Mean epididymis epithelial height (um) by month for 1970 and 1971. Solid line represents 1970; dotted line, 1971.

209.6 μm (range 185-225 μm). Epididymis epithelium was in a pseudostratified condition, with a height of 18.2 μm (range 15-21 μm). Both testes averaged .21 g per lizard in March, with a range of .13 to .35 g. Adults in April ranged from stages 3 to 6 and seminiferous tubules had reached their maximum diameter (mean = 221.0 μm , range 196-260 μm). Epididymis epithelium was proliferating and had an average height of 24.7 μm (range 10-31 μm). Gonad weight in April averaged .25 g per lizard, with a range of .14 to .34 g.

Adult males in May were at stages 6 and 7. The average diameter of seminiferous tubules was 206.4 μm (range 164-225 μm). The first males with spermatozoa in the epididymis were collected on 29 May 1970. Epididymis epithelium height averaged 34.6 μm (range 32-35 μm). Gonad weights reached their peak in May, averaging .30 g per lizard (range .23-.37 g).

In June males were still at stages 6 and 7, with the predominance at stage 7. All had spermatozoa in the epididymis and were capable of inseminating females. Seminiferous tubule diameter was 157.7 μm (range 145-203 μm). Epididymis height averaged 34.0 μm , with a range of 26 to 45 μm . Gonads averaged .14 g per lizard (range .09-.18 g).

In July males were predominantly at stage 8, with only one at stage 7. Seminiferous tubules reached their lowest level at 73.8 μm , with a range of 54 to 90 μm . The epididymis contained spermatozoa until 11 July. Epididymis height for July averaged 22.5 μm (range 17-32 μm) and began to decline on or before 11 July. Gonad weights in July reached their lowest level with a mean of .01 g per lizard (range less than .01-.02 g).

In August and September males reached stages 8 or 1, with the majority at stage 1 (26 out of 31). July and August were seemingly the end of one reproductive cycle and the beginning of the next. Diameter of seminiferous tubules for August and September averaged 107.2 and 175.6 μm , with a range of 71 to 184 and 138 to 195 μm , respectively. The epididymis height was at its lowest level with an August average of 15.8 μm (range 10-21 μm). September epididymis height was uncertain because of insufficient sample size. Only one specimen had an epididymis of 10.0 μm . Gonads averaged .04 and .15 g per lizard for August and September, with ranges of .01 to .17 and .07 to .19 g, respectively.

In 1971 males emerged in March, at which time the gonads were in stages 1 to 3. Seminiferous tubule diameter averaged 186.2 μm (range 164-210 μm). Epididymis epithelium was

pseudostratified, with an average height of 16.1 μm (range 10-20). In March gonad weight was .21 g per lizard, with a range of .11 to .26 g.

Males in April, May, and June followed essentially the same sequence in development as in 1970. There were more discrepancies in July, however. Individuals were observed to be in stages 7, 8, and 1. By late August and September males in 1971 were predominantly at stage 1, with only two at stage 8. The seminiferous tubule diameter began to increase and averaged 110.0 and 165.7 μm (ranges of 50-144 and 138-195 μm). Epididymides were pseudostratified and their heights were 18.7 and 9.0 μm (ranges 10-27 and 10-18 μm). The weights of gonads were beginning to increase, with averages of .04 and .15 g per lizard, with ranges of .10 to .12 and .04 to .22 g.

The spermatogenic cycle in 1970 was approximately fifteen days later than in 1971. In March 1970 lizards were at stages 3 and 4, while 1971 lizards were at stages 1 to 3. It appears that males in 1970 were more advanced than those in 1971 even though in both years they emerged at approximately the same time. However, by the first half of May 1971, lizards were more advanced than those in 1970. By April 1971 epididymis epithelium had proliferated almost to its maximum for the year, whereas 1970 epididymides were considerably lower in epithelial height (Fig. 12). In addition, epididymides in 1970 were not found with spermatozoa until 29 May. However, to be comparable to 1971 this should have occurred on approximately 15 May. In contrast to the date of 15 May for 1970, 1971 lizards contained spermatozoa in the epididymides ten days earlier on 6 May.

General Trends

Even though adult and juvenile males enter hibernation with gonads approaching maximum size, they continue to increase during hibernation and develop more rapidly after they emerge. Peak development of gonads is in the latter half of April and the first of May. Male epididymides usually contain spermatozoa in late May and are capable of insemination. Spermatozoa remain in the epididymides until mid-July. By the latter part of June, the epididymis epithelium is sloughing and the lumen is full of cellular debris. Thus, active spermatozoa are in the epididymides from 1.5 to 2 months each year, a period much longer than that normally used for copulation (as based on field observations over three seasons). By the end of May the gonads are regressing. They continue to regress through June, and by mid-July are at their smallest size

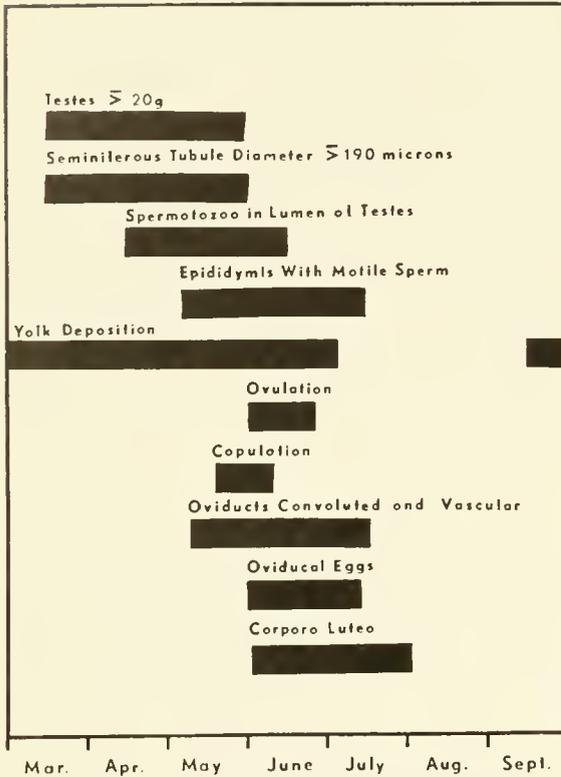


Fig. 15. Summary of various reproductive stages of adult *S. g. graciosus*. Both 1970 and 1971 data are combined in order to simulate the average yearly trend.

(Fig. 12-14 and Table 8). In August the gonads again begin to increase in the size of seminiferous tubules and weight, continuing until the lizards hibernate in late August and early September.

Male stages are compared with those of females in Fig. 15. The combined time periods (1970-71) are used to give the general yearly trends of male lizards in relation to females. Our data for reproductive cycles in this species are generally similar to that reported by Woodbury and Woodbury (1945).

Pre-anal Gland

After considerable handling of lizards to obtain field measurements, it was noticed that males left a moist area on the transparent ruler. This moist area was directly in front of the vent and was discolored in relation to other areas anterior to it on the abdomen. At first the moistness was suspected to be from the normal cloacal discharges; however, careful checking determined it to be a glandular secretion which darkened the scales in the pre-anal area of adult males during the copulatory period. Histological sections of adult males show that there is indeed

a gland just anterior to the cloaca, under the epithelial tissue—a duct gland, with cells lining a lumen. The details are presented in a separate report (Burkholder and Tanner, 1974).

Color in Males

Adult males are most brilliantly colored from April until mid- or late July. During this time, the ventral and ventrolateral portions of the head, neck, lateral and ventral chest, abdomen, and the lateral part of the tail are colored. These colors differ from the white ventral base color and brown dorsal ground color. The range of color varies from black to light orange. During the height of color display, an average male has barring of black and light blue interspersed with white on the throat scales. The chest has black areas (irregular) on a white base. The ventral patches begin behind the axilla and extend to the groin, with the inner edge lined with one or two rows of black scales. Proceeding from the black edge, the scales are deep blue and gradually lighten from the ventral to the lateral, becoming greenish yellow in the region of the light lateral body bar. The patches are separated by 3 or 4 rows of white scales. Laterally, starting in the axilla, the scales of the light lateral bar exhibit some orange, but it is faint and—in contrast to females—usually does not extend to the groin region.

Fat Body Relationships in Adults

In the sections on ovarian cycles and spermatogenesis, considerable emphasis was placed on time difference between the cycles. In the analysis of fat bodies, the data for 1970 and 1971 are combined to increase the number of samples and demonstrate the difference between male and female cycles. Differences between the two years are discussed briefly, but the bulk of this section will deal with male and female differences in all ages. All figures are based on mean fat body weight divided by mean body weight, giving a percent of body weight for the fat body.

In 1970 fat bodies in males were smallest in June; 1971 males had already started their increase (by weight) prior to July. This difference is significant because in both years fat bodies began to decline in size and weight by late April. In 1971, lizards completed their gonad peak (by weight and size) in the first half of May. In 1970 males reached their gonad peak in the latter half of May and did not begin fat body buildup until June (Fig. 16).

Comparisons of females for these years indicate the same time lag as males in fat body decline and buildup, although the decline in



Fig. 16. Fat body fluctuations by month during 1970-71 for males and females. A, females 1970; B, females 1971; C, males 1971; and D, males 1970.

1971 was considerably faster than in 1970. Fat bodies in 1971 were at about the same level in April as those of 1970 were in May (.2 percent difference). In May 1971 they were near their smallest size-weight (.1 percent weight), but in 1970 fat bodies were almost the same weight as in 1971. By June both were at their lowest weight and began an almost identical increase from that period to hibernation.

In Fig. 17 the mean body weights by month and the percent of body weight for fat bodies are compared. It is apparent that females had larger fat bodies than males except in June and July. The June discrepancy is explained by noting that females were at their lowest fat body average and their highest average body weight (1.08 g greater than males). If the average weight of oviducal eggs is subtracted from body weight, the percent of body weight for fat bodies will also be higher in June for females. With few exceptions, all sexual activity is over by July, and female mean body weight is almost the same as that of males. This similarity in body weight in July makes it apparent that females have larger fat bodies than males in August and September (1.9-1.2 percent, respectively).

Juvenile Gonad and Fat Body Relationships

Juvenile fat body fluctuations are depicted in Fig. 18, along with average weight per month. These data indicate that juvenile males follow a fat body and gonad cycle similar to that of adult males, which is most apparent from July to hibernation. In addition, hatchlings also show a buildup of fat bodies before hibernation.



Fig. 17. Comparison of fat body fluctuation, by month in adult males and females (1970-71 combined). Upper lines, mean body weight; lower lines, fat bodies. Males are represented by solid lines and females by dotted lines.

Hatchling Home Range

Hatchlings actually do not have a home range; therefore, the term *area of activity* is proposed. They reside in their areas of activity after hatching and are slowly dispersed before hibernation. Retrapping data suggest that some

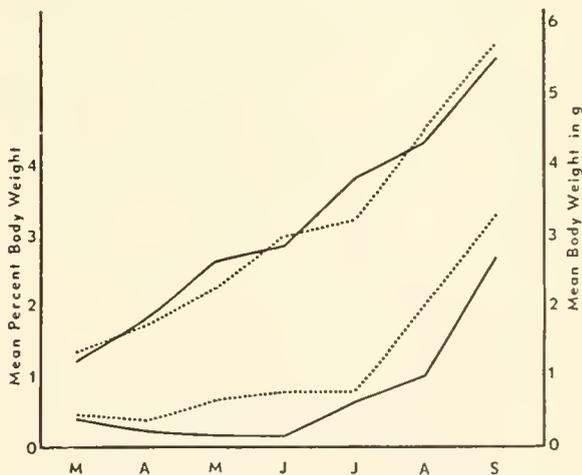


Fig. 18. Comparison of fat body fluctuations by month in juvenile males and females (1970-71 combined). Upper lines, mean body weight fluctuations; lower lines, fat body weights. Males are represented by solid lines and females by dotted lines.

moved considerable distance from the place of their first capture, whereas others were captured many times in the same general area. The areas of activity for male and female hatchlings are .0114 and .0110 ha.

There is a definite tendency for hatchlings to set up a small area of activity. We observed a male hatchling exclude a female hatchling from a particular bush he occupied. Two representative hatchling areas of activity are diagrammed in Fig. 19.

Juvenile Home Range

Juveniles were often observed being chased from the established residence of adult males. The recapture data indicate some juveniles establish a home range in the same area they used as hatchlings. Five records of juvenile movement from their initial capture as juveniles to a new home range (periphery of new home range) averaged 75.6 m, with a range of 56.0 to 92.6 m. This indicates that many, if not all, juveniles had established new home ranges during June and July.

Female 1-6-9 traveled 77.7 m from her initial capture on 27 May to a home range in which she remained from 20 July until 6 August of the

same year. She was captured four times and on 31 August was found 12.5 m from the capture point of 27 May (a return distance of 62.8 m). In addition, she was found in this same home range as an adult the following year. This movement was from the south-facing slope through the wash across the north-facing slope to the west-facing area and then back. A male (1-4-10) lived in a specific area as a hatchling in October and during the following year from 12 June to 27 July. On 13 August he was found 67.0 m north of his previous home range and on 17 August was 65.5 m east of the 13 August capture, a total of 95.1 m (straight line) from the center of the original home range.

Juvenile home ranges averaged 2.8 times larger than the area of activity of hatchlings. The areas were essentially the same for males and females (.0314 and .0316). Two typical home ranges are diagrammed in Fig. 19.

Adults

As adults, the first differences in the size of the home range between the sexes became apparent (.0423 ♀♀ and .0563 ♂♂). Male home range size averaged 24.9 percent larger than that of females. There was an overlap in the size, with the ranges for males 76.1 to 1521.5 and for females 71.4 to 887.6 sq m.

Home ranges of adult females and males averaged 25.0 and 44.2 percent larger than those of juveniles, though there was some overlap in size between their home ranges. The home range of two adults is shown in Fig. 19.

It appears that some adult home ranges may increase slightly in size, but the majority remain generally the same size and in the same area. A male (5-6) remained in his 1970 range at least until 28 May 1971. In 1972 he was captured 102.4 m southeast of his former range. Extended forays by males do not seem to be common. During the spring and early summer males are involved in courtship and in the defense of their territories.

Adult females appear to be restricted to home ranges except for extended forays to lay eggs. We have four such records, but the percentage of those leaving to lay eggs is not known. Adults show an overlap in home ranges, as do juveniles and hatchlings. The majority were located on the south-facing slope.

Age Classes

Three age groups are used in this study. The first group, hatchlings, appears in the population from about the last week of July through the first three weeks of August and remains active until hibernation in October. Upon emer-

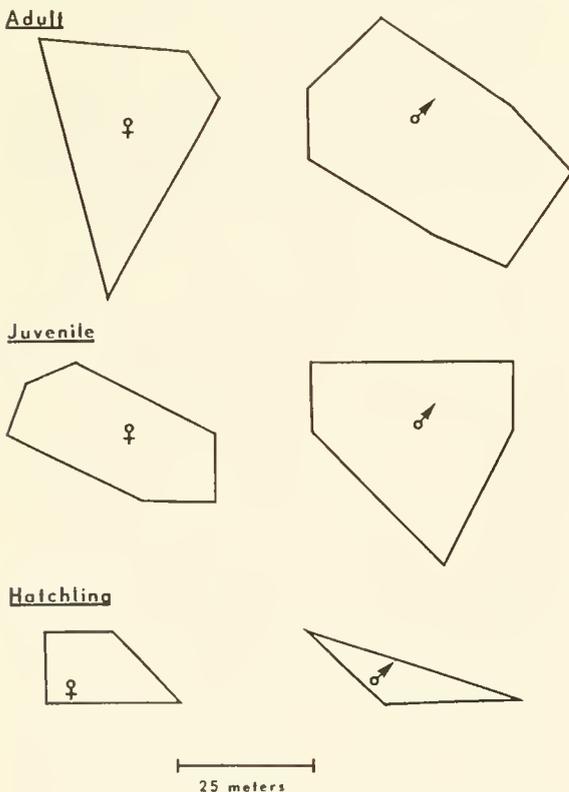


Fig. 19. Diagram of typical home range for female and male *S. g. graciosus* in three age classes.

gence from their first hibernation in March, they are referred to as juveniles. Lizards remain juveniles during one entire activity season, although by August or September they attain minimum adult size. Lizards emerging from their second hibernation are adults. This group may be divided into first-, second-, and third-year reproductive classes. Our data do not go beyond the third reproductive year.

Hatchlings

In 1970 the first hatchlings did not appear on the study plot until 17 August. The 1971 and 1972 hatchlings appeared on 1 August and 10 August, respectively. In 1972, 13 adult females, kept in captivity, laid 68 eggs, of which 34 hatched. Measurements (SVL and total length) and weights were taken prior to 24 h after hatching and after five to seven days. The different measurements before and after the five to seven day period were .56 mm SVL increase, .92 mm increase in total length, and .107 g weight loss per lizard. For detailed data see Burkholder (1973). Using a paired *t*-test of difference, all means were significant at the 95 percent level. This indicates that the yolk present in the gut after hatching keeps hatchlings alive up to a week or more and may allow for some growth. Thirty hatchlings were measured, and only one was smaller (SVL) when measured after five days. However, in all hatchlings the weight decreased. The normal metabolism of the lizard would provide for some growth, the amount depending on the amount of yolk available. The average increase in size for six days was .080 mm SVL per day. It is seemingly very important that hatchlings have yolk in the midgut after hatching to sustain them until they can capture prey. Two hatchlings approximately three hours old were able to recognize prey and strike at it but were only able to handle small, soft-bodied insects (a 12-mm lacewing and a 5-mm leafhopper). It was only after six or seven tries that they could grasp the prey and swallow it. Although they had an instinctive ability to recognize prey and attack it, several days were necessary before they became successful in feeding. Recently hatched lizards in the field usually had empty stomachs.

Size at Hatching and Growth

Based on laboratory hatchlings, males and females averaged 24.81 mm SVL ($N=19$) and 25.27 mm SVL ($N=13$), respectively. Mean weight was .53 g for males and .56 g for females. Total length averaged 56.21 mm for males and 57.58 mm for females.

Once hatchlings were foraging, growth pro-

ceeded at a continuous rate. The average rate of growth in SVL and grams per day for 1971 and 1972 activity seasons are summarized as follows: males, .0841 mm and .0086 g; and females, .0841 mm and .0070 g.

These figures depict the average growth rate for all lizards (pooled $N=99$ and 162 for males 1970 and 1971 and $N=113$ and 175 for females in 1970 and 1971) in each year for the study plot population. A starting point for weight and SVL was taken from the average size and weight at hatching. The range was .813 to .087 mm, with an average of .0841 mm per day, which approximated the 30 laboratory hatchlings (.0800 mm per day without additional food). Weight increase was slightly different, with males showing a higher average than females (.00865 g to .00700 g per day). Considering the extreme fluctuations in weight, size in mm (SVL) may be a better indicator of growth. From these data it is apparent that males and females grow at essentially the same rate from the time of hatching until hibernation in October (Burkholder, 1973). In October 1970 males averaged 30.1 mm SVL and 1.09 g and females 30.2 mm SVL and 1.02 g. In 1971 both males and females averaged 32.3 mm SVL; however, males weighed more (1.28-1.13 g). Hatchlings in 1971 reached a larger average size than in 1970 (Fig. 20) because of a longer growing period brought about by an earlier oviposition. Individual growth rates for 20 hatchlings in 1970 and for 30 in 1971 are listed by Burkholder (1973).

The percentage of increase from hatching to hibernation in 1970 (65-day period) was 20.64 in SVL and 48.57 in weight; in 1971 (86-day period) it was 22.60 in SVL and 55.00 in weight.

Juveniles

The period of greatest growth is during the year after emergence from the first hibernation. Juveniles usually attain adult size by August, depending on the environment, and level off in September (Fig. 20-22). Study plot populations entered their first hibernation at an average SVL of 33.0, 31.6, and 33.1 mm for 1969 through 1971. Differences between hatchlings before hibernation (maximum size $N=40$ and 45 for 1970 and 1971) and juveniles in 1971 and 1972 (March) were .95 and 2.06 mm SVL. Data indicate that little, if any, growth occurs during hibernation. This assumption is based on the similarity of the average size of the latest hatchlings seen in 1970 and 1971 and the earliest juveniles of the following years and is supported by losses in fat body weight (Fig. 18). Since fat stored in the tissues and fat bodies is the only source of energy during hibernation (approx-

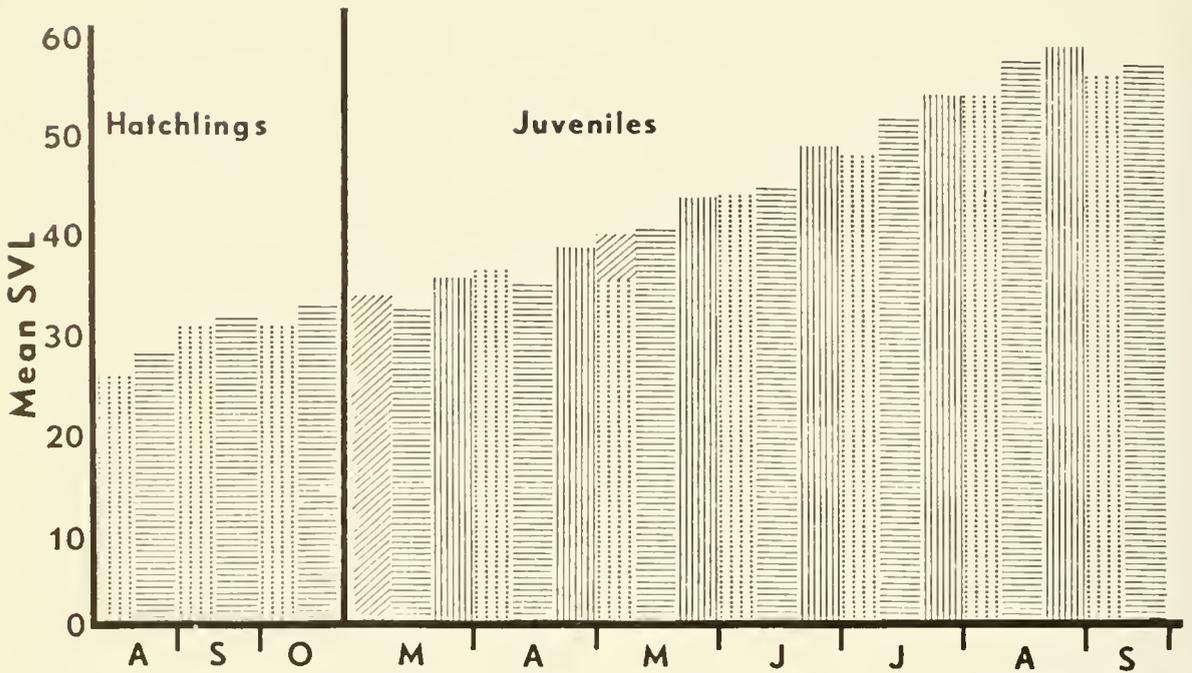


Fig. 20. Growth of hatchlings (1970-71) and juveniles (1970-72) by month. Vertical dotted lines represent 1970, horizontal lines 1971, and vertical lines 1972. Diagonal lines are estimates.

mately six months of cold and snow) it is unlikely that such storage is large enough to provide energy for growth. Temperature is also a limiting factor, since lizards are just below the frost line and metabolism is thus at a low level.

Each year (1970-1972) juveniles reached adult size at different times (Fig. 20). Some were adult size in early August of 1970 as compared to late July of 1971. Individual growth rates per day for 11 juveniles in 1970 are listed in Table 9.

The average rate of growth in mm (SVL) and g per day in 1970 and 1971 for males was

.1230 and .1489 mm and .0200 and .0285 g (N=53 and 96); for females it was .1230 and .1489 mm and .0214 and .0282 g (N=81 and 109). Mean size and weight by month and season and a comparison of 1970-1972 juveniles by month (average SVL in mm) are indicated in Fig. 20-22. These monthly findings are based on the study plot population—except March, April, and May of 1970, whose data are based on field animals. Data indicate that for the entire season

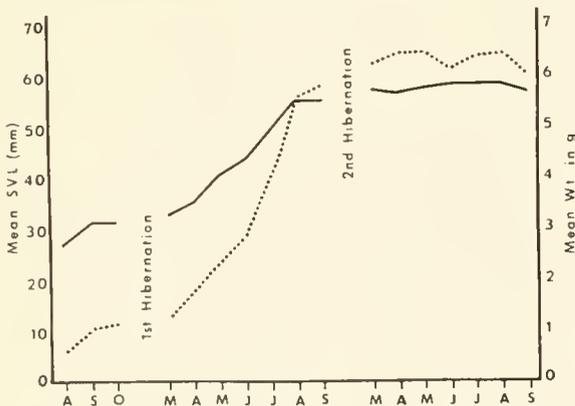


Fig. 21. Growth of male *S. g. graciosus* from hatchlings to adults (1970-71 combined). Dotted line represents weight; solid line, SVL.

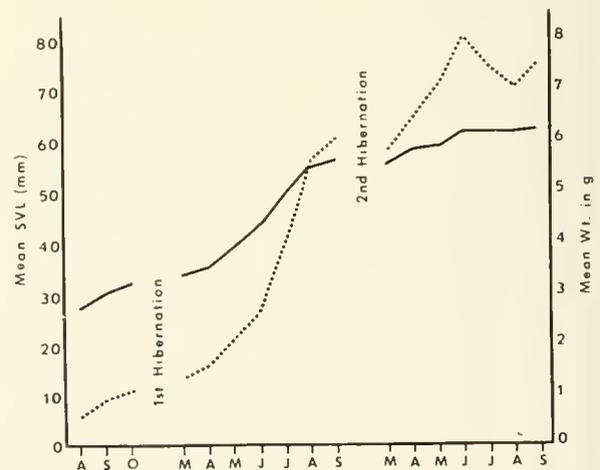


Fig. 22. Growth of female *S. g. graciosus* from hatchlings to adults (1970-71 combined). Dotted line represents weight; solid line, SVL.

TABLE 9. Individual growth of juveniles in 1970 of known age. First figure shows weight in grams; second figure shows snout-vent length.

June	July	August	September	Total Growth	Days Growth	Growth per Day
2.29-39.0		5.06-52.0		2.77-13.0	72	.0384-.1805
4.92-43.0	4.67-51.0		6.32-55.0	1.40-12.0	80	.0175-.1500
1.93-41.0		5.60-57.0		3.67-16.0	68	.0539-.2352
1.62-32.0	2.59-43.0	4.05-46.0		2.43-14.0	60	.0405-.2333
3.06-48.0	2.76-48.0	5.45-55.0		2.39- 7.0	67	.0356-.1044
2.55-46.0	3.68-49.0	4.85-53.0	5.84-54.0	3.29- 8.0	86	.0382-.0930
2.42-43.5	4.32-51.5	4.84-52.0	6.50-56.5	4.08-13.0	72	.0566-.1805
2.95-45.0		5.19-53.0		2.24- 8.0	61	.0367-.1311
3.59-45.5	3.43-46.0	6.56-57.0		2.97-11.5	59	.0503-.1949
	3.21-45.0	5.55-55.0		2.34-10.0	58	.0403-.1724
	2.89-42.0	5.15-51.0	5.33-54.0	2.44-12.0	65	.0375-.1846
Total				30.02-111.5	748	
Mean						.0401-.1490

through August males and females fluctuated in size. In the seasonal tally, males and females had essentially equal growth rates in 1970, and these juveniles were larger than 1971 juveniles in March and April. The May 1970 sample size was small and, therefore, an estimate was made for Fig. 20. This estimate was 39.9 mm SVL, which is intermediate between April and June of 1970. Using this estimate, the May 1970 growth rate seemed to be less than that of 1971. This lower growth rate is attributed to cool temperatures. However, in June 1970, juveniles again outgrew those of 1971. From July on, 1971 juveniles outgrew those of 1970. This higher growth rate results in an average 3.6 mm SVL greater size in August for 1971 juveniles.

Data for 1972 juveniles were incorporated in Fig. 20. These juveniles were larger than those of 1970 or 1971 in all months measured and attained the largest size (58.9 mm SVL) by August, an average of 5.5 mm SVL larger than 1970 juveniles and 2.0 mm larger than 1971 juveniles. The major factor is seemingly the greater number of days for growth (14 in 1972). If the average value for growth per day in 1972 juveniles is multiplied by 14 additional days of growth, the value attained is an increase of 2.07 mm SVL, an approximation of the 2.01 mm SVL difference in the two years. Another apparent reason for the larger size of 1972 juveniles compared to 1971 is a larger mean size at emergence (33.1 mm as compared to 31.6, a difference of 1.5 mm SVL) indicating the larger size of hatchlings in 1971. However, 1971 juveniles had a greater growth rate than 1972 juveniles (.005 mm SVL per day). The 1972 season was one of the driest on record in Utah and on the study plot (Fig. 3). This undoubtedly affected the flora and arthropod population, and perhaps the growth rate of 1972 juveniles.

Adults

Data concerning adult growth are indicated in Fig. 21 and 22 and Table 10. The means for males and females of the study plot and those of other parts of Utah County are not significantly different, thereby allowing us to use the study plot animals to make inferences about Utah County populations.

In comparing first-year adults and older individuals of known age, study plot females were significantly larger than males (Table 10). This fact is also substantiated in the growth curves in Fig. 21 and 22, which also indicate that males have a reduced rate of growth in relation to females, particularly after the second hibernation.

Weight differences were not as great as they appear to be in Fig. 21 and 22. The large increase and decrease in the weight of females through the season, caused by the yolk of eggs, made it difficult to compare the sexes on the basis of weight for the entire activity season. Female weights taken in July and August after eggs were deposited averaged approximately

TABLE 10. Comparison of SVL in adult males and females from Utah County collections and study plot records.

	Number	Range	Mean
Field males	106	52-63.0	57.39
Field females	121	53-69.0	59.91
Study plot males	59	54-63.0	57.82
Study plot females	62	54-66.0	60.59
Study plot first-year adult males	32	54-61.0	56.67
Study plot first-year adult females	38	54-63.0	58.65
Study plot second-year adult and older males	27	55-63.0	59.18
Study plot second-year adult and older females	24	58-66.0	63.47

TABLE 11. Estimated resident density of adults for 1970-71. Biomass of adults based on an average weight in grams for the season.

	Males	Total	Females
Number	27		36
Average in g	6.36		7.16
Biomass in g	171.7		257.7
Total biomass in g		429.4	

6.86 g per lizard (N=46). Males averaged 6.36 g per lizard (N=42).

There was a significant difference between the adult age groups of males and females, with older individuals showing a larger average size. The largest male measured (SVL) in Utah County was 66 mm and the largest female was 70 mm.

Density and Biomass

Estimated resident density and biomass (1971) for adults, juveniles, and hatchlings are provided in Tables 11, 12, and 13. The density for hatchlings was not calculated in the same manner as that of adults and juveniles. Only the number of hatchlings captured each month was used to compute density values. Recapture data were not used because few hatchlings were captured more than once. The biomass was calculated by using the average weight of the hatchlings captured each month, the totals depicting the approximate biomass added to the population from August through October. The total number of hatchlings captured is also given. The estimated resident density per hectare for adults and juveniles is provided in Table 14.

Sex Ratio

In 1971 the most complete data were available for both adults and juveniles on the study plot. These data (Table 15) were based on single captures per month of each group and not

TABLE 12. Estimated resident density of juveniles (1971). Biomass based on average weight in grams for April through August.

	Males	Total	Females
1971 density	25		31
April mean weight	1.38		1.44
Biomass	34.5		44.6
May mean weight	2.39		2.17
Biomass	59.7		67.3
June mean weight	2.67		2.64
Biomass	66.7		81.8
July mean weight	4.33		4.16
Biomass	108.3		128.9
August mean weight	6.00		5.80
Biomass	150.0		179.8
August total biomass		329.8	

TABLE 13. Density and biomass of hatchlings by month (August-October) in 1970 and 1971 on the study plot.

	1970		1971	
	Males	Females	Males	Females
<i>August</i>				
Number	21	21	62	64
Average in g	.66	.72	.61	.57
Biomass	13.8	15.1	37.8	36.5
<i>September</i>				
Number	42	47	46	41
Average in g	1.00	.96	1.10	.92
Biomass	42.0	45.1	50.6	37.7
<i>October</i>				
Number	20	11	18	15
Average in g	1.09	1.02	1.28	1.13
Biomass	21.8	11.2	23.0	16.9
Total number	81	76	126	120
Combined number for each year		162		246
Total biomass	77.6	71.4	111.4	91.1
Combined biomass for each year		149.0		205.5
Grand total biomass		351.5		

on recaptures. This was done in order to effect a random sampling of the population in Utah County, rather than to figure sex ratio fluctuation in an area where only one or two lizards were seen each day. Field data showed the sex ratio to be 1:1 during April, May, and early June, after which males are seen less often than females.

Estimated Potential

Production and Survivorship

Data showing potential production of eggs on the study plot are listed in Table 16. The number of eggs is based on the average clutch

TABLE 14. Density per hectare of study plot animals (1970-71).

	1970		1971	
	Male	Female	Male	Female
Adults	19	25	27	36
Animals/ha	11.0	14.3	15.6	20.7
Sexes combined animals/ha		25.4		36.3
Animals/ha		28.4		40.5
Juveniles	25	29	25	31
Animals/ha	14.3	16.8	14.6	18.0
Sexes combined animals/ha		31.1		32.4
Animals/ha		34.8		36.3
Study plot size 1.72 ha				
*Excluding uninhabited areas 1.55 ha				
Animals/ha for adults and juveniles in 1970				56.8
Animals/ha for adults and juveniles in 1971				69.2
*Animals/ha for adults and juveniles in 1970				63.2
*Animals/ha for adults and juveniles in 1971				76.8

TABLE 15. Changes in sex ratio of juveniles and adults on the study plot in 1971.

	Juveniles		Adults	
	Male	Female	Male	Female
April	3	5	10	12
May	11	15	20	20
June	18	23	17	29
July	13	17	11	23
August	11	16	7	11
September	5	4	1	4

size of females in each age and/or size class found on the study plot in June and the first part of July who may have potentially laid a clutch at the study plot. As was expected, this potential production of eggs was greater than the total number of hatchlings captured. If the actual number of hatchlings captured in each year is compared with the number of potential eggs laid, there is an approximate egg and/or nest failure of 31.0 and 32.5 percent for 1970 and

TABLE 16. Estimated potential production for 1970 and 1971 as compared to actual numbers of hatchlings captured. Survivorship of hatchlings to juveniles and juveniles to adults. Based on study plot data.

	1970	1971
Potential production	232	364
Number marked	162	246
Estimated nest failure	31.0%	32.5%
Hatchlings surviving to next year	44 (27.1%)	45 (18.3%)
Hatchling mortality	72.9%	81.7%
Estimated number of juveniles surviving from 1970 to adults in 1971	36 (81.8%)	36 (81.8%)
Mortality of juveniles		18.2%

1971. Hatchling survival in 1970 was 24.7 percent and in 1971, 18.3 percent. The number of juveniles surviving to adulthood after the second hibernation was 36, or 81.6 percent.

Life Table of S. g. graciosus

A life table is presented in Table 17. Since the population was not studied long enough to take one generation completely through its cycle, the values used for survivorship between first year, second year, and third year adult females were based on the proportion found in the population, with the fourth year given as an estimate. The *X* represents age classes (months), *Lx* is survivorship, and *Mx* is one-half the mean number of eggs that a female will lay in each age group. The sum of *LxMx* (*LxMx*) is the *R₀* (capacity for increase) .909. The *T₀* (cohort generation time) is calculated by dividing $\sum LxMx$ by *LxMx*. In the case of *S.g. graciosus*, cohort generation is approximately 30.13 months.

TABLE 17. Estimated life table of *S. g. graciosus* in Utah County, Utah.

Age Class			<i>LxMx</i>	$\sum LxMx$
	<i>x</i>	<i>Lx Mx</i>		
	0	123.0 0	0	0
	11.0	27.0 0	0	0
	23.0	21.6 2.8	60.48	1391.0
	35.0	7.2 3.2	23.04	806.4
	47.0	1.8 3.9	7.02	329.9
	59.0	.9 4.0	3.60	212.4
			90.90 100	<i>R₀</i> 2739.7/100 = <i>T₀</i>
			<i>R₀</i> = .909	<i>T₀</i> = 27.39
			Cohort generation time ($\sum LxMx / LxMx$) = 30.13 months	

DISCUSSION

Sceloporus g. graciosus is commonly found in the upper Sonoran and Transition life zones in Utah County, Utah, and Woodbury and Woodbury (1945) found it in this same habitat in Salt Lake County. The sagebrush swift requires open, well-illuminated areas between scattered vegetation. The Utah County population was found primarily at elevations of 1,371 to 1,829 m, and records of other collectors indicate that *S. g. graciosus* may occur at elevations higher than 1,829 m. The study plot population was at approximately 1,495 to 1,569 m. When found at higher elevations, they occurred principally on south-facing slopes covered with oak-maple and sagebrush, juniper-pinyon, and sagebrush, or combinations of these.

Woodbury and Woodbury (1945) stated that *S. graciosus* was first noticed in April, and

Mueller (1969) reported that Yellowstone populations did not appear until May. Stebbins (1944) observed them first in late May in California, while activity of Utah populations begins in March.

In 1970 and 1971 sagebrush swifts appeared on 20 and 22 March, and in 1972 they were first observed on 5 March. Adult males and juveniles of both sexes appeared first in all three years, with adult females emerging later. Adult males appeared an average of 16.3 days earlier than females, which allows them time to set up territories. Woodbury and Woodbury (1945), Newman and Patterson (1909), and Noble and Bradley (1933) stated that other members of the genus *Sceloporus* also establish territories before females emerge. Two additional reasons explaining the early emergence of males might

be the noticeable reduction in fat body size (Fig. 17) at the time of emergence as compared to before hibernation, a stimulus to emerge and seek food. Also, males may tolerate lower temperatures than females and would thus be activated at lower temperatures resulting in earlier emergence. Firm evidence for the second reason is not available, however, as both male and female juveniles emerge with adult males. Juveniles are about one-sixth the size of adult males in late March and should warm faster and adjust to short periods of sunshine in the early spring. A positive reason for the early emergence of adult males is not known. We only suggest that a need for food and temperature relationships are possible stimuli.

Sagebrush swift temperature relationships pose several questions when compared to the studies of Brattstrom (1965), Cole (1943), Cowles and Bogert (1944), Larson (1961), Mueller (1969), and Tanner and Hopkin (1972). Average lizard temperatures of March were the lowest for the activity season (Fig. 4); they continued to increase until they reached their highest average in early August, which was also the period with the highest air temperatures (1 m and 3 mm). Mueller (1969) also observed a similar temperature relationship for Yellowstone National Park populations, in which the average temperatures of lizards increased along with the average environmental temperatures. However, average temperatures in Utah populations are seemingly higher than those for Yellowstone populations, possibly the result of adaptation to the lower average temperatures resulting from greater elevation and latitude. Brattstrom (1965) suggests that the average body temperature is in inverse relationship to increasing altitude. This relationship appears to be true in contrasting Yellowstone and Utah populations, with the exception that Utah populations do not follow Brattstrom's curve.

Juveniles emerging from their first hibernation follow essentially the same daily temperature increase as adults (Fig. 4) from March through May, even though they are much smaller. Hatchlings cannot endure exposure to temperatures above 36 C. Perhaps there is a lag in the development of temperature control mechanisms, which are gradually developed in juveniles. The small size of hatchlings may allow for a rapid heating or cooling of the body, causing rapid body temperature fluctuations which may be critical if not controlled. In mid-August daily temperatures may be high; however, nights begin to cool and the average daily temperature turns downward. It is at about this time that fewer adults are seen. By September

hatchlings have averages essentially the same as those of the remaining adults and juveniles, indicating an attainment of temperature control.

Adults and juveniles emerged from retreats at temperatures of 16 to 21 C, comparing closely with the observations of Tanner and Hopkin (1972) for *Sceloporus occidentalis longipes* at 15 to 20 C. Critical thermal maxima (CTMax) for adult lizards from the study plot are close to those found by Mueller (1969) for Yellowstone populations averaging 43.6 C (spring), 42.6 C (summer), and 43.4 C (fall).

In all age classes (Fig. 4) the mean body temperature for each month was higher than air temperatures at 1 m and 3 mm above the substratum. Mueller (1969) reported similar findings in Yellowstone National Park; however, his air and substratum temperatures were taken one inch above the surface and at the surface. Mueller compared these two temperatures and found them not significantly different; however, he states the possible reason for such equality to be thermal activity and lack of air mixing at the surface because of rough substrate material. Cowles and Bogert (1944) and Larson (1961) found mean cloacal temperatures to be intermediate between substratum and air temperatures, with substratum being higher.

It is difficult to compare temperatures of Utah populations with others because of the methods of measurement; however, it can be stated that lizards have a higher temperature than substrate up to June and again in September. During the intervening months, few, if any, lizards were found abroad during the hot periods of the day (Fig. 5). In June, July, and August, lizards have higher body temperatures in the morning and lower during the afternoon, when the substrate has warmed. This is in contrast with Mueller (1969) and Cowles and Bogert (1944), who indicated body temperatures are greater than or intermediate to the air and substrate.

Another aspect of thermoregulation is related to the acquiring of body heat either from substrate, radiant heat, or both. Mueller (1969) believes that direct radiant energy is the primary source, but that substrate is utilized when radiant energy is unavailable. He based this on data indicating higher lizard temperatures than either air or substrate. This is in contrast to Cole (1943), Cowles and Bogert (1944), and Larson (1961), who stated that substrate is the primary source. Observations of Utah populations lead us to conclude that radiant energy is the primary source for warming in the morning (basking) before the substrate temperatures (which

increase much more slowly) reach the appropriate temperature for lizard activity. For example, thunderstorms cool the air and substratum; however, after a storm, lizards are out basking. It is unlikely that this warming came primarily from substrate, even though the lizards were on rocks. Tamer and Hopkin (1972) observed *S. occidentalis longipes* emerge and warm to an optimal temperature by basking while the temperature of the morning air was still cool. It is presumed that the substrate temperature was also cooler than the lizards when they reached their optimal temperature. Their general conclusion is that solar energy provides the prime source of body heat.

By flattening the body against the substrate, lizards eliminate circulating air under the body and thus speed up the process of heating. This flattening also increases the surface area of the body directed toward the sun. While some heat may be conducted from the lizard to the substrate, in full sun this is much less than that received. Interestingly, *S. graciosus* does not darken the surface of the body as *S. o. longipes* does in order to increase warming. Activity begins once the preferred temperature is reached. As air and substrate temperatures continue to increase during July and August, lizards avoid excessive heat by seeking shade and reducing activity. It was our observation that lizards utilize radiant heat first and use substrate only when the former is unavailable.

The mean preferred temperature for adults and juveniles in Utah County was 32.8 C, which is between that reported by Mueller (1969) for *S. g. graciosus* (30.9 C) and by Brattstrom (1965) for *S. g. vandenburghianus* (37.5 C) and *S. g. gracilis* (34.9 C).

In March, lizards were active for 6 to 7 hours per day (Fig. 5). This time gradually increased to 12 or 13 hours per day in June, July, and August. September activity decreased to 7 or 8 hours per day for adults and juveniles, and 9 or 10 hours for hatchlings. Pianka and Parker (1972) noted this behavior in *Callisaurus draconoides*. Stebbins (1944) reported two periods of activity during the day for *S. g. gracilis*. Utah populations also manifest this bimodal activity.

Stebbins stated that the late afternoon peak was from 1400 hours to 1700 hours Pacific standard time. Utah populations have a late afternoon peak centering around 1700 hours to 2000 hours mountain standard time, which is approximately two hours later than that of California populations. A possible explanation for the lag in activity peaks is their geographical location. Stebbins's study of *gracilis* took place at 1,829 m in a conifer forest in Mt. Lassen Volcanic

National Park, whereas Utah populations were at 1,524 m in a scrub oak-maple, sagebrush association. Pianka and Parker (1972) indicated this same separation of activity during the hottest period of the activity season in *Callisaurus draconoides*. Mayhew (1964, 1968), Pianka (1969, 1971), and Tinkle (1967b) have also reported these seasonal shifts.

The development of this bimodal activity is apparent from June through August and is probably necessary to keep the body temperature from reaching a critical level. This intermediate period of reduced activity with an activity temperature may also facilitate digestion of food gathered in the early morning and thus provide for reproduction in June and fat body build-up in July and August before hibernation.

Bimodal activity was also manifest in hatchlings in August (Fig. 5). The retreat from high afternoon temperatures by hatchlings is explained by their apparently lower tolerance for high temperatures. In adults, juveniles, and hatchlings the late afternoon peak is probably triggered by the reduced temperature from 1600 hours into evening. Late afternoon activity was not as great as the morning activity peak.

According to Stebbins (1944), *S. g. gracilis* seeks well-illuminated areas and their seasonal activity may vary with the changes of the incident rays of the sun. *Sceloporus g. graciosus* activity also appears to be affected by the incident rays and the slope of the habitat they occupy. Slope preference was observed on the study plot, an area nearly ideal for slope exposure. The south-facing slope was frequented most by all age classes throughout the activity season, except juveniles in September (Table 1). This preference is explained by the following factors: first, it has the most continuous exposure to sunlight (highest temperature) throughout the year. Second, it supports more open areas, which seem to be preferred by the lizards (Stebbins, 1944). Third, it offers a better place for incubation of eggs (Rand, 1972).

Seasonal fluctuations in activity are explained primarily by the angle of exposure, which affects temperature and ultimately the ability of lizards to warm up to an activity temperature. In March, adults and juveniles were absent from north- and west-facing slopes. March temperatures were sufficiently high to bring lizards out of hibernation on the south slope, but none were seen on other slopes. By mid-April adults were found on all slopes, but not in the same abundance as south slopes.

Exposure and temperature exert a considerable effect on hatchlings, as evidenced by

their decreased numbers on the north-facing slope in September and October (Table 1). Hatchlings show little, if any, home range attachments, and either move to the south- or west-facing slope or hibernate, which probably explains the reduction. By October hatchlings on the west-facing slope also show a decline, perhaps by emigration or hibernation.

Hibernation of the different age classes in the field occurred at different times. Adults started to disappear in mid-August. A few remained until the first part of September, when temperatures averaged 29 C, indicating that this early retirement was not the result of cold temperatures. Even the temperatures prevalent in the first part of September were not as cold as those of March and April, when emergence took place (Fig. 3 and 4). Juveniles stayed out later and were significantly more abundant in late August and September than adults. The retirement of adults earlier than juveniles does not seem explained by cooler temperatures or size of individuals because juveniles were only slightly smaller than adults. We believe a biological clock may explain the early retirement of adults, because food is abundant and temperatures were adequate (Fig. 3 and 4).

Perhaps hibernation is triggered by photoperiodism and/or the size of the fat bodies, just as migration of birds is dependent on fat storage (Welty, 1962). Hatchlings are active approximately a month later and are not in competition with adults and juveniles during this period of rapid growth. Perhaps their small size enables them to warm easily until a limit of tolerance is reached in October and/or fat storage attains a certain level.

Though lizards were suspected of hibernating singly (Woodbury and Woodbury, 1945), it appears possible that two or more lizards might occupy the same burrow or rock crevice. David Cornelison (pers. comm.) has indicated that *Uta stansburiana* were found in large numbers hibernating together in southwestern Idaho. A hatchling of 42.0 mm SVL was put in an enclosure in sandy loam soil on 18 October 1971 and holes were driven to depths of 30 cm or more. Removed on 18 January 1972, the lizard was frozen because it was not below the frost line. This indicates that lizards do use burrows and that hatchlings do not dig holes for the purpose of hibernation, though newly hatched lizards in the laboratory had the ability to bury themselves in loose sand. This may suggest that many hatchlings are not successful in finding safe areas to hibernate and, subsequently, the reason for their high mortality rate.

Behavior

Behavior is expressed in individual actions and interactions between two or more individuals. Individual lizards were observed feeding in the field and in captivity. As prey items increased in size, they were grasped and shaken more vigorously. Hatchlings were able to recognize prey within an hour after hatching and exhibited the same shaking of prey as adults and juveniles, suggesting that the feeding reflex is inherent.

Aggression was observed in and between all age groups, within and between sexes. In females it was manifested by arching of the back, sides compressed, limbs extended, and the tail pointed upward. Stebbins (1944) also observed this in *gracilis* and referred to it as an act of intimidation. Noble and Bradley (1933) noted this behavior in *S. undulatus* females in addition to their hopping on stiff limbs. Hopping was observed once in *graciosus* in a situation where a juvenile male approached a gravid female. The same general pose was observed when an adult male approached a female that had previously copulated and also when a captive female opposed other females that tried to take away her prey. This behavior is apparently a general pattern followed by adult females and may represent a rejection display. It was not noticed in hatchling females or small juveniles.

Aggression in males was usually manifest in a defense of their territory during the breeding season. The color and pattern of the adult male body is considered necessary for males to recognize each other and elicit aggressive behavior. This was noted by Tanner and Hopkin (1972), for *S. o. longipes*, along with head bobbing. Head bobbing was not noticed in *S. g. graciosus* when the combatants were close to each other. The general aggressive pattern was compression of the sides and lowering of the dewlap, with the body extended laterally to challenging males but not to females. Primarily it was a bluff against intruders, though fighting melees were observed in the field as well as in captivity, with the resident male always dominant over an intruder or challenger. Juveniles and hatchlings were observed chasing intruders of both sexes from areas they were occupying. Adult males also removed juveniles from their territories.

Panting by lizards was observed in the field and in captivity. It is apparently an emergency behavior used when the body temperature is approaching a critical level. Critical thermal maxima studies substantiate that panting takes place just prior to reaching the maximum level

tolerated by the lizard. Mueller (1969) also noticed this behavior.

Pushups were observed in all age classes by both sexes. It seems an inherent behavior necessary for the survival of the population because of its apparent relationship to species identification; consequently, reproduction and other social interactions depend on it.

Reproductive activity is a most important behavior. Courtship activity in April and the first part of May is preliminary and does not result in copulation. The general sequence of events leading to copulation is as follows: the male becomes aware of the female, approaches her with his head bobbing very rapidly, and then, as he reaches the female, grasps her on the neck or shoulder region with his mouth, pauses for a short time and assumes a dominant position over the female's body (a period of usually less than 30 seconds). The male then thrusts his vent into contact with that of the female. At this same time the hemipenis is inserted into her cloaca. Woodbury and Woodbury (1945) describe the male as holding the female with the front and hind limbs; however, in Utah County populations only one of each pair of limbs could be considered as holding the female (Fig. 7C).

The hemipenis undergoes rhythmic contractions while inserted, with duration of copulation only five to ten seconds. Woodbury and Woodbury (1945) state that grasping of the neck does not occur with *S. g. graciosus*. In all the copulations observed, the neck or shoulder grasping was a necessary behavior in order for the male to remain secure. Noble and Bradley (1933) substantiate this in their studies on several species of *Sceloporus*.

Escape behavior usually consists of a retreat to bushes, holes, or rock crevices. Individuals have been observed retreating into heavy leaf litter and playing dead. This appears to be an alternative to running from the predator. Lizards manifesting this behavior, particularly the smaller ones, were difficult to find and often escaped capture.

Tail thrashing and vibration were exhibited when lizards approached large prey, when they were captured by hand, and, in males, during precopulatory activity. This behavior is suggestive of a nervous response and may be an example of a ritualistic type of behavior (Goin and Goin, 1971).

Food

Knowlton, Maddock, and Wood (1946) analyzed the stomach contents of *S. g. graciosus* from various populations in Utah and provided a list of food, by orders and families, similar

to the food items listed in this study. Food analyses indicate that the staple food throughout the activity seasons of 1970 and 1971 consisted of Hymenoptera (mostly Formicidae), which made up 2,806 of 3,807 items taken in 1970 and 1,980 of 3,367 items in 1971, and Coleoptera (Table 2), which made up 353 of 3,807 in 1970 and 399 of 3,367 in 1971. These data compare with Tanner and Hopkin (1972) and Tanner and Krogh (1973), who stated that *S. o. longipes* and *S. magister* fed mainly on ants and any other small arthropods that were in abundance. Stebbins (1944), working on *S. g. gracilis*, found that carpenter ants were the most abundant in the few stomachs they examined.

Before juveniles reach adult size they are eating essentially the same prey as adults, in the same priority, and apparently of the same size. Davis (1967) agrees, stating that as *S. occidentalis* juveniles reach adult size they eat the same prey items as adults, becoming competitive for the food supply. Similar competition was apparent in *S. g. graciosus* before adults retired in August. Since hatchlings appear in August and utilize smaller prey in smaller quantities than adults or juveniles, it is doubtful they provide competition.

The sagebrush swift is not an extremely selective feeder (Table 3) but, rather, an opportunist whose diet tends to fluctuate monthly as different insects and other arthropods appear. There may also be yearly fluctuations based on the greater number of arthropods present in one year than in others. Fluctuations in flowering time for various floral types also affect the arthropods present throughout the activity season.

Hymenoptera and Coleoptera were the prey most often eaten by adults and juveniles in 1971. Hatchlings fed predominately on Formicidae (Hymenoptera), small Coleoptera, Homoptera, and Arachnida.

Tanner and Hopkin (1972) noticed that *S. o. longipes* does not appear to move about foraging for food but basks in the sun and loaf in the shade, eating available arthropods of suitable size that attract attention. In contrast, *S. g. graciosus* does forage for food and was observed feeding in the scrub-oak maple thickets and in sagebrush during the morning activity peak. However, during hotter periods of the day these behaved as *S. o. longipes*. Tanner and Hopkin also noticed materials such as rocks and plant parts, feathers, red plastic, pinyon needles, etc., in the stomachs. Rocks and plant parts were found in *S. g. graciosus* stomachs, but other materials were not. The rocks and plants were probably ingested accidentally while capturing

prey, or the plants were possibly moving in the wind and were mistaken for prey.

The sexes differed in variety of food items consumed. Adult and juvenile females consumed more Hymenoptera (mainly Formicidae) than did males. Most other orders were consumed in equal numbers. The average number of items per male and female would suggest that males, being more aggressive, ate larger prey and therefore fewer items than females. This dichotomy was not found in hatchlings.

Another factor in food relationships was the difference between numbers and volume of prey items. In *Callisaurus draconoides* (Pianka and Parker, 1972) the frequency of a particular order utilized may be high while the volume is not. It is possible that volume is a better indicator than number of items. Order of priority for staple food items by volume is different from that by frequency. For adults it was Coleoptera, Hymenoptera, Orthoptera, Lepidoptera and Arachnida in descending order; for juveniles, Arachnida, Coleoptera, Hymenoptera, and Lepidoptera; for hatchlings, Hymenoptera, Arachnida, and Lepidoptera. It is very likely that caloric studies would prove more enlightening than either frequency or volume studies.

In some cases stomachs were completely filled with certain insect orders, again indicating the opportunistic feeding of *S. g. graciosus*. They appeared to rely on sight for finding prey, in contrast to *Cnemidophorus hyperythrus beldingi*, which, according to Bostie (1966a), uses olfactory senses for procuring food.

From the standpoint of practical importance, Knowlton, Maddock, and Wood (1946) stated that *S. g. graciosus* is an important predator of insect pests which compete with livestock for forage and also of insects which multiply in range land and then migrate to nearby cultivated fields. This also applies to Utah County populations. It is our conclusion that *graciosus* as well as other insectivore species are economically important and a necessary link in the Great Basin ecosystem.

Parasites

Stebbins (1944), Knowlton, Maddock, and Wood (1946), and Woodbury (1934) have noted nematode parasites in the stomachs of *S. graciosus* from California and Utah. No nematodes were observed in the 385 stomachs of lizards from Utah County. In 690 stomachs removed from lizards for food analysis, we observed only two tapeworms (*Oochoristica scelopori*). The presence of nematodes in Utah populations outside of Utah County suggests geographical iso-

lation or that appropriate intermediate hosts are not present (Pearce and Tanner, 1973).

Ectoparasites were found mainly on lizards collected from West Canyon in northwestern Utah County. Ticks (*Ixodes*) in both larval and nymphal stages were found in April and May. In July and August mites (*Trombiculidae*) were also found mainly on lizards from West Canyon. This suggests that ticks and mites are prevalent at different times of the year and tend to be localized; therefore, lizards occupying some areas may have a higher incidence of infestation than others.

Predation

Predation was not witnessed in the field at any time. Suspected predators are *Coluber constrictor*, *Masticophis lateralis*, and *Pituophis melanoleucus* when sympatric. *Hypsiglena torquata* is a known predator in Utah County. The sparrow hawk occurs in the same habitat and is known to prey on *Cnemidophorus tigris* in Utah County (Smith, Wilson, and Frost, 1972) and *Phrynosoma platyrhinos* in southern Nevada (Tanner and Krogh, 1973). It is therefore considered to be a possible predator. *Crotaphytus collaris* has been observed preying on *graciosus* in captivity. Taylor (1912) reports a *Crotaphytus icislizenii* preying on *graciosus* in Nevada, and, since both species are found in Utah County, they are considered possible predators.

Tail ratios and breakage

As lizards grow, the ratio of tail length to body length increases (Fig. 8). Mueller and Moore (1969) noted this for the Yellowstone population and Blair (1960) observed similar changes in *S. olivaceus*. Our data also indicate that the proportion of tail to body length is greater in males from the time they reach approximately 50 mm SVL. In both sexes there is a reduction of the ratio after reaching approximately 60 mm or more. *S. olivaceus* does not show the reduction of relative tail length. The difference in tail ratio of male and female *S. g. graciosus* may be caused by the portion of the tail occupied by the hemipenis. In adult males (54-60 mm SVL) this amounts to an average of 6.3 mm. Blair states that males have longer tails because they do not carry eggs. He also considers natural tail breakage in *olivaceus* as an indicator of predation in the population. However, fighting between adult males during the breeding season (to protect the activity center) and certain situations where the male may grasp the tail of the female during copulation may also result in tail breakage. The percentage of tail breakage in *graciosus* increased with age. Blair

concludes that males have a higher predation rate than females because of coloration, display, home range patrolling, and mating activity. Also, males have a greater ability to elude predators, based on the high percentage of tail breaks. It would seem that the greater ability to elude would result in less predation, and not in a significantly greater density of females as Blair reported for *S. olivaceus*, *S. g. graciosus* and *S. olivaceus* males have a higher percentage of tail breakage and perhaps predation than females. Gravid females are orange laterally and less agile until the eggs are laid. It was our observation that males and females are almost equal in attracting predators. Two possible reasons for the differences in the percentage of tail breakage in males are that they are more aggressive and they emerge earlier. This probably contributes to a higher predation rate and may be responsible for a slightly greater density in females (8 percent). In *S. olivaceus* females are significantly (statistically) more abundant. In comparing the Utah County population with Blair's population in Texas, it was concluded (based on natural breaks as an indicator of predation) that predation of northern forms is less than that of southern forms. Pianka and Parker (1972) observed this in *Callisaurus* populations ranging from central Nevada to Estero de Tastiota, Sonora, Mexico. Pianka (1965 and 1970) reported similar latitudinal shifts in *Uta stansburiana* and *Cnemidophorus tigris*. Studies of southern populations should be undertaken to test if this is true in *S. graciosus*.

In tail regeneration, color pattern and certain colors (blue greens in males and orange in females) were not present in the regenerating portion, only a uniform ground color. This suggests that the cells producing the colors were absent. The regenerating portion was also lighter ventrally. Stebbins and Robinson (1946) reported this same phenomenon in California populations of *S. g. gracilis*. Data were not available to make conclusions concerning advantages or disadvantages in the lack of color and pattern.

Age groups and Reproduction

Females were considered adults if they contained yolking follicles, oviducal eggs, or corpora lutea. The minimum age of reproductive females is 22 to 23.5 months.

Hatchling females show an increase in number and size of follicles as they grow. Tinkle (1961) found this same situation in *Uta*. Follicle growth continues during their juvenile year until June and July (Table 3). The reduction in follicle size in juveniles is possibly caused by greater activity, heat, fat deposition, and diet

during May, June, and July. Overall, the average number of follicles increased from the time of hatching and reached a plateau (average) of 18 follicles per female in the second reproductive year. The phenomenon of producing more follicles than can be developed and laid in one breeding season appears to be a general characteristic in saurians. It appears to occur in *Sceloporus*, and Tanner (1957) observed it in *Eumeces*.

In adult females unyolked follicles exhibit some seasonal fluctuations (Table 4 and Fig. 9), with decrease in size and numbers of follicles occurring during the breeding season. The reason for a reduction appears to be the use of lipids and fats contained in the unyolked follicles for yolk deposition, similar to their use in fat bodies (Hahn and Tinkle, 1965). The increase in number and size of unyolked follicles after the breeding season may be in response to the buildup for the next year.

Yolk deposition started in late August and the first part of September in adult and juvenile females, just before they retired for the season. These follicles were 1.9 to 2.0 mm in diameter and began to appear yellowish. Activity in the ovaries apparently ceased during hibernation. Meiosis was observed in *S. o. longipes* collected in August and September from Nevada. Woodbury and Woodbury (1945) state that female *graciosus* entering their second hibernation (juveniles) had ova that were enlarging (2-3 per lizard). Our data suggest that not all females (adults or juveniles) were undergoing meiosis in August and September or had large, yellowish follicles, though all showed increased size of follicles (Tables 3 and 4, Fig. 10). After yolk deposition is well underway in the spring, ova increase rapidly in size. Ovulation took place when ova averaged approximately 7.09 mm in diameter and .21 g in weight. The majority of this growth takes place over a period of about 60 days. Data from a female captured in the process of ovulation indicate that the process of ovulation and passage into the oviducts is rapid and probably lasts no longer than twenty-four hours. The period of ovulation appears to occur as females reach their most brilliant nuptial color. Apparently copulation precedes ovulation, thereby avoiding the obstruction of sperm by eggs that have already passed into the oviducts.

Transceolomic migration of ova has been observed in various species of reptiles (Legler, 1958; Tinkle, 1961; Mayhew, 1965, 1966a, 1966b, and 1971; Bostie, 1966b; Hoddenback, 1966; and Burkholder and Walker, 1973). In *S. g. graciosus*, the ova have a migration rate of about 42

percent (48/20). There seems to be a limit of 4 or 5 ova per oviduct, and, therefore, migration does not occur after an oviduct has received this number. This percentage is higher than that recorded in other reports, except that of Hoddenbach (1966), who reported 66 percent in five individuals of *Cnemidophorus sexlineatus*. Telford (1969) criticizes Hoddenbach for his small sample size, and yet 50 percent or more does not seem impossible. The physical features of the coelomic cavity suggest a passage of ova into the adjacent oviduct in all cases. Hoddenbach (1966) suggests that the stomach position on the left side might cause a movement of ova from the left ovary to the right oviduct. In *graciosus*, movement is from left to right, and it would seem that a full or empty stomach may have an effect on ova migration.

Corpora lutea in *S. g. graciosus* disappear rapidly after oviposition. This is similar to reports on *Uta*, *S. orcutti*, and *Uma* species. In *Takydromus* studied by Telford (1969), however, corpora lutea persist for the life of the female.

The left and right ovaries produced an equal number of eggs (Table 7). This is similar to Johnson's (1960) and Mayhew's (1965, 1966a, and 1966b) findings in *Holbrookia texana* and *Uma* spp.

Approximately 13 percent of the females examined had atretic follicles. Tinkle (1961) found 10 percent as a maximum in *Uta stansburiana*. Atretic follicles in *S. graciosus* were present during and after the active season of egg production. In contrast, Telford (1969), Hoddenbach (1966), and Tinkle (1961) reported on the period when atretic follicles occurred in *T. takydromus*, *Cnemidophorus sexlineatus*, and *Uta stansburiana*. In *Takydromus takydromoides* atretic follicles were present only in the postactive season, whereas *C. sexlineatus* and *U. stansburiana* were seen only during the active season.

Based on counts of corpora lutea and oviducal eggs, there were no cases of partial oviposition observed. Females had either laid the entire clutch or all remained within the female. Recently oviposited eggs averaged 13.7 x 7.9 mm, which is larger than those reported by Van Denburgh (1922) at 13 x 7 mm. Grinnell, Dixon, and Linsdale (1930) reported a length of nearly 10 mm. Females that had just oviposited lost between 2.24 and 2.72 g. of body weight, a loss of about 36 percent. Females measured (SVL) less than 10 days after they had oviposited were shorter (6) or equal (2) to their size before oviposition (Table 6), suggesting that females carrying a clutch of eggs possibly in-

crease their length by relaxing the ligaments and muscles in the axial skeleton. Approximately two weeks after females had laid eggs they were gaining weight and had reached their approximate previous length.

Sceloporus graciosus in Utah County lays one clutch of eggs per year. In contrast, Tinkle (1973) reported two clutches (4.2 eggs each) in southern Utah. However, his evidence is inconclusive since he states that only 1 of 72 females examined had both corpora lutea and ova undergoing vitellogenesis. This fact would cast considerable doubt on all life table studies based on two clutches per year. We recognize that an occasional year with an early warm spring may permit some females to produce two clutches. Also, those populations in the southern limits of the range may be more likely to produce two clutches. In Utah our three-year study has not convinced us that two clutches occur often enough to be an important factor in the fecundity of these populations. Fitch (1970), reporting on northern (Washington, Oregon, and Idaho) and southern populations (California and Baja California), found them laying single clutches averaging 3.60 and 4.24 eggs, respectively. The average clutch size for Utah County populations was 6.03, as determined from 143 clutches. This was significantly larger than the size reported by Fitch (loc. cit.) but similar to the clutch size of five or six eggs reported by Woodbury and Woodbury (1945) for Salt Lake County populations. Mueller and Moore (1969) reported 3.2 eggs per female in Yellowstone Park populations. These females were only 47 to 51 mm SVL, which is significantly smaller than mature females in Utah County. The maximum size of Yellowstone females was 56 mm SVL. This compares well with the observations of Stebbins (1944) on *S. g. gracilis*, which had a maximum size of 57.5 and a mean clutch size of 3.3 (Stebbins and Robinson, 1946). In addition, Yellowstone and California populations had approximately 150 to 160 days of growth. Comparing these populations with those of Utah County, the mean clutch size in Utah was almost double. Furthermore, females reached a greater maximum SVL (70 mm) and had approximately 185 days for growth. Length of the growing period limits the average SVL attained by individuals in the population, and this size limitation directly reduces the clutch size. This appears to be a general relationship in Sceloporine lizards (Tanner, 1972; Davis, 1967; and Blair, 1960).

Clutch size increases as females grow in size. In Fig. 11 the first two categories approximate first-year reproductive females, with the third

category being second-year and the fourth category being third- and fourth-year reproductive females. Hoddenbach (1966) and Johnson (1960) reported that there was no difference in size of clutches as females increased in body size in *Cnemidophorus sexlineatus* and *Holbrookia texana*. However, Blair (1960) considered clutch size to be a function of size and age. In his study, increased size was considered more important than age for first-year females. First-year individuals had a greater variation in size (SVL) than older individuals; also, larger first-year females produced larger clutches.

Some researchers indicate there is a relationship between size of eggs within a clutch and number of eggs to the size of the female. Tinkle (1961) believed that larger clutches had smaller eggs. Telford (1969) reported that, in *T. takydromoides*, the larger the female the larger the clutch and the larger the individual eggs. In *S. g. graciosus* neither of the above consistently occurs. It seems that the size of eggs depends on the fat stores and food availability in the particular niche where the female is living, regardless of age or body size (Table 5).

The incubation period in *S. g. graciosus* was approximately 48 days, with a range of 44 to 52, based on field and laboratory data. This is a shorter period than the 62 days reported by Woodbury and Woodbury (1945). The assumption that the incubation period is only from oviposition to hatching may not be entirely true. Fertilized eggs in laboratory animals were in the oviducts about 22 to 27 days. Adding part of this time to the above incubation period gives a more accurate time of 65 to 70 days from the time of fertilization (if fertilization occurs as ova enter the oviduct) to the time of hatching.

The gonadal cycle of females in 1970 was approximately 15 days later than in 1971. This lag between years is explained by fluctuating factors in the environment. Since 1970 and 1971 individuals emerged at about the same time, emergence time should have been a minor factor. However, prevailing weather conditions in the late spring in the form of cold fronts and possibly inadequate food supply appeared to be the most important factors. This same lag was also evident in the male gonadal cycle.

Males were considered sexually mature if they were 52 mm SVL or greater by 1 July. This is 2 mm greater than reported by Stebbins and Robinson (1946) for *S. g. gracilis*. Woodbury and Woodbury (1945) reported that the male testicular cycle reached its peak volume in late April and May and then dropped to its lowest level in July, picking up again before hibernation. They reported that gonads did not enlarge dur-

ing hibernation, an observation at variance with our data, in which some increase in the diameter of seminiferous tubules occurred (Fig. 12). A slight increase in tubule size would partially explain the failure to notice changes when using volume measurements, suggesting a weakness in using them. Using the volume of testis as a criterion for lack of change during hibernation or any other period is an example. In addition to an increase in tubular size, there was a significant change in testicular weight during hibernation (Fig. 13). Another evidence for change in the testis during hibernation was the stage of the tubules at the time of hibernation as compared to that at the time of emergence, indicating that changes during hibernation are not apparent from volume studies. Other basic trends of the spermatogenic cycle of Utah *graciosus* are in agreement with the findings of Woodbury and Woodbury (1945).

The general trends in the gonadal cycle of male *S. g. graciosus* follow that reported for *S. occidentalis longipes* in Nevada (Tanner and Hopkin, 1972), but are in contrast to the cycles in *Uma* spp. and *Dipsosaurus dorsalis* reported by Mayhew (1965, 1966a, 1966b, and 1971). The differences are in the time of year and the duration of each stage. These variations appear to be caused by the locations of the populations and the length of the growing seasons.

One significant adaptation is the presence of spermatozoa in the epididymis for a period of 1.5 to 2 months, apparently essential to ensure insemination of females. Natural selection seemingly would favor the use of energy required to keep the sperm viable in the epididymis before and after the copulation period to insure a maximum number of inseminated females.

In 1971 we noticed that the pre-anal area of males was moist during the breeding season. To our knowledge this has not been previously described. The area was moist for approximately 45 days from the last of May to the first of July, overlapping and continuing after the copulation period. The use of this secretion is unknown. It is undoubtedly associated with reproduction, since it coincides closely with it, and may be a pheromone used as an attractant to females, or a lubricant used during copulation (Burkholder and Tanner, 1974).

Hahn and Tinkle (1965) studied postecolomic fat body cycles in relation to reproduction in *Uta stansburiana* and found a definite usage during yolk deposition. Fat bodies in *S. g. graciosus* males were smaller than those found in females as a percentage of body weight (Fig. 16 and 17). This compares well with their findings for *U. stansburiana*; however, *S. graciosus*

had smaller fat bodies (percentage of body weight). The cycle followed by *U. stansburiana* was also different than *S. graciosus*, which may be explained by latitudinal differences and length of growing period in the two populations. In addition, *U. stansburiana* in Texas laid more than one clutch of eggs per year whereas *S. graciosus* in central Utah laid one. In *U. stansburiana* and *Cnemidophorus sexlineatus* (Hahn and Tinkle, 1965; and Hoddenbach, 1966) the fat body was used to provide energy for the first clutch only. Males used most of their post-hibernation fat body for general activity (i. e., courtship, home range patrolling, and defense of activity center) as suggested by Hahn and Tinkle (1965). Males and females began to replenish their fat bodies in late June when reproductive activity had ceased and only a few females still had oviducal eggs. In females, yolk deposition seemed to provide the greatest drain on fat bodies. In July males and females weighed essentially the same and had fat bodies of approximately the same size. By August and September males lagged in fat body buildup, suggesting that the next reproductive cycle was beginning.

Fat bodies in southern populations were not used in hibernation, according to Hahn and Tinkle (1965). In contrast, central Utah populations must retreat for a period of six months. Even though metabolism is very low, a certain amount of energy is needed and fat body stores are considered the main source of support. A comparison of fat body weights of September individuals with those recently emerged in March and April showed a decrease of 1.9 in males and 1.4 percent in females, which was apparently used during hibernation. The greater loss in males was perhaps the result of continued enlargement of the gonads during hibernation (Fig. 16 and 17). Females do not follow precisely this cycle because most of their reproductive activities occur in the spring. If hibernation curtails most metabolic activity, except for survival, gonad size and tubule diameter in males should be similar between entrance into hibernation and emergence. Fat bodies in males should also be similar to that of females.

Although there was less than a 10 percent overlap in fat body data for juveniles and adults in August and September, the basic relationships between juvenile males and females are obvious. Even though juveniles increased equally in body size (SVL) and weight, female fat bodies grew faster than those in males from mid-July through September. The size of fat bodies in juvenile females increased over that in males from mid-July to September for the

same reasons observed in adults. Hatchling fat bodies were essentially equal in males and females. The smaller fat bodies of hatchlings at emergence as juveniles indicate that fat bodies are used during hibernation.

Home Range

According to Turner (1971), home range has usually been studied simply because it existed. He suggested that home range should instead be studied in order to solve problems, and he referred to the studies of McNab (1963) and Schoener (1968) and their comparisons of the size of the home range to energy requirements. White (1964) suggested that there is an inverse relationship of density to home range size. Home range size is also useful in studies of density per unit of area and in lizard spacing within a given area. Milstead (1972) stated that home range is important in relation to social behavior and is probably not inherited as display patterns but is environmentally determined by factors such as food and the genetics of the individual. In future studies, telemetry should be explored as a possible method of home range measurement for a three-dimensional area where lizards occupy trees, boulders, etc. Several studies have also considered the subject of home range and territoriality in lizards (Stebbins, 1944; Jemrich and Turner, 1969; Jorgensen and Tanner, 1963; Minstead, 1961 and 1970; Tinkle, 1967a; and Tanner and Hopkin, 1972). However, the subject is still open for further study.

Adult males have a center of activity within their home range, where they are found more often than in other parts of their territory. From late April through June a male is aggressive toward other males found in his home range, especially if the center of activity is approached. This was substantiated by observations of fighting between males and subsequent chasing of the intruder from the home range by the resident male. Fighting did not occur in every encounter. Though there was some overlap in the home ranges of adults, males would not tolerate juveniles of either sex. Female adults could come and go at will, with males performing their display behavior, especially during April and May. Females did not defend their home ranges or centers of activity as vigorously as males. The center of activity appeared to be the most familiar portion of the home range since resident lizards driven away from it tried to return. Stebbins (1944) and Tanner and Hopkin (1972) also reported that there were few encounters among *S. o. longipes* in southern Nevada. It may be that spacing of lizards (density) in an area can have a profound effect on the

number of encounters that actually take place. The spacing would also be a reflection of the number of lizards an area could support, which would be controlled to a great extent by environmental factors. Therefore, the number of encounters would fluctuate directly with increased density and consequent reduction in size of home range and center of activity (Stebbins, 1944). The density of *S. g. gracilis* in California was about 10 per hectare compared to 39 per hectare for adult *S. g. graciosus* in Utah, which would explain the higher number of encounters in Utah lizards.

The average size of the home ranges of *Sceloporus g. graciosus* increased as they grew in size from hatchlings to adults, with adult males averaging a larger territory than females. However, overlap in size did exist. *Sceloporus olivaceus* in Texas showed an overlap in home range with males having larger areas than females (Blair, 1960). Utah *graciosus* showed a fixity in remaining in the area they established as adults and, to a lesser extent, as juveniles. Stebbins (1944), Blair (1960), and Tanner and Hopkin (1972) noticed similar behavior in *S. g. gracilis*, *S. olivaceus*, and *S. o. longipes*. *S. g. graciosus* moved from or remained in the area set up while a hatchling, juvenile, or even early in their first adult year (especially males). One reason for these changes may be that hatchlings set up areas in August and September when adult males and juveniles are less aggressive and most have retired for the season. When hatchlings emerge as juveniles they may be within the home range of an adult and be removed. This may happen again to small adult males in their first year. The changes are all by force but this does not rule out passive movement to another area in search of better habitat or food (Stebbins, 1944).

Homing was another aspect of movement in *S. g. graciosus* observed in all age groups. In adult females, homing consisted of extended forays to lay eggs and then return to the home range. Blair (1960) and Tanner and Hopkin (1972) noticed this in *S. olivaceus* and *S. o. longipes*. Mayhew (1963) noted homing in *S. orcutti* in which animals displaced by the investigator were observed returning to their original home range. Extended forays by *S. g. graciosus* males and a subsequent return to the original home range occurred after the breeding season and may be typical wandering for adult males. A juvenile, in at least one case of homing, moved from the area of first capture to another area, was captured four times in 17 days, and then moved back within 12.5 m of the original capture. Other juveniles were noted

moving away from their home ranges an average distance of 76.6 m. It is not known if these juveniles returned to their original home ranges.

Growth

Growth in *S. graciosus* has been investigated by Stebbins (1944) and Mueller and Moore (1969). Growth studies of other species of *Sceloporus* have been done by Fitch (1940), Crenshaw (1955), Mayhew (1963), Davis (1967), and Tanner and Hopkin (1972). *Sceloporus g. graciosus* in Utah County exhibits growth patterns similar to those for other species; however, there are some differences. From March through most of July only two age groups are present, juveniles and adults. In August, when hatchlings appear, there are three age groups for a short time. After the first two weeks in September only juveniles and hatchlings are abroad, and by the end of September there are only hatchlings.

The presence of yolk in the gut is of considerable importance to the survival of *S. g. graciosus* hatchlings immediately after hatching. Our data indicate that hatchlings may survive longer than a week without food. Although prey is recognizable soon after hatching, feeding success is low in laboratory hatchlings. Those recently hatched in the field usually have empty stomachs. The adaptive importance of yolk in the gut is in sustaining the hatchling long enough to become successful in finding food.

Size of hatchlings at the time of hatching (24.8 mm SVL for males and 25.3 for females) compares well with the sizes reported by Stebbins (1944), Mueller and Moore (1969), and Tinkle (1973). The average size of recent hatchlings of *S. g. graciosus* is greater than that reported for *S. o. longipes* by Tanner and Hopkin (1972) and indicates that size of adults of a species does not determine the size of hatchlings.

Hatchling growth rates are equal in the sexes up to the time of hibernation. This is in contrast to growth rates reported by Davis (1967) and Blair (1960), who stated that males grew faster than females in *S. occidentalis* and *S. olivaceus*. Blair stated that growth stopped during hibernation, while Davis believed it continued and at an increased rate in males. In *S. g. graciosus* growth is negligible during hibernation. Stebbins (1944) found the same for *S. g. gracilis*. A possible explanation for the growth during hibernation reported by Davis (1967) is the warm southern location; however, Blair's (1960) populations were also further south than *S. g. graciosus*.

Hatchlings in 1970 compared to those of 1971 indicated a significant factor in growth dynamics (Fig. 20, 21, and 22). These data indicate that even though growth rates were the same, the 1971 hatchlings were larger by the time of hibernation. Thus, longer periods of growth have a significant effect on the biomass of the hatchling population and juveniles the following year. This may also carry over into the average size of females in their first reproductive year, thereby affecting clutch size and, ultimately, reproductive potential and density of the population. Other factors, such as availability of food and weather variables, would also affect growth during this period.

Hatchlings increased an average of 5.4 mm SVL (20.64 percent) in 1970 before hibernation and 7.22 mm (22.60 percent) in 1971. Mueller and Moore (1969) found that Yellowstone populations of *graciosus* grew an average of 5 mm, which is comparable with 1970 populations from Utah County.

Juveniles grew at a faster rate than other age classes (Fig. 20, 21, and 22). Tanner and Hopkin (1972) stated that *S. o. longipes* averaged 64 to 65 mm SVL in its juvenile year, slightly less than its size at sexual maturity (70 mm SVL) and suggesting that some individuals grow an additional year before reaching sexual maturity. The majority of *graciosus* juveniles in central Utah reached adult size in all years studied and required no additional growth to reach sexual maturity in the spring after the second hibernation.

Juveniles reached adult size at different times in all years studied. When growing seasons were equal in length, the variations in size at emergence were seemingly the result of food availability and weather conditions, both significant factors affecting growth. These factors apparently account for the difference in size between 1970 and 1971 juveniles. A comparison of 1972 juveniles with those of 1970 and 1971 indicates that the above factors were involved; however, an additional growing period of fourteen days resulting from an early spring appears to be an important factor in their larger size.

Davis (1967) stated that *S. occidentalis* juveniles became difficult to distinguish from adults by August. In central Utah populations of *graciosus* this was true of late August juveniles in 1970, late July juveniles in 1971, and second-week-of-July juveniles in 1972.

Adult *S. g. graciosus* showed sexual size dimorphism that has been found in species of *Sceloporus* such as *S. olivaceus* (Blair, 1960), *S. occidentalis* (Davis, 1967, and Tanner and Hop-

kin, 1972), and other subspecies (*S. g. gracilis*, Stebbins, 1944). Adult female *S. g. graciosus* were significantly larger than males. This is in contrast to *S. occidentalis* but comparable with *S. g. gracilis* and *S. olivaceus* studied by Stebbins (1944) at Mount Lassen Volcanic National Park, Mueller and Moore (1969) in Yellowstone National Park, and Blair (1960) in Texas. Utah County populations attained an average size significantly larger (70 mm SVL maximum) than those reported for the Mt. Lassen (57.5) or Yellowstone (56.0) populations. The larger size for central Utah populations may be explained by the longer growing season.

Females and males had approximately equal growth rates for the first 13 months. The decline in the growth rate of males at the end of their juvenile year was greater than that of females. Blair (1960) indicated that *S. olivaceus* showed sexual dimorphism as adults. He suggested that increased size in females was an adaptation to allow females to produce a larger number of eggs. This is a plausible explanation and may be operative in *S. g. graciosus* (Fig. 21 and 22); it does not appear to be the case in *S. occidentalis*, where females are equal to or smaller than males (Tanner and Hopkin, 1972). Increased size of older males may be an advantage in maintaining home ranges in strategic areas and, since they are promiscuous, may bring more success in mating. In 1973 Tinkle conducted a study of *graciosus* in southern Utah approximately 300 miles south of the study plot. The density for his plot was 208 juveniles and adults per ha, with a biomass of 980 g. Central Utah populations had a density of 66 juveniles and adults per ha and a biomass of 409 g (August). These differences indicate that different habitats have different carrying capacities. In addition, though Tinkle's densities were three times greater than those of the central Utah study plot, his biomass was just over two times. The apparent reason for the large biomass of Central Utah lizards in proportion to density is their larger average size as adults (6.35 g, males and 7.20 g, females) and proportionately larger juveniles.

Sex ratios of *S. g. graciosus* were statistically similar even though females were approximately 8 percent more abundant in resident juvenile and adult populations of the study plot. This is in contrast to findings of Mueller and Moore (1969), who found *S. g. graciosus* in Yellowstone National Park to have an equal sex ratio in all age classes except adults, where it was in favor of females (64 percent). From this it appears that greater mortality in males takes place in the first reproductive year. Blair (1960),

however, reported that the uneven sex ratio in *S. olivaceus* was caused by a differential mortality that began from an equal sex ratio at hatching. He further stated that the greater number of females may be an adaptation for greater production of eggs. He continued by stating that this was explained by differential mortality in males and their promiscuous behavior; therefore, fewer males are needed and this leaves more energy and area in the environment to support the more valuable females. Tinkle (1973) indicated this possibility for southern Utah populations of *graciosus*, where females (adult) were as abundant as those researched by Mueller and Moore in Yellowstone National Park. Even though the abundance of females from the juvenile year on in central Utah is not as great as those mentioned above, the same principles suggested by Blair may operate to a lesser degree in central Utah. These additional factors may be also operative: first, young adult males are less successful in combat and are driven to less favorable habitats where mortality rates may be higher; second, males emerge earlier in the spring and are exposed to predation longer than females; third, males by their display behavior are more often exposed to predation.

It may be that the high number of females observed by Mueller and Moore (1969) was due to females migrating into the area to lay eggs and then leaving, as was noticed by Blair (1960) and Tanner and Hopkin (1972). In Utah populations there was also a significant number of additional females in June and July on the study plot (Table 5). These were not part of the resident females occupying the study plot throughout the year.

Rand (1972) suggested that female iguanas select open sandy areas to lay their eggs, where the sun's rays will provide maximum heat to insure fastest development and the most successful incubation. In central Utah, females were observed migrating to the study plot (from adjacent areas) which had a south-facing slope (where most migrants were found) with sandy soil and open areas. It was also noticed that there was little migration of females at the time of oviposition, which may account for the high number of females noticed by Mueller and Moore (1969) migrating to the thermal areas to lay eggs.

Population dynamics in Utah County are best compared with the study conducted by Stebbins and Robinson (1946) on *S. g. gracilis* at an elevation of 1,829 m in Lassen Volcanic National Park in Montane forest (Transitional Boreal). This population was approximately

305 m higher than those in central Utah, at about 1,524 m in an oak-maple and sagebrush association primarily in the Transitional Life Zone. The two populations are compared as follows: California lizards were smaller in size and had a longer life span, population replacement was slower, the growing period was less (150-160 days vs. 180-190 in Utah), and the average clutch size was much less (3.3 in California vs. 6.03 in Utah). These differences seem explained on the basis of the habitats of the two populations. Stebbins and Robinson (1946) compared the population of *S. g. gracilis* with the lowland *S. occidentalis* studied by Fitch (1940) and suggested that possible reasons for lower clutch size and longer life span were fewer predators; a shorter activity period, which reduced exposure to predators; and fewer young, leading to a slower turnover in the population. Though these factors are connected with a longer life span and lower clutch size, there are possibly other factors.

California populations are adapted to the higher altitude and its abiotic and biotic environments. This creates a combination of factors such as shorter growth period, reduction in size (SVL), and an increase in the life span compared to Utah. Also, there are fewer days of exposure to predators and possibly fewer predators. The reduction in SVL is associated with reduction in clutch size; therefore, the only way for the population to remain stable is to increase the life span and number of reproductive years. Thus environmental factors associated with the greater elevation evidently have reduced the number of predators, the growth period, and exposure to predation. The growth reduction may have a fortuitous effect in that lizards would warm faster, an advantage at higher altitudes. Mueller and Moore's (1969) study of *S. g. graciosus* at 2,316 m in Yellowstone National Park lends support to the suggestion that increased altitude reduces individual size and consequently clutch size, with essentially the same values as those of California populations.

In contrast, Utah populations produce a clutch almost twice as large and attain an individual size 5 to 7 mm SVL larger, which allows for the larger clutches. These differences appear to be connected to the longer growing period and greater turnover in the population (possibly due to greater predation), which is manifest by the shorter life span; therefore, a larger clutch size is necessary to maintain the population at a stable level. It appears from these comparisons that different populations of *S. graciosus* have adapted to different habitats

by modification of their life cycle. Tanner (1972) observed the reverse situation in *Uta stansburiana*, which attains a larger size at higher elevations and also larger clutches but is similar to California populations of *graciosus* in having a longer life span. The effects of elevation and latitude on various habitats occupied by a species have also been discussed by McCoy and Hoddenbach (1966) and Burkholder and Walker (1973) for *Cnemidophorus tigris*.

Demography

Lizard demography and reproductive strategies have been studied by Turner, Medica, Lannom, and Hoddenbach (1969); Turner, Hoddenbach, Medica, and Lannom (1970); Tinkle (1967b); Tinkle (1969); Tinkle (1973); and Tinkle, Wilber, and Tilley (1969). Tinkle (1973) reported on the life strategy and demography of *S. g. graciosus* in southern Utah. In central Utah *S. g. graciosus* is a single-brooded, late-maturing subspecies with a reproductive life span of about four and possibly five years, a mean life expectancy of 30.13 months, and a breeding age of 23.0 months. A comparison of these data with those of Stebbins (1944-1948) and Stebbins and Robison (1946) indicates that Utah populations mature faster (23 vs. 48 months [after Tinkle, 1969]), have a longer mean life span (30.1 vs. 25.5 months [after Tinkle, et al., 1969]), and a larger clutch size (6.03 vs. 3.33). However, California populations apparently have a longer life span, nine years, in contrast to six or seven years in central Utah. According to Tinkle (1973), it would appear from these data that California populations would have difficulty maintaining themselves.

Tinkle (1973), reporting on a southern Utah population of *graciosus*, had the following breakdown of demographic statistics: breeding age 21 to 22 months; mean life expectancy of approximately 3.0 years or 36 months; clutch size of 4.2, with two clutches produced in one season; and a life span identical to that reported by Stebbins (1948) of nine years, in fact using Stebbins's ages rather than what may be the ac-

tual longevity in southern Utah. These statistics differ considerably from those of central Utah populations. The only similarity in the two populations is the age of breeding (about 22 months). Contrasting points are mean life expectancy, clutch size, number of clutches per year, and longevity of the animals. These contrasting features are reduced in magnitude when we consider the R_0 values of .909 for Central Utah *graciosus* and .975 for those in southern Utah which are approaching unity, suggesting that both populations are at approximate stability and possibly at the carrying capacity of their separate habitats. A noteworthy point is that central Utah *graciosus* achieve near unity with one large clutch and southern forms with two small clutches. In addition, the R_0 values for central Utah populations are conservative, since only four reproductive years were used and not five. A possible explanation for the different demographic statistics and/or method of achieving stability in the two populations is yearly survivorship. Survivorship of hatchlings to juveniles (yearlings) for the two populations is about the same at 23 percent (mortality being caused by overwintering). However, the big difference occurs in juveniles to first-year adults: 80 percent in central Utah and 60 percent in southern Utah. The 20 percent difference is perhaps sufficient to compensate for higher total egg production and longevity of southern Utah *graciosus*. The lower survivorship of southern Utah populations (yearlings to adults) may be due to higher predation of southern populations as suggested by Blair (1960).

In conclusion, we agree with Tinkle (1973) that *S. g. graciosus* is a late-maturing species. Otherwise, our data are at variance either in detail or in such major aspects as SVL, clutch size, longevity, and density. In view of the differences noted in the four studies (Stebbins and Robison, 1946; Mueller and Moore, 1969; and Tinkle, 1973), it is obvious that *graciosus* is a species with considerable adaptive flexibility.

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