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# CONTRIBUTIONS IN SCIENCE

DECEMBER 31, 1970

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THE STATUS AND HABITS OF GRAUER'S BROADBILL  
IN UGANDA (Aves: Eurylaemidae)

*By* HERBERT FRIEDMANN



LOS ANGELES COUNTY MUSEUM OF NATURAL HISTORY • EXPOSITION PARK  
LOS ANGELES, CALIFORNIA 90007

CONTRIBUTIONS IN SCIENCE is a series of miscellaneous technical papers in the fields of Biology, Geology and Anthropology, published at irregular intervals by the Los Angeles County Museum of Natural History. Issues are numbered separately, and numbers run consecutively regardless of subject matter. Number 1 was issued January 23, 1957. The series is available to scientific institutions and scientists on an exchange basis. Copies may also be purchased at a nominal price. Inquiries should be directed to Virginia D. Miller, Los Angeles County Museum of Natural History, 900 Exposition Boulevard, Los Angeles, California 90007.

ROBERT J. LAVENBERG  
*Managing Editor*

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VIRGINIA D. MILLER  
*Editor*

THE STATUS AND HABITS OF GRAUER'S BROADBILL  
IN UGANDA (Aves: Eurylaemidae)

By HERBERT FRIEDMANN<sup>1</sup>

ABSTRACT: Five examples of the very rare broadbill, *Pseudocalyptomena graueri*, from the Impenetrable Forest, southwestern Uganda, prove to be the same as toptotypical east Congo birds, and not to have consistently narrower bills as was earlier suspected. The field notes accompanying the specimens cause a complete revision of our knowledge of this bird. It is primarily a denizen of the forest undergrowth, not of the tree-tops, and it feeds largely on seeds, buds and flowers, plus such insect larvae and beetles that may occur with them, and is not primarily an aerial feeder on flying insects as has been assumed in the literature.

In the course of a second collecting survey of the vertebrate fauna of the Impenetrable Forest, Kigezi, extreme southwestern Uganda, under the sponsorship of National Science Foundation grant GB 7787, to the Los Angeles County Museum of Natural History Foundation, Robert Glen and Andrew Williams obtained five specimens of Grauer's green broadbill, *Pseudocalyptomena graueri*, in May and June, 1969. These were particularly significant because two years earlier A. L. Archer had collected one male in that area, which had a very narrow, laterally compressed bill, only 8.5 mm broad at the gape, and 5.2 mm wide at the proximal (basal) end of the nares, compared with 10.6 to 11.5 mm at the gape and 7.3 to 7.6 mm at the basal edge of the nostrils in eastern Congo examples. In discussing this specimen Friedmann and Williams (1968: 22) stated that additional specimens would be of interest to determine whether or not the Impenetrable Forest birds might prove to be a racially distinct narrow billed population. The present five examples show that this is not the case, that the first one was merely unusual in the narrowness of its bill. The measurements in millimeters of the five 1969 examples, now in The Los Angeles County Museum of Natural History, are as follows: 2 males—width of bill at gape 13.2, 13.6; width of bill at basal edge of nostril 6.9, 7.1; 3 females—width of bill at gape 13.4, to 13.6; width of bill at basal edge of nostrils 7 to 7.5. As may be noted from these figures, kindly measured for me by J. R. Northern, the present series have slightly broader, not narrower, bills than the eastern Congo toptotypical examples measured earlier. No Congo material was studied in connection with these five specimens, but it is obvious that the variational range in bill width in the Kigezi birds completely overlaps that of toptotypical *graueri*, and that the two populations are not separable.

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That the two are not different is actually easier to understand than was the impression of a local difference suggested by Archer's single specimen in 1967. The extreme limits of the entire, and relatively narrow, area of highland forest known to be inhabited by this broadbill are barely more than 150 miles apart, an area that seems to be too small and ecologically too continuously uniform to allow for geographic differentiation. It is true that all the eastern Congo records are from the mountains to the west of the deep gorge of the Ruzizi river, but this valley does not constitute a barrier between those highlands and the mountainous forests of Kigezi. The eastern Congolese highlands extend north from the northern end of the Ruzizi river along the west shore of Lake Kivu to the Rwanda border and to that of extreme southwestern Uganda, where they are coterminous with the so-called Impenetrable Forest. Furthermore there is no reason for thinking that the broadbill is either very local or sporadic within this small total area, even though the actual specimen locality records are still few in number. Definite records from the Kivu district, eastern Congo, are the type locality about 80 kilometers west of the Ruzizi river, northwest of Lake Tanganyika; Miki, Muusi and Luvumba. In southwestern Uganda, the bird is known only from the Bwindi and Ruhizha areas of the Impenetrable Forest, Kigezi Province.

Knowledge of Grauer's broadbill as a bird, and not merely as a museum taxon, is drastically altered by the field observations by Glen and Williams that accompanied the specimens. Archer, in his field notes on the first (1967) Kigezi specimen, wrote that he shot the bird from a perch about 60 feet up in a tall tree. Rockefeller and Murphy (1933: 28) similarly found this species moving about in the upper branches of fairly tall trees. Chapin (1953: 23) noted that the green broadbill was usually found 25 to 75 feet up in forest trees near native plantations, and that in their behavior the birds were quite flycatcher-like, making short but rapid dashes after insects, which they apparently caught on the wing.

Chapin's statements were based entirely on the notes of Rockefeller and Murphy as at that time he had had no personal experience with the bird in life. Therefore the observations of Rockefeller and Murphy are taken directly from their paper. The first individual they saw was in a ". . . large tree with abundant juicy berries, a feeding place for many other species of birds"; it was not active and seemed not to be feeding. "When shot, it was catching insects about twenty feet above the ground in a vine-draped forest tree . . ." Another one was seen later ". . . slumped down close to the end of one of the uppermost boughs, then with a hop and a flit of the wings it caught an insect over its head, realighting on the perch it had just left . . ." These two observers wrote that the "normal level" for Grauer's broadbill was from 20 to 75 feet up in trees.

The picture one gets from the reports of Glen and Williams is quite different. They found the species to be a denizen, not of the higher branches,

but of the upper portions of the undergrowth, about eight feet from the ground. When an individual of the species was seen high up in a tree it had just flown there from the nearby lower vegetation. Glen considered its general behavior and actions very much like those of a waxbill rather than a flycatcher. The species looks extremely small in the field, and the short tail gives the bird a crombec-like (*Sylvietta*) appearance in flight, especially when seen from above. The birds were found, not always singly, but at times in loose groups of 2 or 3 individuals, searching about for food among the branches of a euphorbiaceous tree, *Neoboutonia* sp., with apparent lack of concern about the approach of the observers.

The stomach contents of the five present specimens reveal not the slightest indication of any aerial feeding habits. The stomach of one of them contained a single small beetle, some small seeds, and small flower buds; the second contained only flower buds; the third had the remains of small pulpy fruits; the fourth only small white flowers; and the fifth contained one small snail, one beetle, several insect larvae and a white seed.

These stomach contents are in general agreement with the fact that Rockefeller and Murphy saw one of these broadbills in a berry-laden tree, even though they witnessed no feeding. In their paper they failed to report on the contents of the stomachs of any of their specimens.

Inasmuch as the only other African broadbill genus, *Smithornis*, is known to indulge in a specialized courtship flight behavior, one wonders if the statement referred to above, of *Pseudocalyptomena* making short rapid flights might relate to a similar courtship behavior and not merely to a feeding pattern.

On one occasion Glen and Williams watched this species making short flights through the upper undergrowth of the forest and noted that the flight was of a slow and gliding nature. Even on short flights the birds rarely flapped their wings after starting but seemed to glide by preference. In *Smithornis rufolateralis* Chapin (*loc. cit.*: 18) was convinced that the noises accompanying the flights was produced in the wings. He noted that the primaries had unusually stiff shafts and that the plane of their webs was twisted slightly on their distal portions. "... four or five of the outer primaries (but not the outermost) have unusually narrow webs toward the base, and it seems possible that air may pass between them during this special flight . . ." He noted (*loc. cit.*: 22-23) that in *Pseudocalyptomena* the same remiges were fairly similar, but with "... just a little of the downward twist of the inner web toward the tip . . ."

Whether this slight difference could be responsible for the absence of the flight sound in the green broadbill is not at all clear, but as our collectors made no entry in their notebooks of any such sound, it would seem that these flights were unaccompanied by any special noises. The collectors did report two types of call notes from Brauer's broadbill: on one occasion they heard one of these birds give a soft *cree-cree* repeated three times; and at another

time they heard a one-syllabled high-pitched *prrrp* at intervals of about thirty seconds.

The new field notes are also of interest in that they tend to allocate *Pseudocalyptomena* ecologically more closely with *Smithornis*. The latter genus is known to nest and to feed fairly low down in the forest vegetation, the nests so far reported having been close to the ground or not more than eight feet from it. The earlier observations that conveyed the impression that the green broadbill was entirely a tree-top bird and an aerial feeder on insects must be emended in the light of new knowledge.

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# CONTRIBUTIONS IN SCIENCE

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FEBRUARY 25, 1970

A NEW SPECIES OF *NEADMETE* (NEOGASTROPODA)  
FROM THE PLIOCENE OF CALIFORNIA

By JACK D. MOUNT



LOS ANGELES COUNTY MUSEUM OF NATURAL HISTORY • EXPOSITION PARK  
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A NEW SPECIES OF *NEADMETE* (NEOGASTROPODA)  
FROM THE PLIOCENE OF CALIFORNIA

By JACK D. MOUNT<sup>1</sup>

ABSTRACT: *Neadmete schwartzi*, a new species of gastropod belonging to the family Cancellariidae, is described from the Upper Pliocene Fernando Formation near Newport Bay, Orange County, California.

INTRODUCTION

During February, 1967, earth moving equipment on the east bluff of upper Newport Bay, Orange County, California, uncovered a highly fossiliferous portion of the lower part of the Fernando Formation. This locality remained exposed until August of the same year when further construction destroyed it. Between these months extensive collecting at the exposure by me and my associates yielded an interesting fauna of over 200 species of larger invertebrates characterized by *Nuculana fossa* (Baird, 1863), *Patinopecten healeyi* (Arnold, 1906), *Pecten hemphilli* Dall, 1879, *Glycymeris grewingki* Dall, 1909, *Exiloidea rectirostris hertleini* Bentson, 1940, *Neptunea tabulata colmaensis* (Martin, 1914), *Boreotrophon raymondi* (Moody, 1916) and *Mya truncata* Linné, 1758. This assemblage suggests a Late Pliocene age based on a two-fold division of the Pliocene of California (Vedder, 1960).

While studying the material several new species of mollusks were noted. One of these belongs to the genus *Neadmete* Habe, 1961, which was only recently recognized in the west American fauna (Kanakoff and McLean, 1966). This new species is described herein.

References to the Los Angeles County Museum of Natural History, Section of Invertebrate Paleontology are hereafter abbreviated as LACMIP.

ACKNOWLEDGMENTS

I am grateful for the assistance of the following persons. Dr. Robert F. Meade, California State College at Los Angeles, and Dr. James H. McLean, Los Angeles County Museum of Natural History, gave helpful advice and critically reviewed the manuscript. Mr. Jack Schwartz, Mr. Boris Savic and Mr. and Mrs. F. L. Grouard aided in collecting the type material. Photographs are by Mr. Louis W. Kundraeth and Mr. James W. Shuttleworth of Kundraeth Studio of Photography, Baldwin Park, California.

<sup>1</sup>Department of Geology, California State College, Los Angeles, 90032.

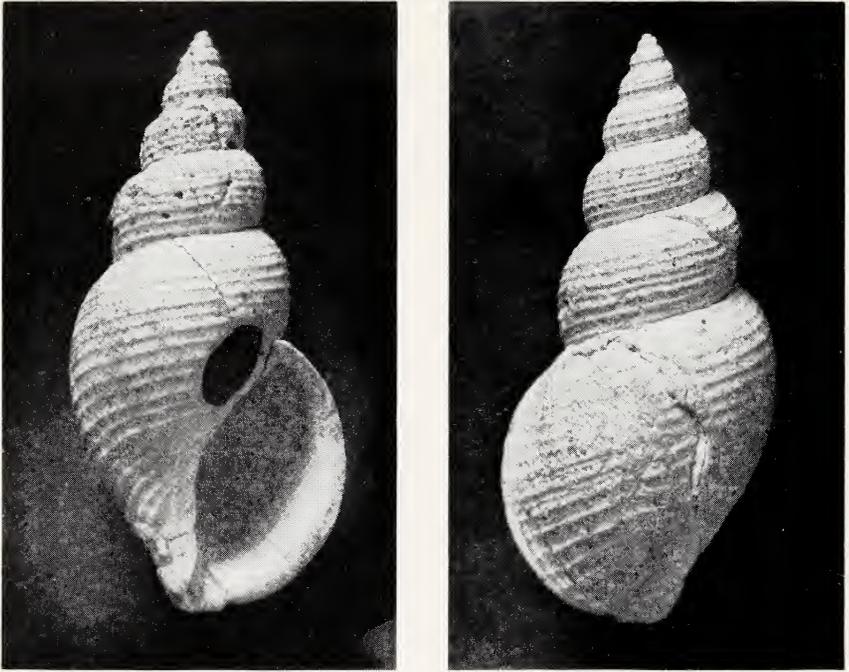


Figure 1. *Neadmete schwartzi*, new species. Holotype, LACMIP 1779. Height 35.6, diam. 16.9 mm.

## SYSTEMATIC DESCRIPTION

Family Cancellariidae Gray, 1853

Genus *Neadmete* Habe, 1961*Neadmete schwartzi* new species

## Figure 1

*Diagnosis:* Shell relatively large; whorls 8, evenly convex, weakly tabulate; 16 spiral ribs on body whorl; outer lip reflected.

*Description:* Shell relatively large for genus, long, slender, fusiform; spire elevated. Whorls 8, moderately inflated, evenly convex, weakly tabulate on early whorls becoming obsolete on penultimate and body whorls. Nucleus simple, smooth, whorls 2. Axial sculpture of approximately 16 low, rounded ribs, becoming obsolete on last four whorls. Spiral sculpture of low, narrow, rounded ribs, 3 on postnuclear whorls and 16 on body whorl; with single smaller rib intercalated between major ribs on the apical whorls and the first nine ribs of the body whorl; interspaces slightly wider than ribs. Sutures moderately impressed. Aperture subelliptical, approximately one half the height of the shell; outer lip smooth, thin, slightly reflected, with 15 internal spiral lines; canal short and shallow. Columella long, straight, with two folds and eight plicae formed by extension of primary spiral ribbing.

*Type Material:* Holotype, LACMIP 1779. Four paratypes: LACMIP 1780; California Academy of Sciences (CAS), Department of Geology type collection 13203; University of California at Los Angeles (UCLA), Department of Geology type collection 47313; and collection of Jack D. Mount (JDM) 106. Measurements for the type specimens are listed in Table 1.

*Type Locality:* LACMIP locality 471; 33° 38' 21" N, 117° 53' 02" W; in a 6 foot thick lens of sandy cobble conglomerate which occurs approximately 425 feet stratigraphically above the base of the formation. At the present time it is located under the residence at 2161 Vista Entrada, Newport Beach, California.

*Age and Formation:* Late Pliocene, Fernando Formation.

*Discussion:* *Neadmete schwartzi* is nearest to the Recent *N. circumcincta* (Dall, 1873:59) but differs from that species principally in the larger size, more evenly convex, less tabulate whorls, more spiral ribs and in the presence of the reflected outer lip. *N. circumcincta* is recorded from Alaska, with a specimen in the Los Angeles County Museum of Natural History from Hope Island, off the northern end of Vancouver Island, British Columbia. *N. sutherlandi* Kanakoff and McLean, (1966:4) from the Lomita Marl (Plio-Pleistocene) of Los Angeles County, California, is the only other fossil species of *Neadmete* and it is readily distinguished from *N. schwartzi* by its larger size, more pronounced tabulation, and smaller number of spiral ribs.

*Etymology:* This new species is named for Mr. Jack Schwartz, who

collected the holotype, in recognition of his contributions to the mineralogy of California.

TABLE 1.  
Measurements (in mm) of the type specimens  
of *Neadmete schwartzi*, new species.

Specimen no.	Height	Diameter	Height of Aperture
LACMIP 1779	35.6	16.9	16.8
LACMIP 1780	28.2	14.8	13.3
CAS 13203	35.3	17.9	16.5
UCLA 47313	33.7	17.1	15.7
JDM 106	31.3	15.7	15.1

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(DIPTERA: BLEPHARICERIDAE)

By CHARLES L. HOGUE



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CONTRIBUTIONS IN SCIENCE is a series of miscellaneous technical papers in the fields of Biology, Geology and Anthropology, published at irregular intervals by the Los Angeles County Museum of Natural History. Issues are numbered separately, and numbers run consecutively regardless of subject matter. Number 1 was issued January 23, 1957. The series is available to scientific institutions and scientists on an exchange basis. Copies may also be purchased at a nominal price. Inquiries should be directed to Virginia D. Miller, Los Angeles County Museum of Natural History, 900 Exposition Boulevard, Los Angeles, California 90007.

ROBERT J. LAVENBERG  
*Managing Editor*

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VIRGINIA D. MILLER  
*Editor*

DESCRIPTION OF A NEW SPECIES OF NET-WINGED MIDGE  
FROM THE GREAT BASIN, WITH A KEY TO THE NORTH  
AMERICAN SPECIES OF THE GENUS *DIOPTOPSIS*  
(DIPTERA: BLEPHARICERIDAE)

By CHARLES L. HOGUE<sup>1</sup>

ABSTRACT: The adult, pupa and larva of a new species of *Dioptopsis* are described and figured from material collected in Great Basin ranges in northeastern California and Nevada. The adult is peculiar among its congeners in lacking mandibles and having infusate wings. It is further characterized along with the immature stages in a key presented for all the North American member of the genus.

The amandibulate condition (with associated modifications of other head structures) of this species and others is discussed and a new term, colocephalous, is introduced to designate it.

Thanks to the exceptional field work of John F. Emmel and Oakley Shields over the past three years, material has accumulated of a previously undiscovered species of *Dioptopsis* in the Great Basin. For this contribution to my studies on the Blephariceridae of North America, I wish to express my appreciation to these spirited collectors. I wish also to thank J. A. Powell and A. Stone and their respective institutions, University of California, Berkeley—California Insect Survey Collection [CIS] and Agricultural Research Service, U.S. Department of Agriculture—U.S. National Museum [USNM], for the loan of additional and comparative material. The majority of the specimens recorded are in the Los Angeles County Museum of Natural History [LACM].

*Dioptopsis dismalea*, new species  
(Figs 1-13)

*Dioptopsis* n. sp. Hogue, *in press*. Bull. Calif. Insect Survey.

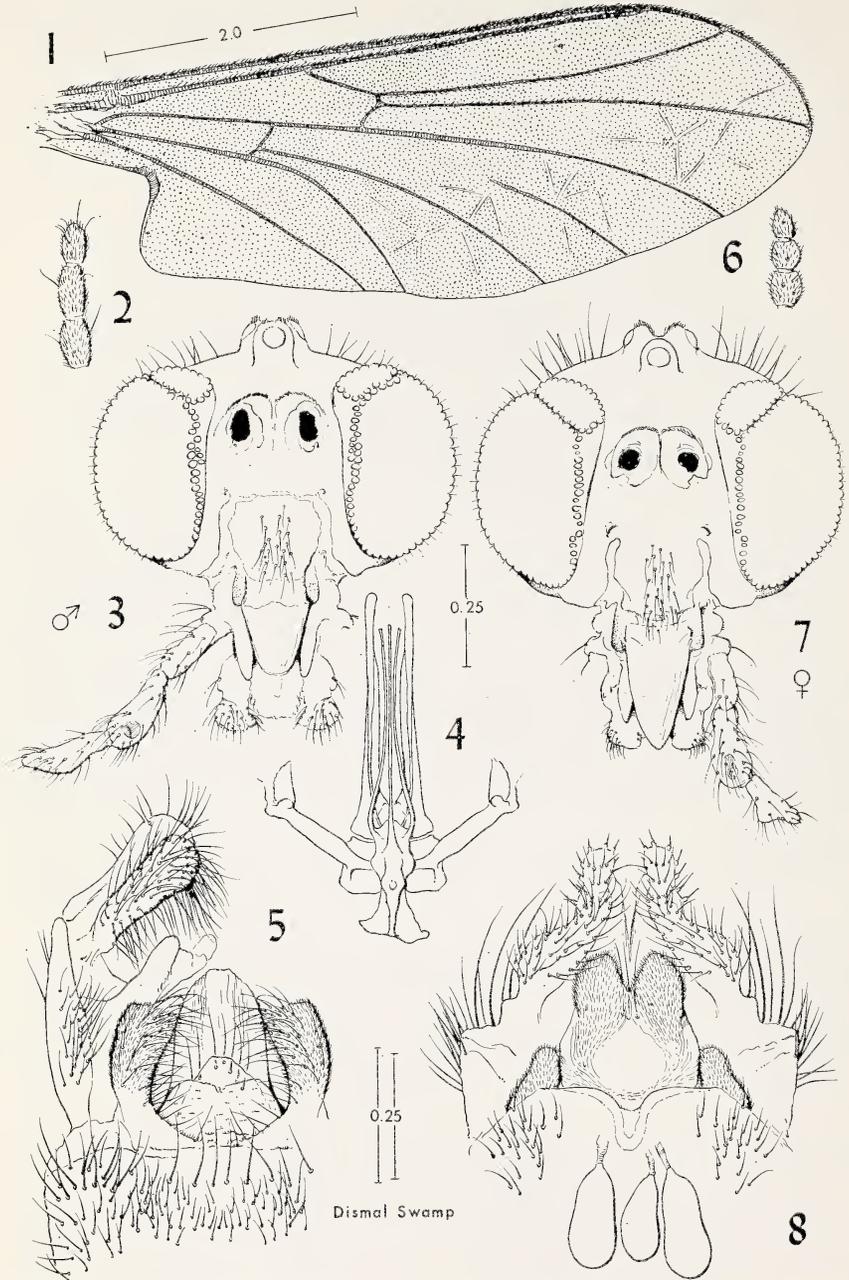
FEMALE (based on allotype; Figs. 6-8)

*Size*.—A medium sized blepharicerid. Measurements (lengths in mm):

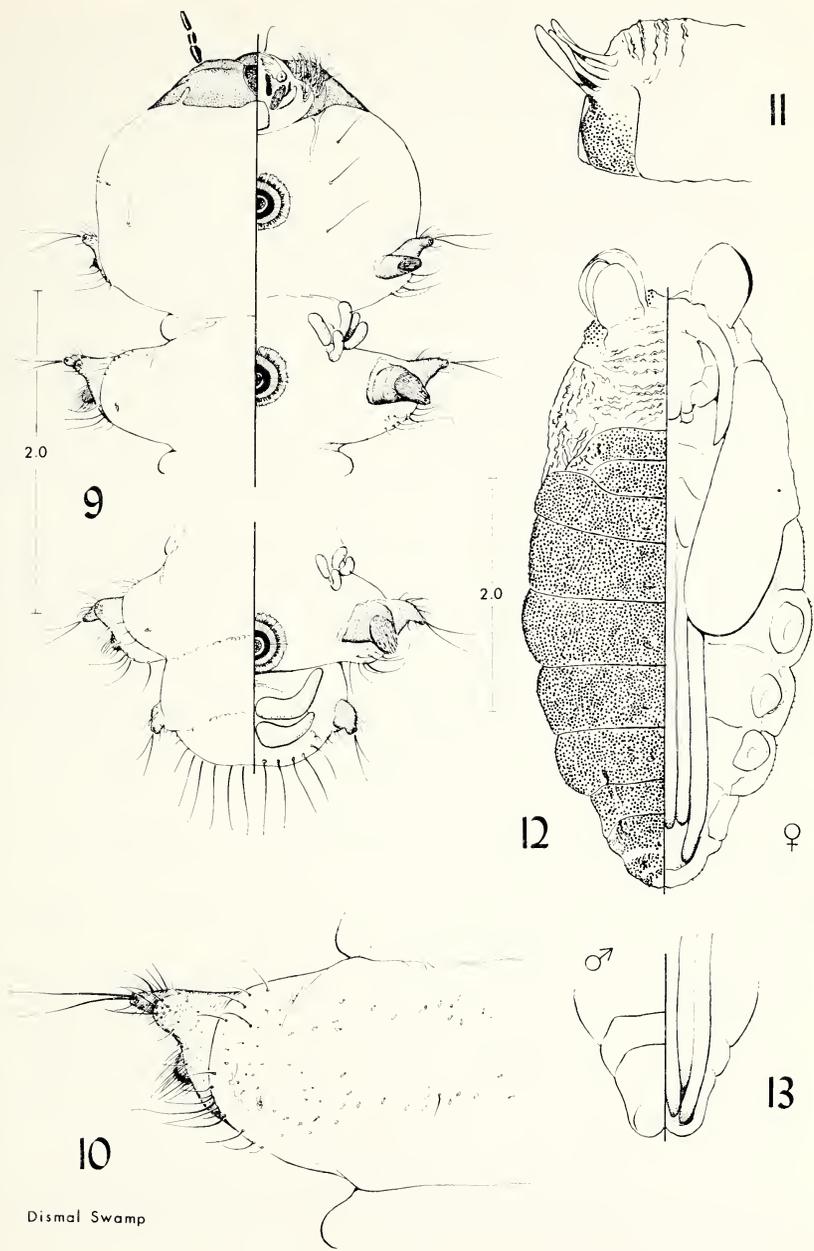
Body: 3.6      Wing: 5.7

Legs:	fore	mid	hind
femur	2.5	2.5	3.4
tibia	2.5	2.3	3.1
tarsus 1	1.2	1.0	1.4
2	0.3	0.3	0.4
3	0.25	0.25	0.25
4	0.2	0.2	0.2
5	0.4	0.4	0.4

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Figures 1-8. *Dioptopsis dismalea*, n. sp., Adult. 1. Wing. 2. Terminal antennal segments, male. 3. Head, male. 4. Phallosome complex, male genitalia. 5. Male genitalia. 6. Terminal antennal segments, female. 7. Head, female. 8. Female genitalia.



Dismal Swamp

Figures 9-13. *Dioptopsis dismalea*, n. sp. 9. Larva. 10. Details of typical median abdominal segment. 11. Pupa, lateral view of anterior end. 12. Pupa (female). 13. Terminal end of male pupa.

*Coloration.*—General integument melanic, well sclerotized. Head, including antennae, all black. Mesoscutum brownish laterad, large antero-medial rectangular area black, pruinose mesad, shiny black laterad; mesonotal sutures, supraanterior pronotal areas, supraalar, scutoscuteellar notches and postscutellum, all shiny black. Scutellum gray pollinose. Pleuron generally brown, lower sternopleuron and metepimeron contrasting black. Haltere even gray. Legs gray-black, darker at joints and distal half of tarsal segments 5. Wing membrane tinged sooty-black. Abdomen evenly black, slightly pruinose.

*Head.*—Figure 7. Eyes widely separated; upper eye division small, 7-9 rows of ommatidia along maximum vertical arc; not well differentiated from lower division, no un-faceted strip, ommatidia of both divisions equal in size. Antenna short, 14 segmented, shape and length of flagellar segments subequal except basal which is approximately 2.0 length of others, ultimate segment slightly smaller than penultimate (Fig. 6). Mouth parts short, mandibles entirely lacking, hypopharynx truncate, with weak marginal teeth. Palpus 4-segmented, terminal segment (4 and 5) swollen ventromesad, subtriangular in shape.

*Thorax.*—Scutellum with dense lateral setal patches, connected by a single row of setae across caudal periphery; a few supraalar and prescutellar bristles, anterior pronotum bare; other sclerites nude. Legs with tibial spurs 0-0-2, spurs of hind tibia unequal. Wing shape, venation and trichiation as figured (Fig. 1).

*Genitalia.*—Figure 8. Oviscapt deeply cleft mid-posteriorly. Spermathecae moderate in size, one smaller than other two and elongate-ovoid, others elongate-ovoid, slightly constricted mesally.

MALE (based on holotype; Figs. 1-5)

*General.*—Slightly larger than female. Measurements (lengths in mm):

Body: 3.6	Wing: 6.0		
Legs:	fore	mid	hind
femur	2.9	3.3	4.3
tibia	3.1	2.8	4.1
tarsus 1	1.8	1.4	1.8
2	0.6	0.5	0.6
3	0.4	0.4	0.4
4	0.3	0.3	0.3
5	0.4	0.4	0.5

*Coloration.*—Generally darker than female. Essentially sooty-black all over; abdominal pleural membranes contrasting white. Wing membrane tinged sooty-black as in female.

*Head.*—Figure 3. Practically indistinguishable from that of female. Eyes widely separated. Hypopharynx truncate, marginal teeth absent. Tip of labrum

entire. Antenna short; 14-segmented, relative size and shape of segments as in female.

*Thorax*.—Chaetotaxy as in female, a few bristles on anterior pronotum. Legs with tibial spurs 0-0-2, hind pair very unequal. Wing as in female.

*Genitalia*.—Figures 4 and 5.

#### PUPA (Figures 11-13)

*Size*.—Small to medium. Measurements (overall length in mm): ♂ range 4.9-5.6, mean ( $n = 4$ ) 5.1. ♀ range 5.2-6.0, mean ( $n = 10$ ) 5.5.

*Coloration*.—Dorsally all black, no pattern.

*Structure*.—Figures 11-13.

#### LARVA (final instar; Figures 9 and 10)

*Variation*.—Fortunately material has recently come to hand from a third locality, in the Jarbidge Mountains, to indicate that this species is discordantly variable in respect to several features of the male genitalia and one pupal character. Formerly, specimens whose differences suggested the existence of two geographical subspecies were only available from the Warner Mountains of California and Ruby Mountains of Nevada.

In the genitalia of the male the following characters are notably variate. (1) Angle of projection of the 9th tergite lobes. The lobes tend to lie straight and parallel, thus angled at about  $90^\circ$  from the posterior margin of the segment, in the Ruby Mountain populations and variously curved and convergent in the other two populations. (2) Extent of bristles on the sides and venter of the basistyle. These bristles are mostly lateral but a few stray mesoventrad, especially in the Nevada populations. (3) Shape of tip of the paramere. Usually the apex of this organ is rounded and slightly inturned with the canal running nearly to the end. In some specimens from the Jarbidge Mountains, the apex is extended beyond the canals to form a spatulate process. (4) Shape of dorsal lobe of outer dististyle. In dorsal aspect this lobe appears club shaped and straight in the Jarbidge Mountains specimens but tend to be capitate and incurved in males from the Ruby and Warner Mountains. (5) Length of ventral projection of the inner lobe of the dististyle. This process variously exists as a short point hardly longer than the body of the main lobe, to a long fingerlike projection curving up and beyond the latter.

A dimorphism occurs in the extent of dorsal integumentary stippling on the pupa. In the California populations, these structures terminate abruptly short of the lateral margins leaving a clear zone around most of the abdominal periphery. Nevada pupae show the stippling strongly up to, and even carrying ventrad of, the lateral edge of the abdominal segments.

*Range*: The species is now known only from extreme western and eastern mountains in the Great Basin and Range geological system. It is certain to be found throughout the intervening ranges where streams occur at elevations of over 7000 feet.

*Diagnosis:* The pigmented wing of this species is unique among *Dioptosis*, the wing membrane of all other species being hyaline. Other characteristics to distinguish adults and the immatures are given in the keys below (see Discussion).

*Type Locality and Material:* The types of this species come from streams draining Mount Bidwell through a large meadow in the Warner Mountains of extreme northeastern California (Modoc County) called Dismal Swamp (119° 10' W, 41° 59' N). Specific collections are as follows:

**HOLOTYPE:** ♂, (genitalia on slide No. CLH 6809-3) and **ALLOTYPE,** ♀, (genitalia on slide No. CLH 6809-6): Dismal Swamp, 7200 feet, 15-16 July 1968 (J. Emmel and O. Shields) [LACM].

**PARATYPES:** 5 ♂♂, 6 ♀♀: same data as holotype (one pair completely dissected, on slides) [LACM, USNM].

8 ♂♂: creek just west of Dismal Creek, 7300 feet, 15 July 1968 (Emmel and Shields) [LACM].

**ADDITIONAL SPECIMENS:** CALIFORNIA, Modoc County. 65 pupae and pupal skins: creek just west of Dismal Creek, 7300 feet, 15 July 1968 (Emmel and Shields) [LACM].

103 pupae: Dismal Creek, 7300 feet, 15 July 1968 (Emmel and Shields) [LACM].

3 pupae: stream west slope Mount Bidwell, 1 mi. S Dismal Swamp, 8000 feet, 16 July 1968 (Emmel and Shields) [LACM].

66 pupae, 75 larvae: Dismal Swamp, 8000 feet, 15 July 1948, 1950 (W. W. Wirth) [USNM, CIS].

NEVADA, Elko County. 27 pupae and pupal skins, 81 larvae: stream connecting Island Lake and Lamoille Creek, Ruby Mountains, 8800-10,000 feet, 8 August 1967, 29 June 1968 (Emmel and Shields) [LACM].

16 ♂♂, 75 pupae: Bonanza Gulch, 7800-8000 feet, Jarbidge Mountains, 23 July 1969 (Emmel and Shields) [LACM].

18 pupae: creek west of Angel Lake, 8600 feet, East Humboldt Range, 26 July 1969 (Emmel and Shields) [LACM].

*Biological Notes:* All localities where *D. dismalea* has been taken lie between 7300 to 10,000 feet elevation. The habitats are accordingly subalpine and alpine but vary to a considerable extent in several features important to blepharicerid ecology. According to Emmel (personal communication), "The Dismal Swamp is a large wet meadow (not a swamp, really) with willow thickets around the edges. There are scattered patches of thick Pine forest on the surrounding slopes. The "swamp" is not in a basin or valley as such, but is on the edge of a high plateau which slopes toward the east, just east of the crest of the Warner Mts. Several very small streams flow into the Dismal Swamp from the slopes above it on the west and south sides. Probably the largest of these streams are two flowing from the slopes of Mt. Bidwell. The streams flow through open aspen forest just above the edge of the large wet meadow; it is in these areas of open aspen forest where blepharicerid material was most

common. Larvae or pupae were not found more than several hundred yards away from the Swamp (although the streams [terminated] not too far above the areas where pupae stopped appearing), nor in the Swamp itself. Larvae and pupae were found on stones ranging in size from 1" diameter up to 6" diameter (which were probably the largest rocks). The stream rocks were generally very dark in coloration, although not usually as dark as the pupae on them. A few pupae were also found in a small stream high on the western slope of Mt. Bidwell where there was no forest; small willow thickets surrounded this stream. In all areas where blepharocerid material was collected, the stream habitat here was in contrast to other blepharocerid stream habitats in which we have collected, in that these streams were mere trickles (although this was a very dry year) rather than rushing torrents of abundant water as is usually the case. The observation that larvae and pupae were on relatively small rocks (the only ones available) is also of interest. The habitat of this species is noticeably different from that of . . . the Ruby Mountains locality . . . [which] . . . looks very much like a typical stream in the high altitudes of the eastern slope of the Sierra Nevada. Lamoille Canyon has been well glaciated; many streams flow down its steep slopes in the early summer. The stream in which larvae and pupae were found flows down an open slope into Lamoille Creek; blepharocerid material was found in the swiftest water, on dark rocks (probably granite). The whole area looks not unlike the higher altitudes of the Sierra Nevada, and it is well watered. Aspens are more abundant than conifers at this altitude; trees occur in scattered patches, never as extensive forest."

The site in the stream above Angel Lake in the East Humboldt Range is like the preceding, a nearly vertical narrow cascade down a rough granite face of a steep glaciated valley. There is scarcely any vegetation in the immediate vicinity of the stream. On the other hand at Bonanza Gulch, in the Jarbidge Mountains, the gently tumbling stream in the bottom of a broad ravine flows through a jumble of log and debris jams and is heavily overgrown with tall clump grass and willows.

*Discussion:* The new species clearly shows a complete lack of mandibles. This is a normal condition in only one other North American blepharicerid, *Blepharicera ostensackeni* Kellogg, but occurs consistently in many exotic species and in populations (subspecies ?) of *Dioptopsis aylmeri* (Garrett) in the eastern drainage of the Sierra Nevada (Hogue, in press). Associated with the amandibulate condition is a complete rearrangement in head proportions including a much shortened labrum and other mouthparts, weak hypopharyngeal teeth, widely separated eyes and reduced upper eye divisions. This type of head may be designated, "colocephalus" (Gr. *Kolos*, stunted, incomplete).

The genetic and phylogenetic significance of colocephaly which is anomalous in some species and normal in others, deserves special study. I have expressed (Hogue, in press), as has Edwards (1929:35-36), the opinion that such a total reorganization of head construction could come about by pleio-

trophic effects of simple mutations. Thus what would appear to be a profound set of differences upon which new species or other taxa might be based actually may easily and frequently arise in individuals or populations (even becoming dominant in one or more geographic areas as has presumably occurred with eastern Sierran *D. aylmeri*) of a single species. A trimorphic or even quadrimorphic condition could exist wherein a species may have males and females alternately with or without mandibles and with associated modified head structure. Such a hypothesis was long ago advanced by Muller but was refuted by other dipterists (Alexander, 1958:814) on the grounds that examples of dimorphic females actually belonged to different species. I believe the phenomenon needs further study to determine its extent, cause, and adaptive significance.

With the discovery of *D. dismalea*, the genus *Dioptopsis* in North America now consists of six species:

1. *aylmeri* (Garrett, 1923). Can. Ent. 55:244 (*cheaini* Garrett, 1925, to be placed in synonymy in forthcoming work by author). Widespread in western Canada and the United States.
2. *sequoiarum* (Alexander, 1952). Bull. Brook. Entomol. Soc. 47:91. California, western Sierra Nevada.
3. *dismalea* Hogue, 1969. Great Basin Ranges.
4. *arizonica* Alexander, 1958. Bull. Brook. Entomol. Soc. 53:50-51. Arizona, Sierra Ancha Mountains.
5. *alpina* Hogue, 1966. Los Angeles Co. Mus. Nat. Hist., Contrib. Sci., 120: 1-5. Northern and southern California.
6. *markii* (Garrett, 1925). Seventy New Diptera, p. 5. Recorded only from northern California, Washington and Alberta.

The first three species are very close relatives and may be united into an Aylmeri group. The primary basis of the grouping is a common larval type. In spite of the colococephalous heads of adult *dismalea* giving it a markedly different character from *aylmeri* (with the exception of certain populations as mentioned above) and *sequoiarum*, the species are indistinguishable in the larval stage. *Arizonica* and *alpina* together form a second natural grouping on the basis of features I have outlined elsewhere (Hogue, 1966:5). *Markii* stands alone with very different larval, pupal and adult characteristics.

The following keys will facilitate identification of the adults and immatures of all these species, with the exception of *arizonica*, whose female, pupa, and larva are unknown.

#### KEY TO NORTH AMERICAN *DIOPTOPSIS* SPECIES ADULTS

(Female of *arizonica* unknown)

1. *General*: Wing membrane infuscated. Palpus four segmented.....*dismalea*  
*General*: Wing membrane hyaline. Palpus five segmented..... 2

2. *General*: Upper eye division at least one-fifth to one-fourth the area of lower in males (at least 11-12 rows of ommatidia), greater than lower in females ..... 3  
*General*: Upper eye division greatly reduced, much smaller than lower in both sexes, a small area of 4-7 rows of ommatidia..... 4
3. *Male genitalia*: Paramere with conspicuous mesal spur. Mesal margin of IX tergite lobe produced into a nude flange (i.e. without micro- or macrochaetae). *Female genitalia*: Spermathecae ovoid.....*aylmeri* (in part)  
*Male genitalia*: Paramere simple, without spur. Mesal margin of IX tergite lobe not produced. *Female genitalia*: Spermathecae elongate-ovoid .....*sequoiarum*
4. *General*: Antenna with 15 segments. Mid-tibial spur present though minute. *Male genitalia*: IX tergite lobe short, only 2 times width. Lobe of outer dististyle short and projecting dorsomesad..... 5  
*General*: Antenna with 14 segments or less. Midtibial spur entirely absent. *Male genitalia*: IX tergite lobe elongate, length 5-6 times width. Lobe of outer dististyle elongate and projecting subparallel to dististyle face ..... 6
5. *Male genitalia*: Tip of inner dististyle lobe recurved.....*alpina*  
*Male genitalia*: Tip of inner dististyle lobe with cup-shaped depression ..... *arizonica*
6. *General*: Ultimate antennal segment smaller than penultimate. Female mandible reduced to absent. *Male genitalia*: Paramere with spur. *Female genitalia*: Spermathecae pear-shaped.....*aylmeri* (in part)  
*General*: Ultimate antennal segment longer than penultimate. Female mandible normal sized. *Male genitalia*: Paramere simple. *Female genitalia*: Spermathecae ovate.....*markii*

## PUPAE

(Unknown for *arizonica*)

1. Branchial sclerite strongly lobed, projecting well beyond cephalic sclerite in lateral aspect.....*alpina*  
Branchial sclerite weakly lobed, cephalic sclerite visible from lateral aspect ..... 2
2. Branchial lamellae spreading, caudal pair strongly convergent, often overlapping .....*markii*  
Branchial lamellae all subparallel..... 3
3. Length/width of anteriormost branchial lamella 1.1 or larger.....*dismalea*  
Length/width of anteriormost branchial lamella 1.0 or smaller..... 4
4. Interbranchial index (=interbranchial distance at base of lamellae/width of anteriormost lamella) less than 0.7. Rugae of posterior region of scutum forming a line running parallel to hind margin of sclerite ..... *sequoiarum*

Interbranchial index greater than 1.0. Rugae of posterior region of scutum random, not forming a line.....*aylmeri*

### LARVAE

(Unknown for *arizonica*)

1. Dorsal tubercles and plates present.....*alpina*  
Dorsal integument without tubercles or plates..... 2
2. Antenna indistinctly segmented, basal  $\frac{3}{4}$  membranous. Ventral gill tuft of segment 6 diminutive, with only 2 filaments. Dorsal pseudopods gently curving cephalolaterad.....*markii*  
Antenna clearly 3 segmented, middle segment much smaller than others. Ventral gill tuft of segment 6 subequal to others, with 5 filaments. Dorsal pseudopods angular, tips project ventrolaterad.....  
.....*aylmeri, sequoiarum, dismalea*

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# CONTRIBUTIONS IN SCIENCE

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GEOGRAPHIC VARIATION AND SYSTEMATIC  
STATUS OF MEXICAN LYRE SNAKES OF THE  
*TRIMORPHODON TAU* GROUP (COLUBRIDAE)

By ROY W. MCDIARMID AND NORMAN J. SCOTT, JR.



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VIRGINIA D. MILLER  
*Editor*

# GEOGRAPHIC VARIATION AND SYSTEMATIC STATUS OF MEXICAN LYRE SNAKES OF THE *TRIMORPHODON TAU* GROUP (COLUBRIDAE)

By ROY W. McDIARMID<sup>1</sup> AND NORMAN J. SCOTT, JR.<sup>2</sup>

**ABSTRACT:** Geographic variation in lepidosis and color pattern was studied in the nominal species *Trimorphodon collaris*, *fasciolata*, *forbesi*, *latifascia*, *tau*, and *upsilon*. Specimens were grouped into seven geographically separated samples which were then compared. Ranges of most characteristics overlap broadly; others vary independently and discordantly. Ventral-subcaudal scales decrease from north to south. Snakes from the Balsas-Tepalcatepec Basin have fewer dorsal bands than do snakes from other areas. They also have a relatively uniform head pattern. Specimens from other areas have a complex head pattern consisting of prefrontal bars, interocular bars, and discrete parietal marks in various combinations. Head pattern and body band analyses indicate limited genetic exchange between the Balsas-Tepalcatepec Basin samples and those from other areas, apparently the result of secondary contact in southern Jalisco and adjacent Michoacán. The Transverse Volcanic Range and the Sierra Madre del Sur apparently are effective in restricting genetic exchange.

The above nominal species are assigned to the synonymy of *Trimorphodon tau*. *Trimorphodon tau tau* is maintained for the foothills and plateau populations and *T. tau latifascia* (new combination) is assigned to the Balsas-Tepalcatepec Basin populations. *Trimorphodon tau* is redescribed and its distribution delimited. Character variation in a brood from Puebla approaches the variation typical of the entire Puebla sample.

## INTRODUCTION

In the years following 1935, rather extensive collections of amphibians and reptiles were made in México. Early reports on many of these collections, culminating in the Mexican checklists by Hobart M. Smith and Edward H. Taylor (1945, 1948, 1950), are extremely useful in elucidating the distribution and relationships of the many components of this complex herpetofauna. During the past 15 years, reports on collections from various parts of México have continued to appear. Unfortunately, some of these reports have confused rather than clarified our knowledge of the distributions and systematics of certain of the Mexican species (see Duellman, 1966, for additional discussion). An example of such confusion is found within the snake genus *Trimorphodon*.

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All 12 nominal species of *Trimorphodon* have been reported from México (Smith and Taylor, 1945). Smith (1941) divided the genus into two apparently natural groups. The *biscutatus* group, characterized by large chevron-shaped marks on the neck and head, included five nominal species (*biscutatus*, *lambda*, *lyrophanes*, *paucimaculatus* and *vandenburghi*) that range generally from the southwestern United States southward through the Pacific lowlands to Costa Rica. The *tau* group, characterized by a light, transverse nuchal collar of varying width, included seven nominal species (*collaris*, *fasciolata*, *latifascia*, *tau*, *upsilon* and *vilkinsonii*) whose ranges encompass upland and mountainous portions of southeastern New Mexico, southwestern Texas and México, north of the Isthmus of Tehuantepec.

We became interested in the *Trimorphodon tau* species group in the course of an extensive study of the herpetofauna of Sinaloa, México (Hardy and McDiarmid, 1969). In attempting to allocate specimens, we realized the need for a revision of this group of snakes and so began a study of the geographic variation and systematic relationships among the described forms, with emphasis on the zoogeographic implications of the distribution of specific characteristics.

#### HISTORICAL REVIEW

Cope (1869) described *Trimorphodon tau* from a single specimen collected by Sumichrast, supposedly from the western part of the Isthmus of Tehuantepec, and *Trimorphodon upsilon* from a specimen collected in Guadaluajara, México by Major (see Zweifel, 1959 for discussion of this collection).

Later in the same year, Peters (1869) described *Dipsas biscutata* var. *latifascia* from specimens collected in Puebla by Berkenbusch.

These descriptions were the first for representatives of the *tau* species group, though specimens of these species were known previously. Jan (1863) listed four specimens of *Eteirodipsas biscutata*, one from México. Nine years later this same specimen was illustrated in Jan and Sordelli (1872) and listed as part of the collection of "Westphal-Castelnau a Montpellier." The Mexican specimen definitely is not *Trimorphodon biscutatus* (Duméril, Bibron and Duméril, 1854), nor is it representative of a species of the *biscutatus* group as presently understood. In fact the color pattern, especially of the head (Jan and Sordelli, 1872: vol. 3, livr. 39, pl. 1, no. 3), is similar to the pattern of the holotype of Cope's *Trimorphodon upsilon*.

Cope (1875) described a fourth species of the *tau* group, *Trimorphodon collaris*. This specimen, also collected by Sumichrast, was from Orizaba, Veracruz. In 1882 Sumichrast pointed out that the type specimen of *Trimorphodon tau* was collected near Quiotepec, between Tehuacán and Oaxaca and was not from the western part of the Isthmus of Tehuantepec as stated by Cope (1869) in the original description. In this same publication, Sumichrast (1882) listed "los individuos típicos" of *Trimorphodon collaris* from Tuxpango, near

Orizaba, Veracruz. However, in the description of *T. collaris* Cope (1875) made no reference to specimens other than the type. The location of any additional specimens of *T. collaris* collected by Sumichrast is unknown.

Günther (1895) pointed out the similarities between *Trimorphodon tau*, *collaris* and *upsilon*, and referred his specimens to *T. upsilon*. Günther considered Peters' *latifascia* synonymous with *Trimorphodon biscutatus*. Boulenger (1896) recognized *Trimorphodon tau* and *T. upsilon* as distinct species. Boulenger followed Günther's suggestion and included *Trimorphodon collaris*, as well as *Trimorphodon biscutatus latifascia* (Peters), in the synonymy of *Trimorphodon upsilon*.

Taylor (1939) reviewed Mexican species of *Trimorphodon* and revived Peters' name *latifascia* for specimens from Puebla and Morelos. Taylor recognized *T. upsilon* and *T. tau* as distinct species but considered *T. collaris* synonymous with *T. latifascia*.

In 1941 Smith surveyed the genus *Trimorphodon* and established the two species groups. He considered *Trimorphodon latifascia*, *T. upsilon*, *T. tau* and *T. collaris* distinct species. In addition Smith (1941) described two more forms in the *tau* group: *Trimorphodon fasciolata* from Tzaráracua Falls, Michoacán (one specimen) and *Trimorphodon forbesi* from San Diego, Puebla (one specimen).

After examining specimens of *Trimorphodon* from Michoacán, Schmidt and Shannon (1947) suggested that *T. fasciolata* might be conspecific with *T. latifascia*. Davis and Smith (1953) and Peters (1954) demonstrated that these two forms probably were representative of a single species.

Smith and Darling (1952) examined some specimens from Tamaulipas and San Luis Potosí and regarded *Trimorphodon upsilon* as a subspecies of *Trimorphodon tau*. Martin (1958) confirmed the conspecificity of these forms.

Duellman (1961) concluded that data were inadequate to support the retention of *upsilon* as a subspecies of *Trimorphodon tau*. He regarded *Trimorphodon tau* as a monotypic species that has a highly variable color pattern. Thus, if the systematic changes since Smith's revision (1941) are accepted, there are currently four species in the *tau* group, *Trimorphodon tau*, *collaris*, *forbesi* and *latifascia*.

Jones and Findley (1963) suggested that *T. wilkinsoni* might be related to *T. lambda*, a member of the *biscutatus* group.

#### METHODS AND MATERIALS

We have examined all known specimens, including holotypes, of the following nominal species of the *Trimorphodon tau* group: *tau*, *upsilon*, *collaris*, *latifascia*, *fasciolata* and *forbesi*. Locality, sex (determined by dissection), and the following features were recorded for each of the 197 specimens: number of ventral scales (counted according to the method outlined by Dowling, 1951), number of subcaudal scales including the tail tip, total number of

ventral and subcaudal scales, nature of the anal plate (divided or entire), number of supralabials, supralabials that contact eye, number of infralabials, the infralabial that is first separated from the chin shields by small gular scales, number of loreal scales (all scales between the preocular and nasal scales), number of preocular and postocular scales, and the number of primary and secondary temporal scales. The dorsal scale rows were counted one head length behind the parietal scales, at midbody and one head length in front of the anus. The number of scales in the light collar counted on the midline was recorded, as was the number of body and tail bands or blotches. The first cross band that showed any indication of splitting (the presence of a light center on the midline) was recorded. For each band-interspace-band sequence the number of scales on the midline was counted beginning with the first dark band-light interspace-second dark band, for the seventh dark band-light interspace-

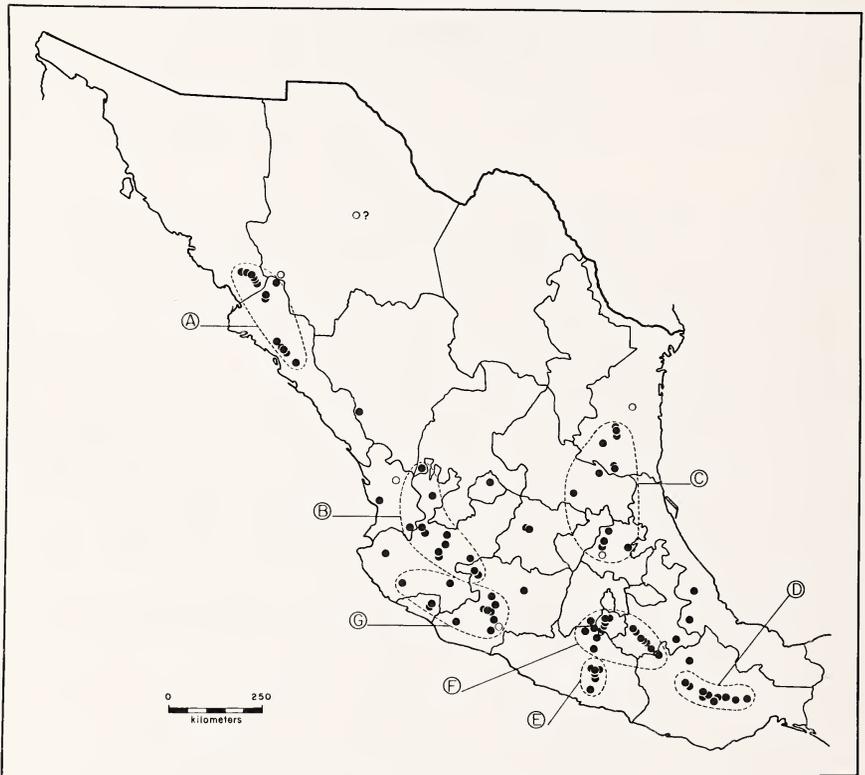


Figure 1. Distribution of *Trimorphodon tau* in México. Each dot represents a locality or localities of one or more specimens. Solid dots indicate specimens examined; circles indicate additional specimens or literature records. Samples analyzed are lettered A through G.

eighth dark band, and at equivalent intervals along the body of the snake. In all instances the band-interspace-band sequence immediately anterior to the vent was counted. Detailed drawings of the dorsal head pattern were made for each specimen.

Specimen localities were plotted on a topographical map of México and grouped into seven geographical units (Fig. 1). These seven samples, hereafter referred to as populations A through G, include specimens from the following areas:

*Population A* (25 specimens,—from localities in the foothills of the Sierra Madre Occidental of southern Sonora and northern Sinaloa. These localities are separated from population B to the south by nearly 480 kilometers.

*Population B* (15 specimens)—from localities in the upper drainage of the Río Santiago and its tributaries in Nayarit and Zacatecas and from the general vicinity of Guadalajara and Lago de Chapala in Jalisco and adjacent Michoacán. These snakes probably are continuously distributed in suitable habitats northward through Sinaloa, as indicated by two specimens from western Durango, but are separated into two populations, A and B, because of the lack of adequate material from the intervening area.

*Population C* (14 specimens)—from localities in Tamaulipas, San Luis Protosí and Hidalgo in the eastern drainage systems of the Río Pánuco and Río Tamesí. There are six specimens known from within the 400 kilometer hiatus that separates population C from population B, the latter of which is restricted to western drainages.

*Population D* (20 specimens)—from localities in central Oaxaca. This sample is situated about 480 kilometers southeast of population C with only a few specimens known from the intervening area. The uplifted southern section of the Mexican Plateau effectively separates populations C and D.

*Population E* (51 specimens)—a large sample from the vicinity of Chilpancingo, Guerrero located in the central part of the Sierra Madre del Sur. These localities are isolated from sample D by the eastern extension of the Sierra Madre del Sur and the mountains in northwestern Oaxaca.

*Population F* (25 specimens)—from areas in northeastern Guerrero and adjacent México and Morelos and from southwestern Puebla. These localities are in areas drained by the northeastern tributaries and headwaters of the Río Balsas. Population F is separated from E by the arid Balsas Basin and from D by the mountainous areas of northwestern Oaxaca. Population F is separated from sample C south of the volcanic peaks and high southern portions of the Mexican Plateau.

*Population G* (19 specimens)—from parts of Colima, southern Jalisco and western Michoacán. These localities are situated in areas drained by the Río Armería and Río Coahuayana (Autlán and Contla, Jalisco and Colima) or by the major northwestern tributary of the Río Balsas, the Río Tepalcatepec (Michoacán). This sample is isolated to the northwest of E by the arid Balsas

Basin and to the south of B by the Transverse Volcanic Range and western portions of the Mexican Plateau.

Specimens removed from the geographic range or topographically isolated from these units were considered separately. In other words, we did not extend the geographical coverage of our units to accommodate individual specimens.

After the seven groups were established, the meristic, scale and pattern characteristics were compared within each unit and among the seven units.

#### GEOGRAPHICAL VARIATION

##### LEPIDOSIS

*Ventral and subcaudal scales.*—Ventral scales vary from 20-231 in males and from 210-243 in females. Subcaudal scales range from 61-85 in males and from 55-80 in females. Females average 2-11 more ventrals than males in the various populations. However, males on the average possess 8-11 more subcaudals than do females in the same population. The relatively shorter body and longer tail of males, as indicated by fewer ventrals and more subcaudals, apparently is the result of their more anteriorly placed cloacal opening. This condition is probably an accommodation for the relatively long hemipenes in the tail. The converse probably is true of females which have a longer, more bulky body to accommodate eggs (Klauber, 1956:167).

The number of ventral and subcaudal scales in snakes is indicative of the number of vertebral segments (Dowling, 1951:99). To test the assumption that there is little or no sexual dimorphism in the total number of vertebral elements in members of the same geographic population, we analyzed the number of ventral plus subcaudal scales for males and females in each of the seven samples using the Student's *t*-test. No significant differences (95 percent level) were found. Therefore, for purposes of analysis, we combined the ventral and subcaudal counts of males and females in each population.

The ventral-subcaudal scales range from 265-319. The higher numbers are characteristic of the northwestern population in Sonora and Sinaloa and the lower numbers are from the southern population in Oaxaca. Variation in numbers of ventral-subcaudal scales in the seven populations is illustrated (Fig. 2). The relative geographic positions of specimens from localities outside of the geographic limits of the prescribed populations are plotted by number in Figure 2.

There is a north to south reduction in the number of ventral-subcaudal scales within population A. The specimens from southern Sonora have 298-319,  $\bar{x} = 307$  (N=11). Specimens from the Río Fuerte in northern Sinaloa have 300-306,  $\bar{x} = 303$  (N=4). Specimens from north central Sinaloa have 293-308,  $\bar{x} = 303$  (N=10). Two specimens from Ventanas, Durango (300 and 302 scales), and a specimen from the vicinity of San Blas, Nayarit (294 scales) are the only known specimens from the 480 kilometer distance between

populations A and B (Fig. 2, Nos. 1-3). Their counts are intermediate and suggest that additional material from the intervening area would show that the north to south reduction in the number of ventral-subcaudal scales exhibited in population A continues into B. A specimen from La Cumbre, Jalisco (Fig. 2, No. 4) has 292 ventral-subcaudal scales.

Within population B, three high counts (299, 299, 303) are characteristic of specimens from northwestern localities of population B, at Barranquitas, Nayarit, and near Magdalena and Bolaños, Jalisco, respectively. Two specimens from the southeastern parts of population B near Emiliano Zapata, Michoacán have low counts (282, 287).

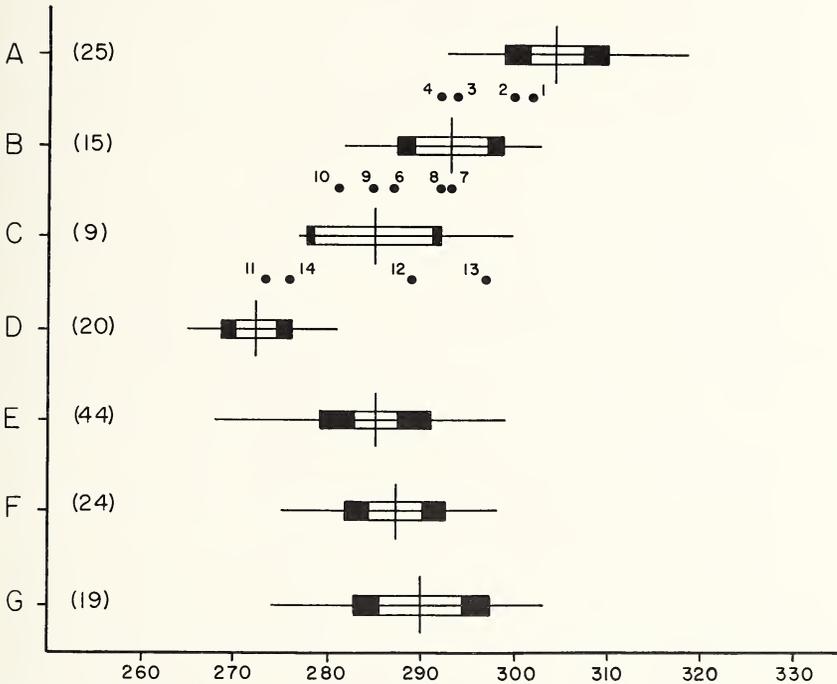


Figure 2. Statistical analysis of the number of ventral plus subcaudal scales in populations A through G of *Trimorphodon tau*. The number in parenthesis indicates sample size of each population. The horizontal lines indicate sample range and the vertical lines sample mean. The black rectangles represent one standard deviation on each side of the mean; the white rectangles represent 2.646 standard errors on each side of the mean (Eberhardt, 1968). Dots represent specimens from the following intermediate localities outside the geographic range of the samples: 1, 2, Ventanas, Durango; 3, N of San Blas, Nayarit; 4, La Cumbre de los Arrastrados, Jalisco; 5, 7 mi S Rincón de Romos, Aguascalientes; 6, 7, Tacicuaró, Michoacán; 8, 10, Guanajuato, Guanajuato; 9, Mt. Cubilete, Guanajuato; 11, Jalapa, Veracruz; 12, Tuxpango, Veracruz; 13, San Diego, Puebla; 14, Quiotepec, Oaxaca.

Specimens from population C in eastern México have fewer ventral-subcaudal scales than specimens from B and in this character indicate a continuation of a cline. The trend is continued within population C in that northern specimens have higher totals than do southern specimens. The highest counts (290, 300) are found in northern specimens from Tamaulipas, while the lowest counts (278, 277) are from snakes from more southern localities in San Luis Potosí and Hidalgo.

Two specimens from Tacícuaro, Michoacán on the interior drainage of the Río Grande de Morelia and three from the vicinity of Guanajuato, Guanajuato in the drainage of the Río Lerma are situated between populations B and C. Four of these five specimens exhibit ventral-subcaudal counts that lie on or between the means for populations B and C, and thus reflect their intermediate geographic position (Fig. 2, Nos. 6-10).

Specimens from population D have the lowest ventral-subcaudal counts and are from localities at the southern limit of the range. Most of these localities lie within the Pacific drainage of the Río Verde although some are from localities in the Atlantic drainage of the Río Papaloapan. These eastern specimens, when considered together with two other specimens from eastern localities north of population D (Fig. 2, Nos. 11, 14), suggest a possible connection between samples C and D along the eastern edge of the Mexican Plateau. The specimen from Jalapa, Veracruz (Fig. 2, No. 11) and the type of *Trimorphodon tau* from Quiotepec, Oaxaca (Fig. 2, No. 14) have ventral-subcaudal counts that are within the range of variation of population D but slightly higher than the average and thus approach populations C and F in this character.

Snakes from the largest sample, population E, average about 13 more ventral-subcaudal scales than specimens in population D and, in this respect, are nearly identical to those in population C (Fig. 2). Sample C is located nearly 400 kilometers north of E and separated from it by the Balsas Basin and the Mexican Plateau.

Population F averages slightly more ventral-subcaudal scales than E, but this difference is not significant at the 95 percent level. All known specimens in sample F are from localities in the upper Balsas Basin. The holotype of *Trimorphodon collaris* from western Veracruz (Fig. 2, No. 12) and the holotype of *T. forbesi* from southern Puebla (Fig. 2, No. 13) are both from localities in eastern drainage systems. These two specimens have ventral-subcaudal counts similar to those of population F. Thus, specimens from southeastern Puebla and adjacent Oaxaca and from Veracruz have two patterns in the number of ventral-subcaudal counts. The holotypes of *Trimorphodon collaris* and *T. forbesi* (Fig. 2, Nos. 12, 13) are more similar to specimens from population F, while the holotype of *T. tau* and the Jalapa specimen (Fig. 2, Nos. 11, 14) are more similar to snakes from population D.

Snakes from population G have more ventral-subcaudal scales than are found in either E or F. In this respect sample G approaches sample B which

lies immediately to the north. There is no significant difference (95 percent level) between samples B and G in the numbers of ventral-subcaudal scales.

This analysis shows that there is a clinal trend in total ventral-subcaudal scales within population A and among populations A, B, C and D, with higher counts in the north and lower counts in the south. Populations E, F, and G are more closely related to each other than they are to either of the two geographically adjacent populations, B in the north and D in the south. However, these three Balsas-Tepalcatepec Basin samples (E, F, G) have the same trend of higher totals in the north and lower totals in the south. In this instance, however, the trend is somewhat less marked.

*Anal scale.*—The anal scale is divided in all specimens except one. A male from Morelos (TCWC 7390) has an entire anal scale.

*Loreal scales.*—The number of loreal scales varies from two to five on each side of the head, with the majority of specimens having either two or three loreal scales (Table 1). Two loreals are more common in specimens from populations B, C and D, while three loreals are typical of populations A, E, F and G.

*Preocular scales.*—Although preocular scales may vary in number from one to four, the majority of snakes in all populations have three (Table 1). Specimens with two preocular scales are found in all populations except D. A single preocular is present in one specimen from population F.

*Postocular scales.*—Three postocular scales are characteristic of most specimens (Table 1). All snakes from sample F have three postoculars. Two postocular scales occasionally occur in the other six samples. Four scales are known only from specimens in populations A and E.

*Temporal scales.*—Most specimens have either two or three primary temporals and three or four secondary temporals. The majority of specimens in populations A, E, F and G have three primary and four secondary temporal scales, while specimens from population B, C, and D usually have two primary and three secondary temporals (Table 1). The differences may reflect the smaller sample sizes of these populations. A single primary temporal occurs only once, in population B; five primary temporals occur only once, in population E. In five instances snakes from sample D have two secondary temporals.

A comparison of the total number of lateral head scales (loreal, ocular and temporal) for the specimens from each sample shows that the higher numbers and means are characteristic of populations A (28-37,  $\bar{x} = 30.9$ ,  $N=23$ ), E (26-39,  $\bar{x} = 30.8$ ,  $N = 48$ ) and F (26-34,  $\bar{x} = 31.2$ ,  $N = 25$ ), while the lower totals and means are found in samples B (23-31,  $\bar{x} = 28.2$ ,  $N=14$ ), C (25-31,  $\bar{x} = 27.9$ ,  $N=12$ ) and D (24-32,  $\bar{x} = 28.2$ ,  $N=20$ ). Population G (24-32,  $\bar{x} = 29.0$ ,  $N=19$ ) is somewhat intermediate in total head scales but is slightly closer to the lower than to the higher values. There is considerable variation in the number of head scales within some populations and some variation among several populations. We do not consider the different head

scale characteristics to be of systematic importance in distinguishing any of the samples.

*Labial scales.*—Most snakes have either eight or nine supralabials, except in population C where all specimens have eight (Table 1). Eight is the more common number of supralabials in all populations except F, in which nine occurs more frequently. Only in sample D are specimens with seven supralabials found. The type specimen of *Trimorphodon tau* has six supralabials on each side, the lowest number known.

Although the fourth and fifth supralabials border the eye in the majority of specimens examined, some variation was noted. In populations A, D, E, and F occasional individuals have the fifth and sixth supralabial bordering the eye. One specimen from each of populations F and G has the third, fourth and fifth supralabials bordering the eye on one side while the fourth and fifth border the eye on the other. The fifth supralabial borders the eye on one side in two specimens from population F; the usual condition is found on the other side.

There is considerable variation in the number of infralabials from population to population and within populations (Table 1). Twelve is the most common number, although ten, eleven, and thirteen infralabials are found in nearly all samples. Population D has the lowest recorded number of infralabials (nine) and has a lower mean than do the other six samples.

The small gular scales usually separate the infralabial series from the chin shields at the level of the fifth or sixth infralabial scale. In population A this separation occurs in the majority of snakes at infralabial six. In population D this separation occurs in most specimens at infralabial five. In the other five populations the separation occurs about equally at the fifth or sixth infralabial. Occasionally the infralabial series may be separated from the chin shields at a level as far anterior as the fourth infralabial or as far posterior as the seventh.

*Dorsal scales.*—The dorsal scales of *Trimorphodon* are smooth, with paired apical pits. The scales are arranged in diagonal rows and vary considerably in number. The anterior count at one head length behind the head ranges from 21-27 rows; 75 percent of the individuals have 22, 23, or 24 rows. The number of scale rows at midbody varies from 17-25; 80 percent of the snakes have 22 or 23 rows. At one head length in front of the vent, there are between 14 and 18 rows, and at this level 83.33 percent of the sample have 15 or 16 rows.

The reduction in scale rows is similar to the reduction found in *Leptodeira* (Duellman, 1958:20). The reduction involves changes in the paravertebral row. The level (ventral scale) at which reduction in scale rows take place is highly variable with no geographic consistency.

#### PATTERN AND COLORATION

*Cross bands.*—The number of dorsal body bands (body and tail blotches) in individuals with complete tails ranges from 18-46, though evidence suggests

TABLE 1.

Range and Percent Distribution of Various Head Scales in  
the Seven Populations of *Trimorphodon*

		A	B	C	D	E	F	G
<i>No. of specimens</i>		23	15	14	20	51	25	19
	2	6.5%	66.6%	75.0%	60.0%	18.0%	12.0%	44.7%
	3	87.0	33.4	25.0	35.0	79.0	86.0	55.3
Loreals	4	6.5	—	—	5.0	2.0	2.0	—
	5	—	—	—	—	1.0	—	—
	1	—	—	—	—	—	2.0	—
	2	6.5	13.3	14.3	—	8.9	2.0	15.8
Preoculars	3	93.5	83.3	85.7	97.5	88.1	90.0	84.2
	4	—	3.4	—	2.5	3.0	6.0	—
Postoculars	2	19.2	3.5	10.7	7.5	1.9	—	10.5
	3	76.6	96.5	89.3	92.5	94.1	100.0	89.5
	4	4.2	—	—	—	4.0	—	—
	1	—	3.5	—	—	—	—	—
	2	19.6	55.2	39.3	60.0	23.5	24.0	31.6
Primary	3	78.3	41.3	57.2	37.5	71.6	74.0	68.4
Temporals	4	21.0	—	3.5	2.5	4.0	2.0	—
	5	—	—	—	—	0.9	—	—
	2	—	—	—	12.5	—	—	—
Secondary	3	26.1	44.8	63.0	50.0	25.7	12.0	47.4
Temporals	4	60.9	55.2	37.0	35.0	72.3	86.0	52.6
	5	13.0	—	—	2.5	2.0	2.0	—
	7	—	—	—	10.0	—	—	—
	8	60.9	69.0	100.0	72.5	63.9	39.5	57.9
Supralabials	9	37.0	31.0	—	15.0	29.9	58.1	39.5
	10	2.1	—	—	2.5	6.2	2.4	2.6
	9	—	—	—	2.5	—	—	—
	10	2.1	3.3	9.5	27.5	2.1	4.6	—
	11	28.4	30.0	28.6	50.0	14.9	23.3	26.5
Infralabials	12	47.8	43.4	47.6	20.0	45.8	44.2	44.1
	13	21.7	20.0	14.3	—	35.1	25.6	20.6
	14	—	3.3	—	—	2.1	2.3	8.8

that higher numbers do occur (see below). The higher values are found in samples A, B, C and D while the lower numbers are characteristic of the three Balsas-Tepalcatepec Basin populations, E, F and G. The numbers of body bands for the seven populations and for geographically intermediate specimens are shown in Figure 3.

There is a decrease of dorsal body bands within population A from north to south. Specimens from Sonora have 27-36,  $\bar{x} = 32$  ( $N=11$ ); specimens from northern Sinaloa have 29-33,  $\bar{x} = 30$  ( $N=14$ ); specimens from central Sinaloa have 25-31,  $\bar{x} = 28$  ( $N=10$ ). Snakes from population B on the average have more body bands than specimens from population A, and snakes of population C tend to have more bands than those from B. Specimens that are geographically intermediate between samples A and B have an intermediate number of bands. The same is true for two specimens from the area between samples B and C (Fig. 3, Nos. 8, 9).

In population C the Hidalgo specimens apparently have more bands than

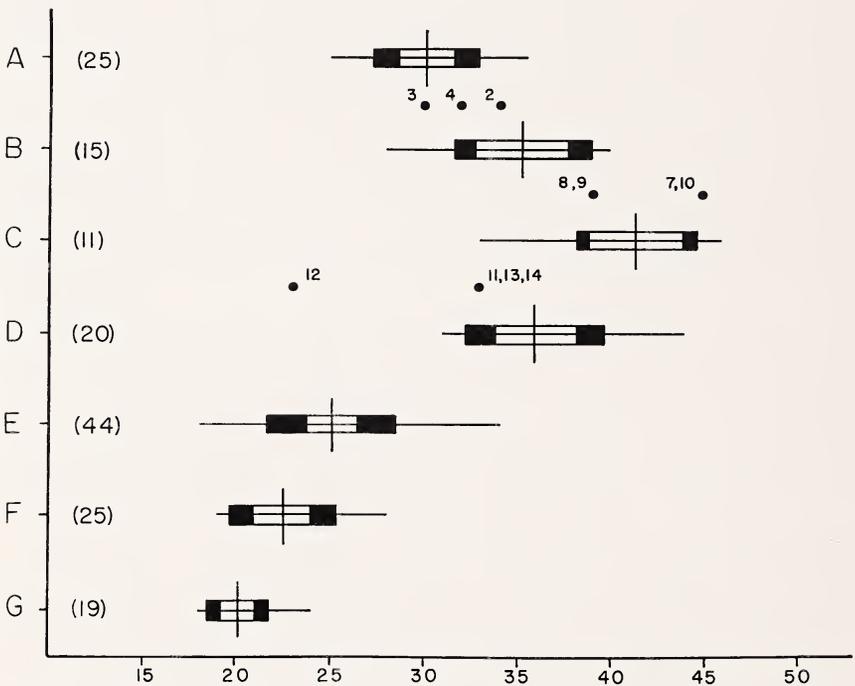


Figure 3. Statistical analysis of the number of cross bands in populations A through G of *Trimorphodon tau*. See legend to Figure 2 for explanation of diagrams and symbols.

do the Tamaulipas specimens. The only Hidalgo specimen with a complete tail has 43 body bands. Three other snakes from Hidalgo appear to have 40, 42 and 49 bands or more. These three specimens have damaged tails and, for this reason, are not included in Figure 3. The higher number of bands indicated for southern specimens in population C may account for the high numbers found in two of the intermediate specimens between B and C (Fig. 3, Nos. 7, 10). Both of these specimens (FMNH 105193, USNM 11370) are from localities slightly farther south than most of the localities in either B or C.

Specimens from population D, like population B, have fewer dorsal blotches than those from population C. Three of the four snakes from localities intermediate between C and D in eastern México are more similar to D than to C. The fourth snake (Fig. 3, No. 12), the holotype of *Trimorphodon collaris*, is much closer in band number to specimens from sample F.

Snakes from populations E and F average 11 to 13 fewer blotches than specimens from population D, the sample that is closest geographically. They are most similar to snakes from population A which is the farthest removed geographically. In band count, samples E and F are most similar to sample G. These populations (E, F, G) are significantly different from all of the other populations. Although populations B and G are in close geographic proximity, there is no overlap in the number of body bands. In fact these two samples are separated by a mean difference of 15 dorsal body bands.

The lengths of the bands may vary considerably on a single individual and among individuals of the same or different populations. In order to evaluate the differences in band size, the lengths on the middorsal scale row (as indicated by the number of included scales) of three band-interspace-band sequences were compared. The first sequence behind the collar (anterior), a mid-body sequence, and the last sequence before the vent (posterior) were used. These values are presented in Table 2.

In all populations the first dark cross band usually is the longest. The second cross band is longer on the average than either of the midbody bands, and they, in turn, always average longer than the posterior body bands. The mean band length of specimens from population A is greater than that of specimens from B, and mean band length in B is greater than in C (Table 2). In all instances the bands on snakes from population D average longer than bands in C but are shorter than bands on snakes in B.

Bands of specimens from populations E, F and G average longer than those of any of the other four samples. The only exception is the mean first band length of sample A which is longer than in sample E but never as long as in samples F or G. In general, specimens from population G have longer bands than specimens from F, and specimens from F have longer bands than specimens from E. The longest mean band lengths at all three body positions are characteristic of specimens from population G while the shortest band lengths are always found in population C.

TABLE 2.  
The Range and Mean of Band-Interspace-Band Lengths at Three Middorsal Positions on Specimens from the Seven Populations

	A	B	C	D	E	F	G
A	N	23	15	13	48	25	18
N	R	12.0-23.0	9.0-16.0	8.0-11.0	7.0-12.0	11.0-22.0	13.0-20.0
T	$\bar{x}$	15.9	11.2	9.6	10.1	15.1	16.6
E	N	23	15	13	20	50	18
R	R	2.0-5.0	2.0-4.5	3.0-4.0	2.5-6.0	2.0-5.0	2.0-5.5
I	$\bar{x}$	2.9	3.1	3.3	3.8	3.3	3.5
O	N	22	15	12	20	51	19
R	R	8.0-13.0	7.0-12.0	5.0-8.5	5.5-11.0	10.0-19.0	11.0-28.0
M	$\bar{x}$	11.0	8.8	7.1	7.5	12.9	14.2
I	N	23	15	13	20	51	19
D	R	6.0-16.5	5.0-9.0	4.5-6.0	4.0-6.0	7.5-16.0	8.0-16.0
B	$\bar{x}$	9.1	6.6	5.1	5.3	10.3	11.2
O	N	23	15	13	20	51	17
D	R	2.0-3.0	1.5-4.0	2.0-4.0	2.0-5.0	1.5-6.0	2.0-6.0
Y	$\bar{x}$	2.7	2.8	3.2	3.2	3.1	3.9
P	N	23	15	13	20	51	19
O	R	7.5-13.5	4.0-9.0	4.5-6.0	4.0-7.0	7.0-13.0	8.0-14.5
S	$\bar{x}$	9.5	6.1	5.1	5.2	11.5	12.5
T	N	24	15	12	20	49	19
E	R	5.0-12.0	4.0-11.0	3.0-5.0	3.0-6.0	6.5-12.5	6.0-10.0
R	$\bar{x}$	7.2	6.2	4.0	4.6	8.6	8.3
I	N	24	15	10	20	50	18
O	R	1.5-4.0	1.5-3.0	1.5-3.0	2.0-4.0	1.0-6.5	2.0-9.0
R	$\bar{x}$	2.2	2.2	2.1	2.1	3.1	4.3
I	N	24	15	11	20	50	19
O	R	5.5-11.0	4.0-8.0	3.5-6.0	3.0-6.0	5.5-14.0	6.0-12.5
R	$\bar{x}$	7.7	5.8	4.5	4.6	8.6	8.8

There is an average decrease in interspace length from anterior to posterior in all samples except F and G. In the former the midbody interspaces average shorter than the posterior interspaces while in the latter the midbody interspaces average slightly longer than either the anterior or posterior interspaces which are the same (Table 2). Specimens from populations A and B have the smallest mean interspace lengths. Specimens from population F have the longest interspace lengths.

There is no consistent number or location of bands which show signs of splitting or fusion (indicated by light centers) in any population. However, there is some consistency within certain populations in the extent of the light central area. For example, in Oaxaca the light areas within the darker bands are relatively large and diffuse. In Sinaloa the central light areas often form discrete spots.

*Collar length.*—The length of the light nuchal collar varies among individuals from the same population. In some specimens the first body blotch contacts the posterior margin of the head cap or the parietal scales on the midline or is separated from them by only half a dorsal scale. Others may have

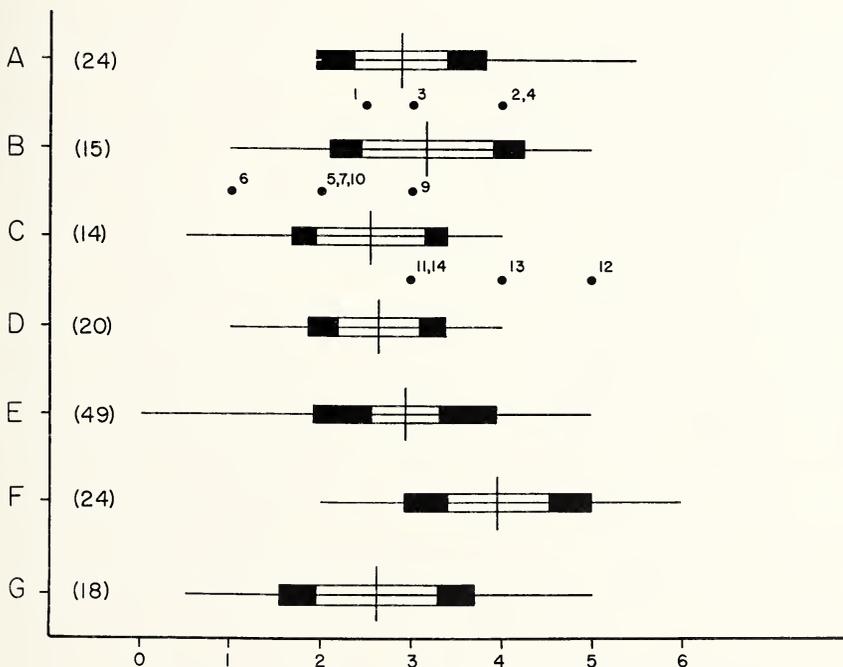


Figure 4. Statistical analysis of the collar lengths in populations A through G of *Trimorphodon tau*. See legend to Figure 2 for explanation of diagrams and symbols.

as many as six dorsal scales separating the first body blotch from the head cap or the parietal scales. However, the collars among the seven samples have nearly the same average lengths as indicated by the number of light scales on the midline (Fig. 4). Only population F has a noticeably higher number of dorsal scales in the nuchal collar. In addition, snakes from population F have the greatest interspace length (Table 2). Most of the specimens from intermediate localities have intermediate collar lengths which fall within the range of variation of the two samples concerned. Notable exceptions, however, are the collar lengths for the type specimens of *T. collaris* and *T. forbesi* which are plotted between populations C and D (Fig. 4, Nos. 12, 13). Both of these have collar lengths most similar to those characteristic of sample F. The type of *Trimorphodon forbesi* has four scales, very near the mean for F, while the type of *T. collaris* has five and is near the upper end of the range of sample F.

*Dorsal head cap.*—The pattern of dark and light colors on the head generally is consistent within a geographic area. Because of this geographic consistency, a detailed analysis of the head patterns is extremely useful in determining the relationships among the seven samples. Although individual head patterns may be very complex (Figs. 5, 6), they can be analyzed in terms of the following components: snout—light or dark rostral and internasal scales; presence or absence of a prefrontal bar—light bar extending across the prefrontal scales with dark anterior and posterior borders; presence or absence of an interocular (interorbital) bar—a light bar extending between the eyes, usually including the supraocular scales and the frontal scale; presence or absence of a parietal mark—a light mark of various design that may or may not connect to the interorbital bar or the light collar; presence or absence of an occipital spot—a medial, dark rounded spot located on the posterior portion of each parietal scale and the adjacent dorsal scales in the collar; posterior border—the shape of the posterior margin of the dark cap where it is bordered by the light nuchal collar.

Most snakes from population A have dark snouts (a few specimens from near Alamos, Sonora have light snouts) and a light prefrontal bar (blending into the snout of the light snouted forms) that is restricted to the anterior third of the prefrontal scales (Fig. 5A). Occasionally (three specimens) the prefrontal bar is connected with the interorbital bar by a straight or irregular medial area. The interocular bar is always present, usually has irregular borders, and generally is continuous between the orbits (interrupted in two specimens). A parietal mark is always present but extremely variable in shape and extent (Fig. 7). Frequently the parietal mark is shaped like an irregular-armed trident, a bell, a teardrop, or consists of two oblong parts arranged at right angles to form an inverted T. The parietal mark (connected medially to the interorbital bar in one specimen) begins at the posterior edge of the frontal scale and continue posteriorly to connect with the collar (56 percent). In the remaining specimens the parietal mark is separated from the light collar. An

occipital spot is present in 12 of the 14 specimens with the parietal mark-collar connection. The posterior border of the head cap may have a single median indentation (16 specimens), a lateral indentation on either side of a median posterior extension (five specimens), or it may be nearly straight (three specimens).

The two specimens from Ventanas, Durango have complete interorbital

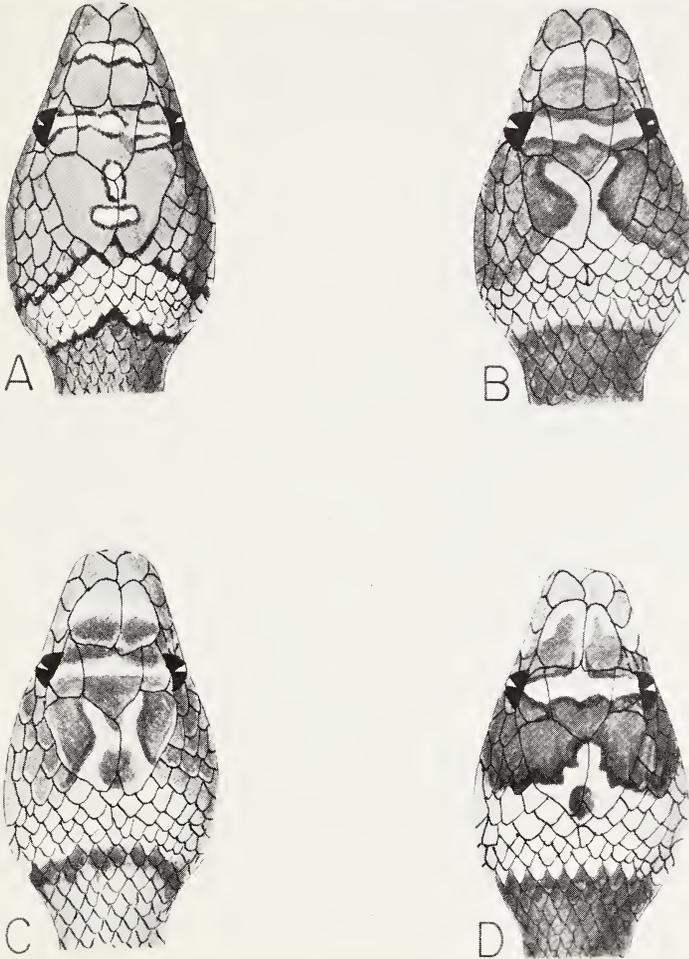


Figure 5. Representative dorsal head cap patterns for specimens of *Trimorphodon tau* from A) Terreros, Sinaloa in population A; B) between Hostotipaquillo and Magdalena, Jalisco in population B; C) S Ciudad Victoria, Tamaulipas in population C; D) intermediate locality at Jalapa, Veracruz.

bars and light snouts that include the area of the prefrontal bar (Fig. 7). The simple parietal marks are restricted to the suture lines between the parietal scales. The parietal mark is connected to the light collar in one specimen and separated in the other. An occipital spot is present in the snake with the parietal mark-collar connection.

The specimen from near San Blas, Nayarit has a dark snout, a prefrontal bar, an interorbital bar, a parietal mark connected to the collar, and an occipital spot. It is very similar to several Sinaloan specimens.

Most snakes from population B have dark snouts (light in the Zacatecas specimen and two Michoacán specimens) and distinct light prefrontal bars (66 percent of individuals). The interorbital bar is present (faint in KU 67735) and complete in all specimens except one (UMMZ 118950), where it is interrupted medially. The arms of the parietal mark, which is usually Y-shaped, edge the frontal scale posteriorly (Fig. 5B; Cope, 1900: fig. 315). The upright base extending posteriorly along the parietal suture may connect to the collar (six specimens) or remain separate from it (five specimens). In one specimen (FMNH 105194) the arms of the parietal mark connect with the interorbital bar on the supraocular scales forming a triangle (Taylor, 1939: pl. 35, fig. 2). The parietal mark is oblong in three snakes and heart-shaped in one. The occipital spot is less common than in population A, being found in only two specimens. The posterior border of the head cap is rounded in two specimens, forms a straight edge in one, is indented medially in five, and has a medial posterior projection in the remaining seven snakes.

A snake from La Cumbre, a locality southwest of population B, has a head pattern very similar to many specimens from B in that it has an interocular bar and a medial posterior projection of the head cap. The snout is somewhat lighter than the rest of the head cap and includes the prefrontal bar. The parietal mark is V-shaped and outlines the frontal scale posteriorly.

Two specimens from Tacúcuaro, Michoacán (southeast of population B) have dark snouts, interorbital bars, and irregular Y-shaped parietal marks that connect to the light collar. An occipital spot is present in one specimen but absent from the other (Fig. 7). Although these two snakes lack prefrontal bars, they are similar in head pattern to other snakes from population B.

Three specimens from Guanajuato (east of population B) have interocular bars and Y-shaped parietal marks characteristic of most specimens from B but resemble the Tacúcuaro specimens in lacking the prefrontal bars. The parietal mark connects to the collar in two specimens and is separate from it in the third. The snout, including the prefrontal bar, is light in one specimen and dark in two.

An Aguascalientes specimen from a locality north of population B has a light snout that includes the prefrontal. In this respect the Aguascalientes snake is similar to one of the Guanajuato specimens and to the Zacatecas specimen in population B. The interorbital bar is complete and the parietal mark, which

is roughly Y-shaped, does not connect to the light collar. The posterior border of the head cap is rounded.

Specimens from sample C have a very complex head pattern. Half of the individuals examined have a light snout that encompasses the prefrontal area. The other specimens have a dark snout with either a well-developed or very faint prefrontal bar. Many specimens, especially those with the lighter snout have a patch of dark color in the center of each prefrontal scale. These patches may be joined medially or separated by a lighter suture line between the prefrontal scales. About half of the specimens have a second light bar on the posterior edges of the prefrontals. The interocular bar is always present and usually expanded on the frontal scale. In one-third of the specimens the interorbital bar is connected anteriorly to the prefrontal bars and posteriorly to the parietal mark. In these specimens the dark head color actually is restricted to six spots, one in the center of each prefrontal scale, one at the anterior edge of each supraocular and adjacent frontal scale, and one on the posterior part of each supraocular and adjoining frontal and parietal scales.

In most of the specimens from Tamaulipas and San Luis Potosí, the arms of the parietal mark form a V and outline the posterior edges of the frontal scale. The posterior part of the parietal mark bifurcates and encloses a large occipital spot before joining the collar (Fig. 5C). In these specimens the posterior border of the head cap is indented medially.

The parietal marks of the four specimens from Hidalgo differ from the more northern representatives of sample C. One specimen (LACM 53023) has a Y-shaped mark outlining the frontal edges and connecting to the collar. It lacks an occipital spot and has a postero-medially indented head cap. In two other specimens (AMNH 93432 and ANSP 14770) the parietal mark is lyre-shaped and not connected to the light collar. The arms of the lyre extend to the frontal borders, connecting with the interorbital bar on one side in one specimen. They do not outline the postero-medial edges of the frontal scale. In both specimens the occipital spot is incorporated into the head cap, thereby extending the posterior border of the cap medially. In the fourth specimen (USNM 110401) the interocular bar extends posteriorly to the tip of the frontal scale. The parietal mark is fragmented into three parts. On the left side the mark borders the frontal anteriorly and extends posteriorly nearly to the light collar forming a shallow, laterally concave arc. On the right side only the anterior half of the arc is present. The posterior half consists of a light rounded spot on the posterior part of the right parietal scale, just above the light collar. The posterior border of the head collar is nearly straight medially but rounded laterally.

A specimen from Jalapa, Veracruz has a light snout extending over the anterior half of the prefrontals. Each nasal scale is very faintly pigmented. The interorbital bar is complete and connects medially to the light snout along the prefrontal suture. The parietal mark is irregular in shape, restricted to the

parietal suture (Fig. 5D) and connected to the light collar. The occipital spot is well defined.

The type specimen of *Trimorphodon collaris* lacks pigment on the internasal scales. Its interocular bar is broken about the middle of each supraocular, and it has a more rectangular-shaped parietal mark connected to the collar. In other respects it is very similar to the Jalapa specimen.

The type specimens of *Trimorphodon tau* and *T. forbesi* also are from localities in the Atlantic versant and generally are similar to the two specimens mentioned above. The type of *T. tau* has dark circular marks in the center of each internasal scale. The light snout is connected medially and laterally with the prefrontal bar which is also connected with the complete interocular bar along the suture between the prefrontals. The lighter color of the collar continues onto the temporal parts of the head connecting with the postero-lateral portions of the interocular bar. As a result, the dark parietal portion of the head cap is greatly restricted and completely surrounded by the lighter coloration. The parietal mark is connected to the collar. Posteriorly the head cap is nearly straight. The occipital spot is present but small. The type of *T. forbesi* also has a lighter snout that includes the prefrontal area. The interocular bar is complete and connects along the prefrontal suture to the lighter snout. The parietal mark is rounded and broadly joined to the light collar. The occipital spot is small. The posterior border of the head cap is rounded laterally and indented medially. In general these four specimens from eastern México (Veracruz, Puebla, Oaxaca) are very similar in overall head pattern.

The head patterns of specimens from population D generally are more uniform than are those from population C. Most of the specimens (75 percent) have a dark snout and lack a prefrontal bar. Two of the five individuals with a light snout have dark pigment in the central parts of the internasal scales and a suggestion of a prefrontal bar. In this respect they are similar to the type of *Trimorphodon tau*. In several specimens, including light-snouted and dark-snouted individuals, the edges of the internasal and prefrontal scales are lighter than the central portions (Fig. 6A). Ten specimens have a light bar along the suture between the prefrontals. Often this bar is connected to the interocular bar (50 percent) forming the inverted T-pattern characteristic of *Trimorphodon tau* (Cope, 1869: 152). The interocular bar is always present and frequently (50 percent) extends laterally to the orbits. In some specimens (eight of 20) the interocular bar forms a shallow arc, concave posteriorly. The parietal mark has a simple configuration, rarely touching the frontal scale, and is connected with the light collar in all but two specimens (Taylor, 1940: fig. 8). In one specimen (AMNH 10093) the mark is irregular in shape (two lateral arms on each side) and contacts the posterior part of the frontal scale. An occipital spot is present in only five specimens.

The head cap is indented medially in all but two specimens from sample D. In these two specimens the parietal mark and the collar do not connect, and

thus the head cap extends postero-medially. The white collar extends anteriorly along the sides of the head in these specimens, together with 16 of the 18 indented head cap forms, giving the head cap a rounded appearance. In two (Fig. 7) the postero-lateral edges of the cap are nearly straight.

We examined the head patterns of 48 snakes from population E. In only eight of these does the light snout include the prefrontal bar area. Although the

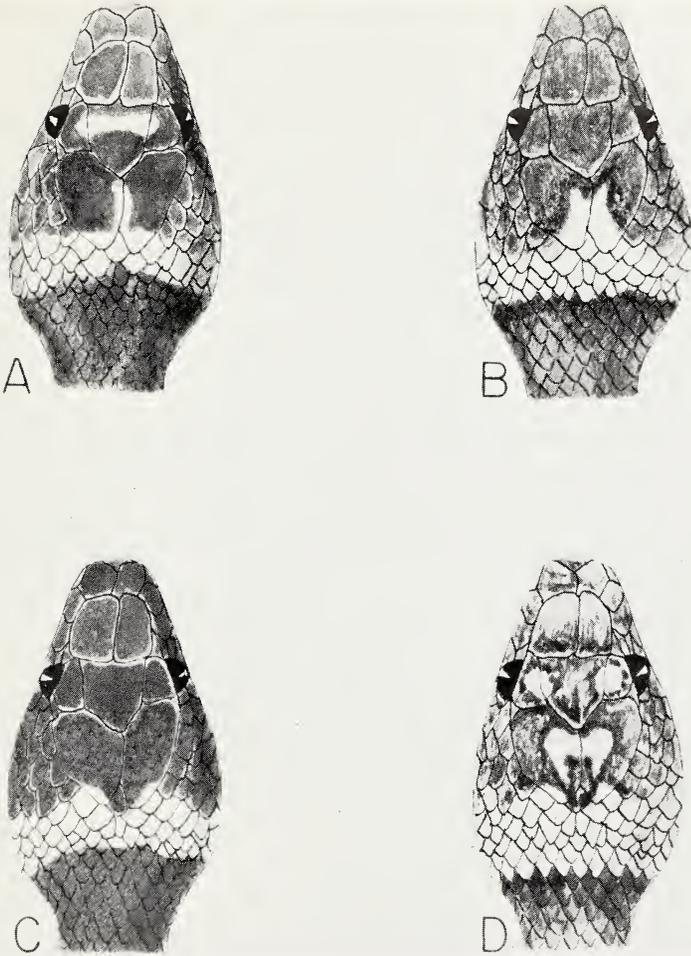


Figure 6. Representative dorsal head cap patterns for specimens of *Trimorphodon tau* from A) 3 mi NE Mitla, Oaxaca in population D; B) Chilpancingo, Guerrero in population E; C) Coalcomán, Michoacán in population G; D) 4 mi S Autlán, Jalisco in population G.

snout in these few specimens is somewhat lighter than the rest of the cap, it is still well pigmented and not the white or very light tan characteristic of certain light-snouted specimens from populations A and C. None have a defined prefrontal bar, although three individuals have a pair of light spots on the anterior prefrontal scales. Three other specimens have a medial light spot on the prefrontal suture. An interorbital bar is lacking in 23 specimens, reduced to a median frontal spot or to two lateral supraocular spots in 21 specimens, and complete in four specimens. None has a connection between the interorbital bar and parietal mark. In all specimens, except four, the parietal mark is connected to the light collar (Fig. 6B) or is absent. Of these four, two have a small circular spot on the parietal suture, one has a small central and two small lateral spots, and the fourth has two lateral spots that appear to be remnants of a V-shaped mark. Of the remaining 44 specimens, eight have no indication of a parietal mark; the posterior margins of their head caps are rounded laterally (Fig. 7). Most of the others have a median extension of the collar connecting to the parietal mark. Usually the parietal mark or anterior end of the collar extension is rounded, but occasionally it may be Y- or V-shaped or may narrow rapidly at its anterior apex near the frontal scale. Occasionally (six specimens) the collar has a double extension onto the parietal region, and the head cap extends posteriorly on the midline. The head cap is rounded laterally in nearly all of these specimens. An occipital spot is present in only nine.

In twelve of 24 specimens from sample F, the snout is lighter than the rest of the head cap and includes the prefrontal bar area. In this respect they are similar to the light-snouted individuals of population E. Only two of the dark snouted specimens have a prefrontal bar. When a complete interorbital bar is present (three specimens), it is faint. In twelve other snakes, the bar is fragmented or reduced to one, two, or three circular spots or short bars. There is not interorbital bar in nine specimens (Taylor, 1940: pl. 52). Four specimens lack parietal marks and have a head cap with a rounded posterior margin. Three specimens have shallow V-shaped parietal marks that outline the frontal scale and are not connected with the light collar. In these specimens the posterior edge of the head cap has a single medial indentation, two lateral indentations, or a postero-medial extension. In the remaining snakes (17) the parietal mark is connected to the collar, and thereby, the posterior edge of the head cap is indented medially. The extended collar-parietal mark may be broadly Y-shaped (Fig. 7), triangular, narrow and restricted to the parietal suture, or wishbone-shaped. There is a large distinct occipital spot in the collar extension in most (12 of 17) of these specimens.

The head patterns are remarkably consistent in population G. None, except the type of *T. fasciolata*, have a light snout or show any trace of a prefrontal bar. In the type specimen of *T. fasciolata* the snout and the edges of the prefrontal scales are somewhat lighter than the rest of the head cap. An interorbital bar is lacking in all specimens (Fig. 6C) except three. In two of these

(UMMZ 112516 and the type of *T. fasciolata*) the supraocular scales have light centers. The third specimen from Autlán, Jalisco (KU 27191) has two light circular spots in the interorbital area. Distinct parietal marks are lacking from all except the Autlán specimen (Fig. 6D) and a specimen from near Apatzingán (UMMZ 112515). In the latter there are two small spots on the posterior third of each parietal scale. The posterior margin of the head cap is indented in one specimen from Apatzingán (FMNH 37079) and the type of *T. fasciolata* and shallowly indented in a third (UMMZ 104696). Occipital spots, lacking in other specimens, are present in these three snakes. The posterior margin of the head cap is doubly indented in nine specimens (Fig. 6C), rounded in four, nearly straight in two, and slightly convex in one.

The geographic distribution of the different head patterns is illustrated in Figure 7.

*Coloration.*—These snakes have considerable variation in coloration from sample to sample and within some samples. Because adequate color descriptions and pictures of specimens from many areas are available in the literature (Taylor, 1939: 364-367; 1940: 474-479; Smith, 1941: 161-167; Peters, 1954: 33; Davis and Dixon, 1957: 24; Duellman, 1961: 111; Brown and Brown,

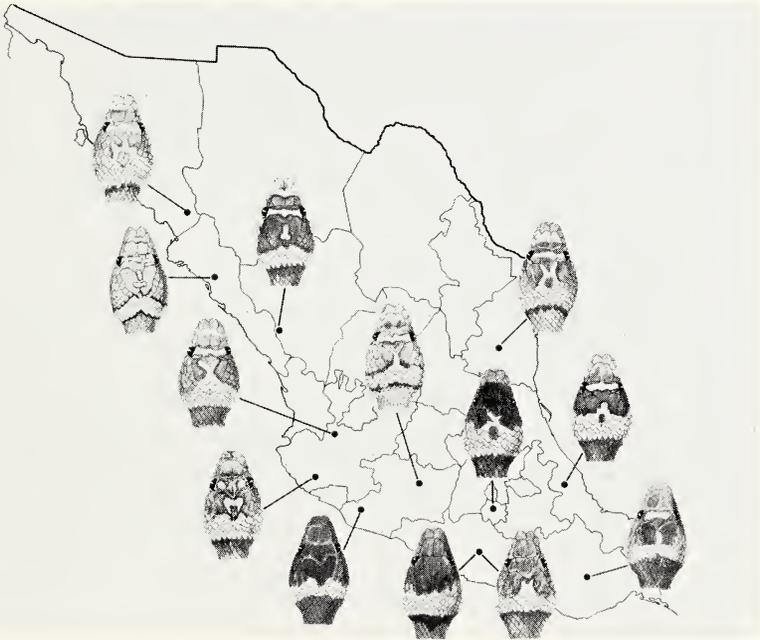


Figure 7. Geographic distribution of representative head cap patterns for specimens of *Trimorphodon tau* from localities within the seven samples and selected intermediate localities.

1967: 325), no detailed color description will be included here. Instead we will summarize this information and present it together with color notes on living specimens from Sinaloa and Puebla.

The ground color of adults ranges from various shades of brown to fawn, pale tan or gray, usually becoming darker posteriorly. Juveniles often have a more reddish or grayish ground color than do the adults. The cross bands of both age groups are darker than the ground color and often yellow-brown or gray-brown to black. In many specimens the center of each band is lighter. The edges of each band are usually bordered with dark brown or black. Juveniles apparently have darker bands than adults from the same area. Laterally, smaller dark blotches are present in the interspaces of some specimens. The head cap is brown, gray-brown or black and nearly the same color as the cross bands. The lips, chin and throat usually are tan or white. The venter may be tan or creamy white, and often with a reddish or salmon tinge posteriorly. In some snakes the venter is mottled by ventral extensions of the cross bands and interspace blotches; in others the venter may be spotted. Some have a nearly immaculate belly. In some juveniles the ventral surface of the tail may be nearly black.

The iris may be yellow-brown, gray-brown or grayish-tan.

#### DISCUSSION CHARACTER ANALYSIS

Much similarity exists among the seven samples. Some characters indicate independent, discordant patterns of variation. Even though most characters are not diagnostic, three are particularly useful in deducing the relationships among the seven samples: number of ventral plus subcaudal scales, number of dorsal body bands, and dorsal head cap pattern.

The number of ventral-subcaudal scales decreases from north to south in samples A through C. The trend continues southward into population D, where the lowest counts are recorded. Two specimens (Fig. 2, Nos. 11, 14) from intermediate areas between C and D are more similar to D than to C in this character, while two other specimens from intermediate areas (Fig. 2, Nos. 12, 13) are more similar to C and F than they are to D. This suggests a connection among the samples through the high river valleys of southeastern Puebla and Oaxaca. Population G has the highest counts and is the most northern of the three Balsas-Tepalcatepec Basin samples. In this character sample G approached sample B, its closest geographic neighbor. The ventral-subcaudal scale counts will not allow for absolute distinction between specimens from geographically adjacent samples.

An analysis of the number of dorsal cross bands (Fig. 3) gives a slightly different picture of the relationships among the seven samples. Among populations A, B, and C there is an increase in number of dorsal blotches from northwest to southeast. The geographically intermediate specimens generally con-

firm this trend. Sample D has fewer bands than does C and thus has a slightly different relationship to A, B, and C in this character than it did in terms of ventral-subcaudal scales. In this respect, however, the number of dorsal blotches of sample D approaches those characteristic of samples E and F. Of the four specimens from eastern México that are geographically intermediate among samples C, D and F, three (Fig. 3, Nos. 11, 13, 14) have counts most similar to the counts of D while the fourth (Fig. 3, No. 12) has a count most like those of sample F.

In dorsal cross bands E, F and G are closely related to each other and well differentiated from sample D. The most striking thing about the dorsal band counts is the difference between samples G and B which do not approach each other even though the two populations are closely adjacent (Fig. 3). This is a notable exception to their similarity in the number of ventral-subcaudal scales.

The same general relationship is present in the seven samples for both dorsal head patterns and dorsal cross bands. An interocular bar, usually complete, and a discrete parietal mark are always present in specimens from samples A, B, C, and D. The remnants of an interocular bar are present in 43 of 91 specimens from samples E, F and G. Only seven specimens from the Balsas-Tepalcatepec samples have a complete interocular bar. A discrete parietal mark, that is one not connected to the collar, is found only in nine of the 91 specimens in samples E, F and G. A prefrontal bar or light snout including the area of the prefrontal bar is found in most snakes from samples A, B and C. In sample D a prefrontal bar is usually lacking, as it is in most specimens from samples E and G. Approximately 50 percent of the specimens from sample F have light snouts that include the area of the prefrontal bar and thus are somewhat intermediate between samples A, B, C and D, E, G.

In summary, the Balsas-Tepalcatepec Basin samples (E, F and G) have a darker, more uniform head cap than is found in specimens from samples A, B, C and D. The Balsas-Tepalcatepec samples generally lack the prefrontal and interocular bars and the discrete parietal marks characteristic of the other samples. In general they lack the ornate head marking characteristic of the other four populations. Except for two snakes (KU 27191 and USNM 110400), there is no indication of any similarity between samples B and G in characters of head pattern. Some specimens from samples E and F show an apparent relationship to samples C and D by possessing remnants of an interocular bar and parietal mark. The head patterns of specimens from areas geographically intermediate between samples A, B, C and D have intermediate head patterns.

#### TYPE SPECIMENS

It seems appropriate to discuss briefly the six type specimens with reference to our seven populations to clarify our systematic treatment of the various samples.

The type specimen of *Trimorphodon tau* is a small snake in relatively poor condition. It was adequately described by Cope (1869) and redescribed by Taylor (1939). Although from a locality northwest of sample D, in all characteristics, it is typical of specimens from that sample.

The holotype of *Trimorphodon epsilon* is typical in all respects of specimens from sample B and was included in that unit. Zweifel (1959) noted that many of the specimens collected by Major probably did not come from Guadalajara, Jalisco as the locality information indicated but possibly were from Colima. However, Zweifel did point out that the type of *Trimorphodon epsilon* may actually have been from Guadalajara as additional specimens of this species are known from the same general area. Our analysis supports Zweifel's contention that Guadalajara probably is the type locality as originally stated.

The cotypes of *Trimorphodon latifascia* from Puebla have the characteristics typical of Puebla specimens from sample F. However, they were not included in sample F because the specific type locality is unknown (Peters, 1869).

For purposes of nomenclatural stability and in accord with Article 74, International Commission on Zoological Nomenclature (1964), we designate ZMB 6652a, the larger of the two syntypes (588 mm total length), as the lectotype. The smaller specimen (417 mm total length), ZMB 6652b, is designated the paralectotype in accord with recommendation 74E. Both specimens are males and have 211, 209 ventrals, 79, 74 subcaudals, and 21, 22 dorsal body bands. The snout is slightly lighter than the head cap in both specimens. In one the interocular bar consists of two short lateral spots and in the other of a median spot. The posterior border of the head cap is indented medially and rounded laterally in both. A faint occipital spot is present in the smaller paralectotype.

The holotype of *Trimorphodon collaris*, like the type of *T. tau*, is a juvenile. Cope's description (1875) is accurate for the characters listed. Some confusion exists concerning the type locality and number of specimens (see Historical Review and Smith, 1941: 166). This specimen, although from a locality somewhat intermediate among samples C, D and F, is typical of specimens from sample F in the important characteristics of ventral plus subcaudal scales, collar length, and number of dorsal blotches. The band-interspace-band lengths also are closest to those characteristic of sample F. The head pattern is similar to the patterns found on specimens from both D and F, although it is more similar to those from D. We consider the specimen to be most similar to snakes from sample F.

The type specimen of *Trimorphodon fasciolata* is a large male collected from a locality on the northeastern periphery of sample G. The specimen was adequately described by Smith (1941: 160-162). In all characteristics except certain details of head pattern (see previous description), it is typical of rep-

representatives of sample G, in which it was included. These differences in head pattern emphasize the marginal nature of the locality and may reflect its proximity to specimens from sample B and the intermediate specimens from Tacúcuaro, Michoacán.

Finally, the type of *Trimorphodon forbesi* is an exceptionally large male that is relatively well preserved but badly faded. In general our findings, on examination of the type, agree well with Smith's description (1941: 163-165) with two exceptions. We recorded five more ventrals and two more subcaudals than listed in the type description. Unfortunately the ventral scales are damaged in some areas and accurate counts are difficult to make. This may account for the discrepancies. However, we believe our count of 297 scales to be accurate.

The other point with which we disagree is Smith's (1941: 164-165) discussion of and reference to the "pattern reversal" characteristic of *Trimorphodon forbesi*. It is quite obvious that this specimen is faded; apparently the brown color of the head pattern faded more rapidly than did the dark borders along the interocular bar and nuchal collar, thus giving the appearance of a light head pattern with a darker interocular bar and nuchal collar. We cannot accept the contention that this is anything other than a badly faded but originally normally colored head pattern. The pattern itself is similar to the pattern of the type of *Trimorphodon tau* and other specimens in sample D.

The remaining characters of *forbesi* that Smith (1941: 165) used to distinguish it from other species include a divided anterior loreal, the fifth and sixth labials entering the eye, a faintly marked belly and white subcaudal surface, the number of cross bands, the narrow black borders of the cross bands, and the length of the cross bands on the mid-dorsal line. All of these characteristics are known from other samples (see previous description of geographic variation) and therefore are of little value in distinguishing this specimen. In ventral-subcaudal scales and collar length this specimen is more similar to sample F. In number of dorsal blotches and in head pattern, it is more similar to sample D. Certain characteristics of head scales and blotch length are intermediate between those for samples D and F.

Thus, the type of *Trimorphodon forbesi* has some characters typical of specimens from sample D, some typical of specimens from sample F, and some that are intermediate. Because of its intermediate locality and characteristics, we consider the specimen to represent a population of *Trimorphodon* that apparently bridges the gap between samples D and F.

In order to evaluate the usefulness of the three characters, ventral-subcaudal scales, body bands and head cap pattern, as indications of phylogenetic relationship, we attempted to correlate their geographic variation with various environmental parameters. Klauber (1941) showed that desert specimens consistently tend to have more ventral scales than coastal specimens of the same species. He also found that specimens of *Trimorphodon vandenburghi* from

the desert had more dorsal blotches than those along the coast. Klauber attributed these disparities to differences in humidity, and possibly temperature. Fox (1948) showed how different temperature regimes can influence scutellation in developing embryos of *Thamnophis*. Gravid females from the same natural population kept at cooler temperatures give birth to young with significantly fewer ventral and subcaudal scales than young from females maintained at warmer temperatures. Stebbins (1949) suggested that physical factors of humidity, temperature and light are important considerations determining the coloration and pattern of the salamander *Ensatina*.

In our analysis we could find no consistent correlation between environmental factors of temperature, rainfall or elevation and the geographic variation in ventral-subcaudal scales, dorsal cross bands or head pattern. In some samples there appeared to be a positive correlation between ventral-subcaudal scales and temperature; in other samples the same character indicated an inverse relationship to mean temperature. These same results generally were found in other comparisons. Unfortunately, the lack of precise microenvironmental information for many areas prevents detailed analysis of the possible correlation between other environmental factors and morphology.

Band lengths (Table 2) and band numbers (Fig. 3) have an inverse relationship. As the average band length increases, the number of bands decreases, and the snakes have a greater dark to light ratio. This is found in samples E, F, and G and is exemplified also by their darker head pattern. The Balsas-Tepalcatepec Basin is characterized by both high mean annual temperatures and high mean annual rainfall (Vivó Escoto, 1964). This suggests that a detailed analysis might show a correlation between mean annual temperature, rainfall, and/or light intensity and the number of dorsal bands and head pattern. Details of vegetation type and density would also have to be considered.

Variation in band numbers among the samples may be the result of splitting or fusion of some of the cross bands. For example, there is an average increase of five body bands from population A to B, but a decrease of about 15 scale lengths (difference between totals of six band lengths in Table 2). Although the light centers of many bands suggest splitting or fusion, there is no consistent location or number of bands which have light centers within any population. In addition, we were unable to derive the various band patterns from one another. It seems unlikely, therefore, that the light centers characteristic of many cross bands are indicative of fusion or division, a possible means of decreasing or increasing the band number. Differences in cross band numbers and lengths may represent adaptive responses to different selective pressures that increase or decrease the overall ratios between dark and light areas on the snakes.

#### SYSTEMATIC TREATMENT

Our data indicate overall similarities among the seven samples and the type specimens in nearly all characteristics examined. The analyses reveal

a geographic trend towards a southern reduction in ventral-subcaudal scales among samples A, B, C and D and among samples E, F and G, and also point to the similarities among samples A, B, C and D and samples E, F and G in number of body bands and head pattern. Specimens with characteristics that are intermediate between these two groups indicate that only a single species is involved. Therefore, we refer our seven samples, their intermediates, and the types of *Trimorphodon tau*, *upsilon*, *collaris*, *latifascia*, *fasciolata* and *forbesi* to one species. After careful consideration and consultation, we conclude that Günther's (1895) use of *Trimorphodon upsilon* did not constitute the action of the first revisor as defined in Article 24, International Code of Zoological Nomenclature. Therefore, the name *Trimorphodon tau* is applicable because of the action of Smith and Darling (1952) who gave priority to *tau* rather than *upsilon*, by their action as first revisor.

#### TRIMORPHODON TAU COPE

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Natur. Sci. Philadelphia, ser. 2, 8, p. 131; 1886, Proc. Amer. Phil. Soc., 23, p. 286; 1887, Bull. U.S. Natl. Mus., 32, p. 68; 1892, Proc. U.S. Natl. Mus., 14, p. 678. Günther, 1895, Biologia Centrali-Americana, Reptilia, pp. 174-75. Boulenger, 1896, Catalogue of the snakes in the British Museum, vol. 3, p. 55. Mocquard, 1899, Bull. Soc. Phil., ser. 9, 1, p. 157. Cope, 1900, Rep. U.S. Natl. Mus. for 1898, pp. 1104-1105, fig. 315. Gadow, 1905, Proc. Zool. Soc. London, 1905, pp. 196, 231, 233; 1910, Zool. Jahrbuch, 29, pp. 697, 701. Mocquard, 1908, in Duméril and Bocourt, Mission Scientifique au Mexique et dans l'Amérique Centrale, 3, pp. 908, 910-11. do Amaral, 1929, Mem. Inst. Butantan, 4, p. 202. Taylor, 1939, Univ. Kansas Sci. Bull., 25, pp. 365-66, plate 35, fig. 2. Smith, 1941, Proc. U.S. Natl. Mus., 91, pp. 162-163; 1943, Proc. U.S. Natl. Mus., 93, p. 494. Smith and Taylor, 1945, Bull. U.S. Natl. Mus., 187, p. 148. Zweifel and Norris, 1955, Amer. Midland Natur., 54, p. 245. Duellman, 1961, Univ. Kansas Publ. Mus. Nat. Hist., 15, p. 112.

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*Trimorphodon tau epsilon*, Smith and Darling, 1952, Herpetologica, 8, p. 85. Zweifel, 1959, Amer. Mus. Novitates, 1949, pp. 3-4, 6-8.

*Description.*—A species of *Trimorphodon* with 201-231 ventral and 61-85 subcaudal scales in males; 210-243 ventrals and 55-80 subcaudals in females; 265-319 total ventral-subcaudal scales; a divided anal scale; usually 3 (2-5) loreal scales, 3 (1-4) preocular, 3 (2-4) postocular, 3 (1-5) primary temporal, 4 (2-5) secondary temporal, 8 (7-10) supralabial with the fourth and fifth (third-sixth) bordering the eye, and 12 (9-14) infralabial scales usually separated from the chin shields at the sixth (fourth-seventh) infralabial; dorsal scales usually in 22, 23, or 24 (21-27) rows at one head length behind the head, 22 or 23 (17-25) rows at midbody, and 15 or 16 (14-18) rows at one head length in front of the anus.

The snakes are usually gray, tan or light brown in ground color and crossed by 18-46 body bands that usually reach the edges of the ventral and subcaudal scales. The cross bands are various shades of brown or black and often darkest along their margins. Most dark cross bands have lighter central areas that approach the ground color. These central areas may be large and diffuse or concentrated into discrete spots. They suggest the splitting of one band or fusion of two bands. The cross bands decrease in length on the midline from anterior to posterior. Often the first cross band is considerably larger than the second. The cross bands are widest dorsally and taper to a broad or narrow base laterally. Laterally, small, irregular interband spots may be present. Frequently the body bands continue onto the abdominal scales giving

the ventral surface an irregular blotched pattern. However, in some specimens the abdominal scales are irregularly spotted or nearly immaculate.

The head pattern is extremely variable (see discussion). It consists of a dark head cap extending from the snout to the posterior parts of the parietals where it usually is separated from the first cross band by a light nuchal collar. In some specimens the snout is light. There may be a prefrontal bar, an interocular bar, a parietal mark and an occipital spot or any combination of these components. In some specimens most or all of the head cap components may be lacking, and the head is uniformly dark brown.

The nuchal collar sometimes extends medially onto the parietal area to connect with the parietal mark. In this instance the anterior border of the collar is chevron-shaped. Often the nuchal collar is straight or slightly indented anteromedially. The posterior border of the collar is nearly always straight. The first body blotch occasionally contacts the head cap or may be separated from it one-half to six dorsal scales. The collar is usually three scales long on the midline.

*Subspecies.*—The numbers of cross bands, the cross band lengths, and the head pattern indicate that gene flow between samples B and G is limited. The geographic barrier of the Transverse Volcanic Range separating these two samples may be partly or wholly responsible for this apparent restriction of gene flow. Presumably these two populations have come into secondary contact after experiencing separate histories. In our opinion, these two samples do not represent a continuum that was split into two components by the uplift of the Transverse Volcanic Range. It seems more likely that population G evolved from ancestors that moved into the Tepalcatepec Basin from the south after the Transverse Volcanic Range reached its present height in Jalisco and Michoacán (see discussion below). The similarities between the Balsas-Tepalcatepec samples E, F and G and their differences from A, B, C and D support this view. The latter four samples are similar in several characteristics and probably are representative of a continuum, as indicated by specimens from intermediate localities. There appears to have been some genetic exchange between the two groups through samples F and D in some of the river valleys of southeastern Puebla, northeastern Oaxaca and eastern Veracruz.

The similarities and differences between A, B, C and D and between E, F and G have been thoroughly discussed. Consideration of these points, combined with the apparent geographic barriers between these two groups, at this time leads us to recognize them as subspecies. The specimens representative of samples A, B, C and D and their intermediates are referred to *Trimorphodon tau tau*. The specimens from samples E, F and G in the Balsas-Tepalcatepec Basin are referred to *Trimorphodon tau latifascia* (new combination).

*Distribution and ecology.*—*Trimorphodon tau* is widely distributed along the coastal slopes and foothills of the Sierra Madre Occidental and Sierra Madre Oriental (Fig. 1). Occasional specimens have been taken on the coastal

plains. The species is found in suitable habitats to the north of the Transverse Volcanic Range and the high southern portions of the Mexican Plateau. *Trimorphodon tau* has also been recorded from scattered localities to the east and south of the Mexican Plateau, from the Valley of Oaxaca south and east of the Sierra Madre del Sur. The species is widely distributed in the foothills of the Balsas and Tepalcatepec Basins. Although the species is reported from localities ranging from 100 to 2600 meters in elevation, most of the range of the species lies between 1000 and 2100 meters.

The lack of adequate material from localities between samples A and B, between samples D and E, and between samples E and G probably reflects the inaccessibility of these areas as well as inadequate sampling of suitable habitat. Only four specimens are known from the eastern versant between samples C and D. We suspect that local climatic factors (high annual precipitation and abundant cloud cover) probably restrict the distribution of *Trimorphodon* to drier, less accessible habitats in this area.

*Trimorphodon tau* is a nocturnal species that occupies semi-arid to seasonally dry habitats. Specimens have been collected in arid tropical scrub, thorn woodland, tropical deciduous forest, mesquite grassland and dry pine-oak woodland (vegetation classifications follow Leopold, 1950). The species is terrestrial and commonly found in rocky areas of irregular relief. Individuals have been collected from beneath rocks, in holes and under bark on fence posts and dead trees during the day and in a flooded rice field at night. Most specimens were found on roads at night. The species feeds primarily on lizards, although frogs and small mammals probably are eaten also. Unidentifiable species of *Sceloporus* and *Cnemidophorus* were found in specimens from Guerrero, Michoacán and Oaxaca.

*Eggs and young.*—Because very little is known concerning the eggs and young of oviparous snakes, the following data for *Trimorphodon tau* are appropriate.

On July 18, 1966 a large female *Trimorphodon tau* (MVZ 81354) was collected 26 miles NW of Huajapan de León on México Highway 190 in Puebla (Sample F) by J. L. LaPointe. Sometime between the date of capture and July 25, this snake deposited seven eggs. The eggs were incubated following the technique outlined by Zweifel (1961: 112-113). On September 25, one of the eggs was opened and found to be developing. On October 10, the eggs averaged 26.1 mm in length, 16.8 mm in width and 4.0 gm in weight. Five of the remaining six eggs hatched between October 29 and November 1, at least 96 days after laying. The hatchlings made from 2-7 ( $x = 5.4$ ) longitudinal slits in the egg shell to escape. The sixth egg did not hatch and was found, on November 4, to contain a well developed, but dead, female (MVZ 81361). Pertinent information for the mother and five hatchlings are presented in Table 3.

The hatchling snakes are typical of sample F in the characteristics studied.

TABLE 3.  
Data for Adult Female and Five Offspring of  
*Trimorphodon tau* from Puebla, México

Specimen No. (MVZ):	81354	81359	81360	81356	81357	81358
Sex	Ad. ♀	♀	♀	♂	♂	♂
Weight - gms.	—	2.73	2.95	2.39	2.86	2.86
Total length - mm.	752	199	207	199	213	219
Snout-vent length - mm.	633	168	176	165	174	179
% tail length % total length	15.8	15.6	14.3	17.1	18.3	18.3
Ventrals	217	218	216	195	205	203
Subcaudals	69	67	68	80	84	78
Ventrals & Subcaudals	217	218	216	195	205	203
Umbilical Scar *	—	186	182	170	174	177
Body Bands	28	24	?	22	22	24
Supralabials	8-9	8-8	9-9	8-8	9-8	8-8
Infralabials	13-13	13-12	13-13	11-11	13-12	12-12

\* First ventral scale with scar

Five hatchlings have 275-289 ( $\bar{x} = 282.8$ ) total ventral-subcaudal scales. These counts are very similar to counts from other Puebla specimens from the same general area (275-290,  $\bar{x} = 284.75$ ,  $N = 8$ ). The same similarities exist in comparing the total body band counts. Four hatchlings have 22-24 ( $\bar{x} = 23.0$ ) dorsal cross bands while other Puebla specimens have 19-26 ( $\bar{x} = 22.3$ ,  $N = 9$ ) cross bands. The hatchlings also agree with other Puebla specimens of *Trimorphodon* in their supralabial and infralabial counts (Table 2).

#### EVOLUTIONARY HISTORY

Some brief comments concerning speciation in the genus *Trimorphodon* seem appropriate. Because no fossil remains are known, our interpretation of the evolutionary history of the species is based primarily on an analysis of the distributions and relationships of living forms correlated with the geohistory and paleogeography of the area.

Savage (1966) considered snakes of the genus *Trimorphodon* to be representative of the Middle American Element. Duellman (1958, 1966) suggested that *Trimorphodon* diverged early from the evolutionary stock that gave rise to *Hypsiglena*, *Leptodeira*, *Eridiphas* and *Cryophis*. We concur, and suggest that the ancestor of *Trimorphodon* diverged early in the Cenozoic and probably occupied areas of relatively low relief in northern and central México. Axelrod (1958) has indicated that most of this region was dominated by a Neotropical Tertiary Geoflora. Based on indirect evidence several authors have suggested that a broad ecotone of Arcto-Tertiary Geoflora extended into the mountains of México at this time (Axelrod, 1960; Brame and Wake 1963; Savage, 1966).

As a result of the general cooling trend in the early Tertiary, the northern borders of the tropics began to move towards the equator. In areas of northwestern México and the southwestern United States, elements of a Madro-Tertiary Geoflora, that developed *in situ*, began to spread. The Miocene was a period of major mountain building and general uplift (Maldonado-Koerdell, 1964). The Mexican Plateau, the Sierra Madre Occidental, the Sierra Madre Oriental, and the Sierra Madre del Sur were uplifted to their present height beginning in the Miocene and continuing to the present. This period of orogeny initiated major volcanic action, especially during the Pliocene and Recent, that formed the Transverse Volcanic Range. By the end of Miocene, in response to the gradual Tertiary temperature depression and increasing aridity, much of the tropical vegetation, except the more xeric type, was eliminated from central and western México. In northern México the derivatives of the Madro-Tertiary Geoflora were segregating into their component parts in the late Cenozoic. The mixed coniferous and deciduous derivatives of the Arco-Tertiary Geoflora were found throughout most of the mountainous areas of México.

We suggest that the ancestral *Trimorphodon* stock gave rise to three distinct lineages, each of which was markedly affected by the continuing trends of cooling and aridity and by the late Tertiary period of mountain building and volcanic activity.

The first lineage probably occupied much of central México and gave rise to *Trimorphodon tau*. As the climatic changes continued, this species adapted to dry habitats throughout much of the present Mexican Plateau perhaps as far south as Oaxaca. Tamayo and West (1964) suggested that much of this area, originally drained by the Lerma River included the lake basins drained by the present Río Lerma as far southeast as the Valley of México. With the late Tertiary volcanic activity that gave rise to the Mesa Central (West, 1964) and the Transverse Volcanic Range and the resultant cooler temperatures, this ancestral species was eliminated from the central part of its range and restricted to a horseshoe pattern of distribution north, east and south of the Mesa Central. One segment of this population gave rise to the subspecies *latifascia* in the eastern Balsas Basin. Subsequently, when conditions were suitable, the Balsas population apparently expanded into the Tepalcatepec drainage system and approached the range of the northern segment of the original population. These two ends of the horseshoe are now separated by the western portions of the Transverse Volcanic Range. At the same time that the Balsas-Tepalcatepec populations were expanding, the population ancestral to the subspecies *tau* was expanding northward along the slopes and foothills of the Sierra Madre Occidental and Sierra Madre Oriental.

The second major lineage of *Trimorphodon* evolved in association with the developing Madro-Tertiary Geofloral derivatives and gave rise to the species found in the arid lowlands of the southwestern United States and north-

western México today. We suspect that *Trimorphodon vandenburghi*, *T. lambda* and *T. lyrophanes*, if indeed they are distinct species, were derived from this second major lineage. *Trimorphodon vilkinsonii*, today found in eastern New Mexico, western Texas and adjacent parts of México, likely was derived from the ancestral *lyrophanes* stock and isolated east of the Rocky Mountain-Sierra Madre Occidental mountain system, where it is found today in mountains and foothills on the margin of the Chihuahuan Desert.

The third lineage gave rise to the species *T. biscutatus* and probably evolved in a xeric tropical lowland environment in the Pacific coastal lowlands of southern México and northern Central America. Savage (1966) referred to this species in his discussion of the history of the Western Mesoamerican Complex. *Trimorphodon biscutatus* subsequently dispersed northward along the developing Pacific lowland route as far north as southern Jalisco.

Areas of sympatry or near sympatry between *Trimorphodon biscutatus* and *T. lambda* occur in the southwestern corner of Jalisco. *Trimorphodon tau* is sympatric with *Trimorphodon biscutatus* at Apatzingán, Michoacán and Huajintlán, Morelos and with *Trimorphodon lambda* at Terreros, Sinaloa and about 10 miles west of Alamos, Sonora. Although *T. tau* has been reported from Chihuahua, Chihuahua (Cope 1900) near the type locality of *Trimorphodon vilkinsonii*, this record needs to be verified.

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#### SPECIMENS EXAMINED

##### MÉXICO

Aquascalientes: 7 mi S Rincón de Romos (UIMNH 27566).

Colima: Colima (AMNH 12777); 4.3 mi SW Colima, 575' (UMMZ 114479).

Durango: Ventanas (BM 83.4.16.68 and 69).

Guanajuato: Guanajuato (SU 4412, USNM 11370), Mt. Cubilete (AMNH 93433).

Guerrero: 15 mi NE Acapulco (LACM 7114); Acahuizotla (TCWC 22142); 3 mi WSW Axixintla (UMMZ 126541); Chilpancingo (FMNH 38412-32; KU 24100-03; MCZ 33657-58, 33663-5; UIMNH 34991-93); near Chilpancingo (UMMZ 85769-74); vicinity of Chilpancingo (AMNH 72522-24); 4 mi W Chilpancingo, 5800' (TCWC 9575); 13 m S Chilpancingo, 3750' (KU 67733); 7 mi E Chilpancingo (UIMNH 19139); 40 mi N Chilpancingo (LACM 53026); 25 mi NNE Iguala, 3800' (TCWC 12608); Ojito de Agua, 2.5 mi S Almolonga, 5600' (TCWC 11602-03); Ojito de Agua, 3 mi S Almolonga, 5400' (TCWC 11601); Omilteme, Sierra de Burro Mtns. (MCZ 42677); Palo Blanco, 4800' (TCWC 9574); 15 mi SE Tonatico (UMMZ 126542); Taxco (MCZ 33901).

Hidalgo: 10 km N Jacala (USNM 110401); Zacualtipán (ANSP 14770); 5.6 mi N of road to Zimapán on Hwy 85 (LACM 53023); 5 mi S Zimapán (AMNH 93432).

Jalisco: 2 mi ENE Acatlán, 5300' (KU 67735); 4 mi S Autlán (KU 27191); 2 mi E Bolaños, 3500' (KU 91428); 1 mi NE Contla, 3800' (KU 80762-63); La Cumbre de los Arrastrados, 8500' [Talpa Mascota] (BM 92.10.31.63); Guadalajara (MCZ 46891; USNM 31358-type of *upsilon*); between Hostotipaquillo and Magdalena (AMNH 19582); 10.4 km NNW Ixtlahuacán del Río (KU 102986); Jamay (AMNH

19841); near Magdalena, 1300 m (FMNH 105194); 1 mi NW El Molino, 5100' (AMNH 96652).

México: Ixtapan de la Sal, 5250' (AMNH 71360).

Miahoacán: Apatzingán, 1000' (FMNH 39078-79); 7.6 mi E Apatzingán, 1600' (UMMZ 112514); 14 mi E Apatzingán, 1700' (UMMZ 112516); 17.6 mi E Apatzingán, 1600' (UMMZ 112515); 3.9 mi S Apatzingán (UIMNH 73730); Coacomán, 945 m (UMMZ 104696-97); 6 mi E Emiliano Zapata, 5350' (UMMZ 118950); 7 mi E Emiliano Zapata, 5400' (UMMZ 118949); 4.3 mi N Lombardía, 2850' (UMMZ 118951); 8.7 mi S Lombardía (UMMZ 124039); Nueva Italia, 1250' (UMMZ 118952); 43 mi S Nueva Italia on Playa Azul Road, 1000' (UAZ 27060); Tacicuaró, 2000 m (FMNH 105193; UIMNH 19138); 5.5 mi W Tangamandapio, 5800' (UMMZ 118948); 1.4 mi N Río Tepalcatepec (UIMNH 73729); Tzaráracua Falls, 6 km SE Uruapan (USNM 110400-type of *fasciolata*).

Morelos: Alpuyeca, 3500' (TCWC 4127); 4 mi S Alpuyeca, 3600' (UMMZ 114478); Campo Agrícola, Progreso (UIMNH 26073); camp near Cuernavaca (UIMNH 19135); Huajintlán (UIMNH 19137); km 128, near Puente de Ixtla (FMNH 105100); 12 mi S Puente de Ixtla (UIMNH 19134); Tepoztlán (UIMNH 19136); 6 mi W Yautepe (TCWC 7390).

Nayarit: Barranquitas (AMNH 75585); 5 mi SE Ixtlán del Río (TCWC 12609); N of San Blas (LACM 53025).

Oaxaca: Juquila Mixes [=Xuquila Mixes] (AMNH 100649); 3 mi NE Mitla, 5800' (AMNH 97985); ca. 2 mi W Mitla, La Fortaleza (AMNH 89629); 17 mi SE Nochixtlán, 6900' (TCWC 12640); Oaxaca (FMNH 105305, 105350); 21 mi SE Oaxaca, 5350' (UMMZ 112522); 59 mi NW Ciudad Oaxaca, (UMMZ 121824); Quiotepec (USNM 30338-type of *tau*); San Felipe del Agua, 6500' (AMNH 97988, 100932-33); 2 km W San Felipe del Agua, (UIMNH 60799); Cerro San Felipe (UIMNH 53121, 73654, 74462-64); San Lucas Camotlán (AMNH 89630); 3 mi N San Miguel del Valle, 6950' (AMNH 97986-87).

Puebla: no specific locality (ZMB 6652-syntypes of *latifascia*); 11.4 mi NW Acatlán (LACM 38206); 16 mi N Acatlán (LACM 9509); 6 mi SE Acatlán (KU 31680); 10.1 mi NW Amatlán (UF 11337); 10 mi NW Huajuapán de León on Hwy 190 (MVZ 81355); 26 mi NW Huajuapán de León on Hwy 190 (MVZ 81354); 3 km W Izúcar de Matamoros (KU 39625); 17 mi SE Izúcar de Matamoros (AMNH 89631); San Diego, ca. 5 mi S Tehuacán (USNM 110402-type of *forbesi*); 6.7 mi NNW Tehuizingo (UF 11335); 6.3 mi SE Tehuizingo (UF 11336).

San Luis Potosí: 10.5 mi W Río Verde, 4000' (UMMZ 126193); 2.5 mi S Pendencia (LSUMZ 298).

Sinaloa: 16 km NNE Choix, 1700' (KU 68754); 22.1 mi N Culiacán (LACM 53024); 4 mi NNE El Fuerte, 300' (FMNH 71531) 2-3 mi ESE Río Fuerte Dam [8 mi NNE El Fuerte, 300'] (FMNH 71532-33) 8.3 mi N Guacamil [=Guamúchil] (UF 12829); 1.6 mi S Guacamil [=Guamúchil] (UF 12830); Terreros (LACM 9510); near Terreros (LACM 7112); 2.5 mi NW Terreros (LACM 7108); 5 mi NW Terreros (LACM 7109); 7 mi NW Terreros (LACM 7111); 10 mi NW Terreros (LACM 7110); 10.2 mi SE Terreros (LACM 7113).

Sonora: La Aduana, 5 mi W Alamos (LACM 53028); Alamos (AMNH 75119); W

side Alamos (KU 24119); 3.5 mi W Alamos (LACM 9157); 9.7 mi W Alamos, 1300' (LACM 53029); 8 mi SSE Alamos on Río Cuchujaqui, 900' (LACM 53030); Guirocoba (MVZ 50833-34); ca. 15 mi SE Navojoa (MVZ 76372); 18 mi SE Navojoa (MVZ 76373); 20 mi E Navojoa (LACM 53027).

Tamaulipas: 10 km N Antiguo Morelos (MU 196); S Ciudad Victoria, on Hwy 85 between C. Victoria and Llera (UMMZ 111255); 13 mi S Ciudad Victoria (UIMNH 19284); 14 mi S Ciudad Victoria (UIMNH 27164); 23 mi S Ciudad Victoria (AMNH 72399); 24 mi S Ciudad Victoria (AMNH 72400); Gruta de Quintero, near Quintero (AMNH 58224); La Joya de Salas, 1550 m (UMMZ 110882).

Vera Cruz: Jalapa (BM 81.10.31.65); Tuxpango, near Orizaba (USNM 26499-type of *collaris*).

Zacatecas: Hacienda San Juan Capistrano (USNM 46334).

Locality Unknown: "Mexico" (FMNH 42066; USNM 9911-12, 25361, 26138-9 [see Taylor, 1939: 366 for comments]).

"Southern Mexico" (BM 95.1.4.7 A and B)

"Districto Federal" (AMNH 19718 [see Zweifel, 1959: 7 for comments]).

#### ADDITIONAL SPECIMENS (*examined but data not included*)

Colima: 4.3 mi SSW Colima, 1300' (UF 24783).

Hidalgo: 10.4 mi NNW Ixmiquilpan, 7500' (UF 27378).

Jalisco: 2 mi NE El Molino (UAZ 27023).

Sonora: 6 mi W Alamos (ASU 6651, 6684); 9 mi W Alamos (ASU 6377); 11 mi W Alamos (ASU 6663, 6712); 14 mi W Alamos (ASU 6648).

#### LITERATURE RECORDS (*specimens not examined*)

Chihuahua: Batopilas (Cope, 1887: 68; Klauber, 1928: plate 22); city of Chihuahua (Cope, 1900: 1105).

Jalisco: "Jalisco" (Mocquard, 1899: 157); Guadalajara [USNM 12419] (Taylor, 1939: 366; Smith, 1941: 163).

Michoacán: San Salvador [BM 1914.1.28.136] (Peters, 1954: 32-34).

Morelos: between Cuernavaca and Tepoztlán; near Huajintlán (Taylor, 1941: 479).

Nayarit: Sierra del Nayarit (Mocquard, 1899: 157).

Tamaulipas: 14 mi SW Jiménez (Brown and Brown, 1967: 325).

#### RESUMEN

La variación geográfica en lepidosis y tipo de coloración han sido estudiadas en las siguientes especies nominales *Trimorphodon collaris*, *fasciolata*, *forbesi*, *latifascia*, *tau* y *upsilon*. Los ejemplares fueron agrupados en siete diferentes muestras geográficas que fueron luego comparadas entre sí. La mayoría de las características tienen una amplia distribución y se confunden mas con otras; otras características varían independientemente. Las escamas ventrales y subcaudales disminuyen en número de norte a sur. El número de bandas dorsales en el cuerpo es menor en culebras del Valle de Balsas-

Tepalcatepec, las cuales tienen también coloración uniforme en la cabeza. Ejemplares de otras regiones tienen una compleja coloración cefálica que consiste en bandas prefrontales, bandas interoculares y marcas parietales discretas en varias combinaciones. Estudios de los bandos en el cuerpo y coloración cefálica indican un intercambio genético limitado entre los ejemplares del Valle de Balsas-Tepalcatepec y aquellos de otras regiones, posiblemente como resultado de contacto secundario en el sur de Jalisco y la región adyacente de Michoacán. La Cadena Volcánica Transversa y la Sierra Madre del Sur aparentemente restringen el intercambio genético.

Estas especies nominales se asignan al sinónimo *Trimorphodon tau*. El nombre *Trimorphodon tau tau* se conserva para las poblaciones de las colinas y la meseta y *T. tau latifascia* (nueva combinación) se asigna a la población del Valle de Balsas-Tepalcatepec. *Trimorphodon tau* es redescribo y se delimita su distribución. La variación en características de un grupo procedente de Puebla es semejante a la variación típica que se encuentra en la muestra total de Puebla.

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STUDIES ON NORTH AMERICAN BEES OF THE GENUS  
*HYLAEUS*. 5. THE SUBGENERA *HYLAEUS*, S. STR. AND  
*PARAPROSOPIS* (HYMENOPTERA: COLLETIDAE)

By ROY R. SNELLING



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STUDIES ON NORTH AMERICAN BEES OF THE GENUS  
*HYLAEUS*. 5. THE SUBGENERA *HYLAEUS*, S. STR. AND  
*PARAPROSOPIS* (HYMENOPTERA: COLLETIDAE)

By ROY R. SNELLING<sup>1</sup>

ABSTRACT: The Nearctic representatives of the two subgenera *Hylaeus*, s. str. and *Paraprosopis* are considered in this paper. Within *Hylaeus*, s. str., eleven nominate species are recognized, one of these with a morphologically differentiated subspecies. One species (*H. granulatus*) is removed from synonymy, one new species (*H. sejunctus*) is described from the southwestern United States, and one name (*H. gaigei*) is transferred to the subgenus *Prosopis*. The distribution and morphological variation of several species are treated in detail, and the hypothesis is advanced that one species (*H. stevensi*) may be adventive from the Palearctic fauna. A key is given for all Nearctic species and facial views of the heads of both sexes of most species, and the male apical ventrites are illustrated.

Fourteen Nearctic species of *Paraprosopis* are recognized and included in the key to the species. Two new species (*H. lunicraterius*, *H. timberlakei*) are described from Idaho and California, respectively. The species *H. hydrangeae* is transferred from the subgenus *Metziella* to *Paraprosopis* as a synonym of *H. georgicus*. The distribution of most species is discussed and facial characteristics and male apical ventrites of all species are figured.

The present paper is a continuation of those comprising the series in Literature Cited (Snelling, 1966 a, b, c; 1968), and includes all the species assigned to the nominate subgenus and to *Paraprosopis*. One additional paper, treating the subgenus *Prosopis* in greater detail than my earlier paper (1966a) is in preparation. Hopefully, the series will conclude with a treatment of the species of Mexico and Central America.

*HYLAEUS* S. STR.

The nominate subgenus is, in the Nearctic Region, one of the larger groups in numbers of species. Except for the ubiquitous *H. cressoni* (Cockrell), however its component species are less abundant than those of *Prosopis* and *Paraprosopis*. As is the case of *Prosopis*, *Hylaeus* s. str., is Holarctic and most of the species are Palaearctic. Our fauna is closely allied to that of the Old World, and one species, *H. ellipticus* (Kirby) shows definite affinities with a small complex of Old World species. Its nearest relative seems to be

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*H. cardioscapus* Cockerell, of Siberia. The females, especially, are difficult to separate.

Our species are definitely of boreal origin and seem to have only comparatively recently invaded the more arid regions of the Southwest. Thus, of the eleven species here recognized, only one is a true xerophile. One other species has evolved a xeric subspecies. Of the remainder all save one are essentially northern and/or montane in distribution. The one exception seems to be restricted to the relatively cool sand dune areas along the California coast.

That the invasion of the New World is a phenomenon of long standing is attested by the extensive southern distribution of the group and by the development of several rather distinctive groups of species. The most primitive of our species seems to be *H. ellipticus* which extends from as far north as the Firth River in the Northwest Territories south to California, Arizona and New Mexico. From Alaska on the west *H. ellipticus* ranges eastward across Canada to the Atlantic Coast in Nova Scotia. From there it ranges south as far as North Carolina and Tennessee at the high elevations in the Appalachians.

Another essentially boreal species is *H. verticalis* (Cresson). The northern limit of this species is unknown to me although I have a few specimens from scattered localities in southern Alaska. It occurs as far south as California, Arizona and New Mexico in the western states, and North Carolina and Tennessee in the eastern. At its southern extremities *H. verticalis* occurs only at high elevations.

Two species comprise the *H. conspicuus* group: *H. conspicuus* (Metz) and *H. maritimus* Bridwell. Both are highly modified from the usual pattern of the *H. cressoni* group, but seem, nonetheless, to be related to that assemblage through *H. rudbeckiae* (Cockerell and Casad). *Hylaeus conspicuus* is the more common and widely distributed, extending along the Pacific Coast states from British Columbia south to southern California. Eastward the range includes northern Nevada and Utah, Idaho, Wyoming and Montana. Although often locally abundant *H. conspicuus* is of sporadic occurrence and is seldom represented in collections by large series. Far more restricted in distribution, *H. maritimus* is known only from coastal sand dunes of California from Sonoma County south to Santa Barbara County.

The one completely isolated species in the Nearctic fauna is *H. stevensi*. This species seems to be unrelated to any species in the Nearctic fauna. This species is most abundant in the north-central and northwestern states, but does not extend very far into Canada. In many samples which I have seen from these areas it is obviously the dominant species of *Hylaeus*. Beyond this region its occurrence is spotty but it may be locally very abundant. For example, it is quite common along the San Joaquin River, ten miles west of Turlock, Stanislaus County, California, where it frequents *Melilotus* spp. At Turlock, where I collected intensively for about ten years, it appears to be very rare.

The remaining group is apparently entirely Nearctic in distribution. This

is the *H. cressoni* group which includes, in addition to *H. cressoni* itself, *H. fedorica* (Cockerell), *H. labiatifrons* (Cockerell), *H. rudbeckiae* (Cockerell and Casad), *H. saniculae* (Robertson) and *H. sejunctus*, n. sp.

The most common, and most widely distributed, member of this group is *H. cressoni* which extends transcontinentally from southern Canada to northern Mexico. Its elevational amplitude exceeds that of all other species in the subgenus, extending from sea level in California to altitudes in excess of 9500 feet in the same state and at the same latitude. Perhaps in response to this extensive distribution, *H. cressoni* has produced a welter of varietal forms, a number of which have been formally named. I recognize only the form which inhabits the southwestern deserts as a valid subspecies. Several additional species are very closely related to *H. cressoni* and their females are extremely difficult to separate from those of *H. cressoni*. Of these species, only *H. rudbeckiae* is at all common and widely distributed, and its range is nearly as extensive as that of *H. cressoni*, the species being absent only from very arid regions. The only other member of the group other than *H. cressoni mesillae* to occur in desert areas is the new species *H. sejunctus*; this species, obviously derived from *H. cressoni*, occurs sporadically in desert regions in southern California and Nevada, western Arizona and extreme northwestern Mexico. Three species, *H. fedorica*, *H. labiatifrons* and *H. saniculae* are found in the midwestern and eastern states. All are rare and very poorly known.

It is not very difficult to visualize the evolution of the *H. cressoni* group from a more primitive bee such as *H. ellipticus*. Such requires only a reduction in size and in punctation, together with some modification of the male secondary characters (scape configuration, extent and orientation of facial maculae). By a similar reasoning, the *H. conspicuus* group can be derived from the same source, through an intermediary form such as *H. rudbeckiae*. The larger size, larger and more clearly defined sculpturation and Holarctic distribution of the *H. ellipticus* group favor the conjecture that this is the more primitive of the two groups. The *H. verticalis* group appears to be still less specialized, and our one representative is structurally a more variable species.

From the above sketchy commentary on our species of *Hylaeus*, s. str., it should be obvious that the species of this subgenus will prove difficult to identify. This particularly is true of those which I have assigned to the *H. cressoni* group. In the key which follows one should not experience any difficulty with the females until those couplets dealing with the *H. cressoni* group are reached (Nos. 7-12). I have been forced to rely on characters which are, at best, exceedingly difficult to work with, and the results are far from satisfactory. During the preparation of this portion of the key, an AO-Spencer binocular microscope, with 18x ocular eyepieces and 6x objectives, was used. A five unit measuring reticle, divided into twenty subunits was used, this calibrated against a stage micrometer for conversion into millimeters. Facial measurements were made with the head in full-face view, i.e., the head so

positioned as to produce maximum distance between the clypeal apex and the posterior head margin. Head length is a useful character although even slight overall size increase usually results in a disproportionate increase in the development of the vertex; this does not become apparent until one has examined many specimens. Far less variable, and hence more useful for some purposes, is the maximum measurable distance between the clypeal apex and the anterior margin of the anterior ocellus, along the mid-line of the face. This I have called the *facial length*. With the head positioned as indicated above, a measurement of the maximum width, across the compound eyes, is made to yield the *head width*. This measurement is subject to some allometric variation and hence is less useful than desired, but its alternative, *facial width* (maximum measurable distance *between* the eyes at the level of the antennal sockets) is less easily made with precision and is only slightly less variable.

Characters of punctuation have also been used to separate females within the *H. cressoni* group. These are subtle and difficult to express, and until one has become somewhat familiar with the various species, they are very difficult to appreciate. Unfortunately, there is a considerable amount of variation, especially in *H. cressoni*, and many (about 15% of those I have studied) females cannot be keyed satisfactorily. The alternative was to bring all females of this group to a single couplet without any attempt to separate them. Others may wish to adopt this alternative and stop keying at couplet 7. Tentative determinations may then be made on the basis of associated males, although this is hazardous since there are few areas where but a single species is found, although in any area one species will be dominant, usually *H. cressoni*.

The portion of the key separating the males should present few difficulties. Two forms (*H. cressoni mesillae* and *H. sejunctus*) are separated by differences in the shape of the ninth ventrite since no reliable external features have been discovered. All specimens from the southern California deserts, southwestern Nevada, the western third of Arizona and adjacent portions of northwestern Mexico must be separated in this manner. Specimens from the remaining areas of the southwestern deserts will all be *H. cressoni mesillae* or intergrades to the typical form (these are particularly common in Utah and Texas). Males of the other species may also be identified simply by comparison with the figures of the faces; these are quite distinctive for each species.

#### KEY TO *HYLAEUS*, S. STR.

- |   |    |
|---|----|
| 1. Females .....  | 2  |
| Males .....   | 13 |
| 2. Anterior coxae not distinctly angulate laterally; facial foveae ending no more than one-fourth of distance between eyes and lateral ocelli; pronotal collar distinctly shorter medially than laterally; pronotal collar usually maculate ..... | 3  |
| Anterior coxae distinctly angulate laterally; facial foveae ending about  |    |

- one-third of distance between eyes and lateral ocelli; pronotal collar usually as long medially as laterally; pronotal collar immaculate.....  
 .....*verticalis* (Cresson)
3. Oblique propodeal carina evanescent or absent; lateral carina evanescent or absent above; mesopleura very densely tessellate, punctures obscure; if mesopleura densely tessellate above only, *then* genae broader than eyes ..... 4
- Oblique and lateral propodeal carinae usually well-defined; mesopleurae frequently punctate and shiny above, if densely tessellate and impunctate, than genae narrower than eyes..... 5
4. Entire mesopleuron densely tessellate, dull, punctures very obscure; genae, seen from side, distinctly narrower than eyes; median length of basal zone of propodeum much shorter than median length of post-scutellum; clypeus usually extensively maculate.....*conspicuus* (Metz)
- Mesopleuron moderately shiny and punctate on lower half; genae, seen from side, distinctly broader than eyes; median length of basal zone of propodeum subequal to median length of postscutellum; clypeus immaculate.....*maritimus* (Bridwell)
5. Mesopleural punctures extremely coarse, several times diameter of those of vertex, distinctly larger than those of mesocutum, integument dull, densely tessellate; postscutellum with deep, distinct coarse punctures, frequently appearing rugose.....*stevensi* (Crawford)
- Mesopleural punctures little, if any coarser than those of vertex or mesocutum; punctures of postscutellum usually obscure, never coarse.... 6
6. Lateral and oblique carinae very strongly developed; transverse carina present, high; entire basal area coarsely rugose; mesopleura deeply, uniformly punctate; postscutellum dull, densely tessellate and roughened; larger species, length to apex of second tergite 5.5-6.7 mm; clypeus frequently with transverse, apical macula.....*ellipticus* (Kirby)
- Lateral and oblique carinae variable, but usually rather faint; transverse carina usually absent; basal area rarely entirely rugose; if rugose, *then* mesopleura tessellate on upper half, punctures sparse, obscure; postscutellum usually slightly shiny, often with evident punctures; smaller, slender species, length to apex of second tergite 2.7-4.2 mm..... 7
7. Head width 1.40 mm or more, usually about 1.5 mm; facial length 1.2 mm or more.....*rudbeckiae* (Cockerell and Casad)
- Head width not exceeding 1.31 mm; facial length not exceeding 1.2 mm 8
8. Punctures of mesocutum fine, separated by 1.5 or more times a puncture diameter; interspaces very densely tessellated so that integument is dull..... 9
- Punctures of mesocutum coarser, separated by about a puncture diameter or less; interspaces usually somewhat shiny; if densely tessellate, punctures quite close.....10

9. Punctures of mesocutellum medially distinctly closer than those on either side, interspaces somewhat polished.....*sejunctus* Snelling  
Punctures of mesocutellum medially little, if any, closer than those on either side, interspaces slightly shining, distinctly tessellate.....  
.....*cressoni mesillae* (Cockerell)
10. Clypeus and lower half of supraclypeal area tessellate, but slightly shining with extremely fine longitudinal striolae.....11  
Clypeus and lower half of supraclypeal area very densely tessellate, appearing almost granular, without fine longitudinal striolae.....  
.....*fedorica* (Cockerell)
11. Pronotal collar immaculate.....12  
Pronotal collar maculate; tegulae maculate; clypeus either maculate apically or strongly suffused with light reddish.....  
.....*cressoni cressoni* (Cockerell)
12. Facial maculae well-developed; tubercules and basal two-thirds of front tibiae maculate.....*cressoni cressoni* (Cockerell)  
Facial maculae greatly reduced or absent; tubercules immaculate; front tibiae with small basal spot.....*saniculae* (Robertson)
13. Sides of face without conspicuous oval concavity; clypeus rarely marked with black .....14  
Sides of face, slightly above level of antennal sockets, with a conspicuous oval concavity; lateral face marks narrow, elongate; clypeus usually partially infuscated along lower margins.....*saniculae* (Robertson)
14. Antennal scape broad, its greatest width equal to one-half or more its length .....15  
Antennal scape narrower, its greatest width not exceeding 0.47 times its greatest length .....19
15. Scape more or less dilated, strongly flattened to concave beneath; lateral face marks variable.....16  
Scape robust, thick, hardly, if at all, flattened beneath; lateral face marks curving away from eye margins over antennal sockets (Fig. 2H).....  
.....*verticalis* (Cockerell)
16. Lateral face marks above well-removed from inner orbits and conspicuously dilated or clavate above (Figs. 2C, D, J); transverse propodeal carina evanescent or absent.....17  
Lateral face marks above not separated from eye margin, but with pointed median extension ending over antennal sockets (Fig. 2C); transverse propodeal carina sharply defined.....*ellipticus* (Kirby)
17. Scape no more than 0.58 times as broad as long; concave surface black, with at most a narrow yellow stripe along lower margin; mesopleura distinctly punctate.....18  
Scape at least 0.70 times as broad as long, concave under surface wholly yellow, with broad yellow stripe along lower margin which

- expands above onto convex surface, (Fig. 2J); mesopleura densely tessellate and roughened, without conspicuous punctures.....  
 ..... *conspicuus* (Metz)
18. First flagellar segment subequal to second; rugulae of basal area of propodeum not attaining posterior margin; the rugulae longitudinal, widely spaced; oblique carina absent; lateral face marks slightly constricted above level of clypeus, separated from inner orbits by less than their width at constriction (Fig. 2D) ..... *maritimus* Bridwell  
 First flagellar segment half, or less, as long as second; basal area of propodeum rugoso-reticulate to posterior margin; oblique carina present, face marks strongly constricted, separated from inner orbits by much more than their minimum width at constriction (Fig. 2F) .....  
 ..... *rudbeckiae* (Cockerell and Casad)
19. Mesopleural punctures little, if any, coarser than those of frons; transverse and oblique carinae usually absent; lateral face marks constricted above (Figs. 2A, G, I); smaller species, length to apex of second tergite, 2.7-3.5 mm .....20  
 Mesopleural punctures much coarser than those of frons; transverse and oblique carinae present, distinct; lateral face marks not constricted above (Fig. 2B); larger species, length to apex of second tergite, 3.0-4.2 mm ..... *stevensi* (Crawford)
20. Lateral face marks expanded above constriction, *or* continued upward and curving inward above antennal sockets (Figs. 2G, I) .....21  
 Lateral face marks not expanded above constriction, rarely extending beyond level of upper margin of antennal sockets, never curving inward above sockets (Fig. 2A) ..... *fedorica* (Cockerell)
21. Punctures of mesoscutum and mesoscutellum coarse, separated by one-half a puncture diameter or less, the interspaces densely tessellate, and dull; rugulae of basal area of propodeum usually extending to summit of declivity .....22  
 Punctures of mesoscutum and mesoscutellum fine, mostly separated by one and one-half times a puncture diameter or more, interspaces lightly tessellated and moderately shiny; rugulae of basal area evanescent beyond middle, rarely attaining summit of declivity .....23
22. Tibiae and tarsi entirely yellow; tegulae maculate; scape largely yellow beneath ..... *labiatifrons* (Cockerell)  
 Middle and hind tibiae yellow on basal-half only; tegulae often black; scape often entirely dark beneath ..... *cressoni* (Cockerell)
23. Apical lobes of ninth ventrite shorter than pedicle .....  
 ..... *cressoni mesillae* (Cockerell)  
 Apical lobes of ninth ventrite distinctly longer than pedicle .....  
 ..... *sejunctus* Snelling

*Hylaeus (Hylaeus) verticalis* (Cresson), NEW STATUS

Figs. 1G, 2H, 3B, 5B

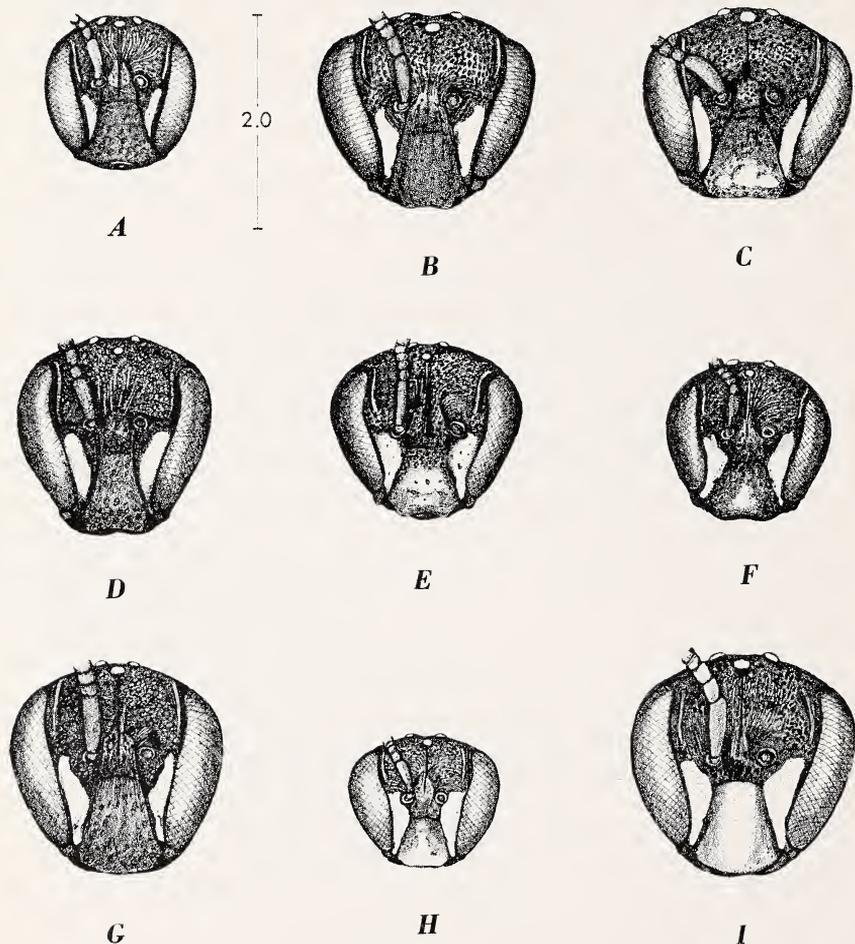
*Prosopis verticalis* Cresson, 1869. Proc. Boston Soc. Nat. Hist. 12:271. ♂.*Prosopis tridentulus* Cockerell, 1896. Psyche 7 (sup.): 27. ♂ NEW SYNONYMY.*Prosopis tridens* Cockerell, 1896. *Op. cit.*: 27. ♂.*Prosopis subtristis* Swenk and Cockerell, 1910. Ent. News 21:70 ♀. NEW SYNONYMY.

Figure 1. *Hylaeus (H.)* spp., female faces: A, *H. fedorica*; B, *H. stevensi*; C, *H. ellipticus*; D, *H. maritimus*; E, *H. rudbeckiae*; F, *H. cressoni cressoni*; G, *H. verticalis*; H, *H. sejunctus*; I, *H. conspicuus*. Figures by Ruth A. DeNicola.

*Prosopis melitina* Lovell, 1911. Ent. News 22:214. ♀.

*Prosopis tridentulus*, Metz, 1911. Trans. Amer., Ent. Soc. 37:116-117.

*Prosopis episcopalus* var. *subtristis*, Metz, 1911. *Op. cit.*: 131. ♀ (*in part*).

*Hylaeus verticalis*, Cockerell and Sumner, 1931. Amer. Mus. Nov. 490: 3-4.

*Hylaeus verticalis tridentulus*, Linsley, *In* Muesebeck, *et al.*, 1951. U.S.D.A., Agr. Monog. No. 2:1050.

*Hylaeus verticalis verticalis*, Linsley, *Op. cit.*: 1052. Mitchell, 1960. N. C. Agr. Exp. Sta. Tech. Bul. 141:76.

With the exception of *H. cressoni* no species of *Hylaeus* is more widely distributed than *H. verticalis*. Throughout most of its range this species is quite common and highly variable. Most of the variation occurs in the females. This variation assumes several different forms. In western populations there is a strong tendency for the apical one-third of the clypeus to be suffused with reddish, rather than entirely black. This variant form is found together with females which have the clypeus entirely black, but there is a noticeable trend toward the maculate condition in those populations which occur at lower elevations in the Sierran and Cascade ranges, and it is a dominant feature in the populations of the Coast Ranges in California. The maculate clypeus is rare in northern and eastern populations. Very rarely are specimens found which have small yellow maculate on the pronotal collar. I have seen only three such specimens among the hundreds I have examined; all were females, one from Idaho, one from Colorado and one from California.

Variation, too, occurs in the shape of the pronotal collar. In the usual condition the pronotal collar, when viewed from above is very nearly as long in the middle as at the sides. In profile it is convex and evenly rounded toward the anterior pronotal neck. Some females, however, have the middle portion flat and somewhat compressed so that it is much shorter here than at the sides. Such specimens, on the basis of the material I have seen, occur only in the western populations, and are especially common in samples from Oregon, California and Nevada. No specimens presenting an intermediate condition are known to me, and these individuals may actually represent a cryptic sibling of *H. verticalis*. I have not, however, been able to associate them with any male variant, so am content to assign them to *H. verticalis* for the present.

I have examined the types of *H. tridentulus*, *H. tridens* and *H. subtristis* and can find no justification for their continued recognition. The first two, both based on males from Colorado, were named because of slight differences in the color of the maculae and slight differences in punctuation from the typical form described from Pennsylvania. With large series of males from the entire range of the species available, it is evident that they fall well within the total range of variation exhibited by any one population. The females described by Swenk and Cockerell from Nebraska as *H. subtristis* are perfectly typical of the western populations of *H. verticalis*; they were merely the, until that time,

undescribed opposite sex of this species. The females which Metz (1911) had called *H. episcopalis subtristis* were a conglomerate association which included, in addition to *H. verticalis*, *H. rugulosus rugulosus* (Cockerell), *H. r. episcopalis* (Cockerell) and *H. modestus citrinifrons* (Cockerell). I have not seen the type of *H. melitina*, but as there is nothing in its description to indicate merit for its further consideration, I have accepted its synonymy as published by Mitchell (1960).

*Hylaeus (Hylaeus) cressoni cressoni* (Cockerell)

Figures 1F; 2H; 6.

*Prosopis pygmaea* Cresson, 1869. Proc. Boston Soc. Nat. Hist. 12:272. ♂. *Preoccupied* by Schenck, 1853.

*Prosopis cressoni* Cockerell, 1907. Annals and Magazine of Natural History (7) 20:131. New name for *P. pygmaea* Cresson, not *P. pygmaea* Schenk. Metz, 1911. Trans. Amer. Ent. Soc., 37:105. ♂ ♀.

*Prosopis pasadenae* Cockerell, 1910. Annals and Magazine of Natural History (8) 5:30. ♂ ♀.

*Prosopis teleporus* Lovell, 1911. Ent. News, 22:213. ♀ ♂. NEW SYNONYMY.

*Hylaeus mesillae* race *pasadenae*, Meado-Waldo, 1923. In Wytsman, Gen. Insect., fasc. 181:30.

*Hylaeus laciniatus* Cockerell and Sumner, 1931. Amer. Mus. Novitates, 490:9-10. ♂. NEW SYNONYMY.

*Hylaeus repolitus* Cockerell and Sumner, 1931. *Op. cit.*, 13-14. ♀. NEW SYNONYMY.

*Hylaeus (Hylaeus) cressoni cressoni*, Linsley, 1951. IN Muesebeck, *et al.*, Hymen. Amer. N. Mex., Synoptic Cat., Monogr. 2, U.S.D.A., p. 1050; Mitchell, 1960, N. C. Agr. Expt. Sta. Tech. Bull. 141:60, 62, 70.

*Hylaeus (Hylaeus) cressoni pasadenae*, Linsley, 1951. IN Muesebeck, *et al.*, Hymen. Amer. N. Mex., Synoptic Cat., Monogr. 2, U.S.D.A., p. 1050.

*Hylaeus (Hylaeus) teleporus*, Linsley, 1951. IN Muesebeck, *et al.*, Hymen. Amer. N. Mex., Synoptic Cat., Monogr. 2, U.S.D.A., p. 1052; Mitchell, 1960, N. C. Agr. Expt. Sta. Tech. Bull. 141:60, 62, 75; fig. 11.

This species extends transcontinentally from southern Canada to northern Mexico. Over most of this range *H. cressoni* is a common species. The populations from eastern, northern and montane regions commonly have the clypeus and pronotal collars immaculate. Some individuals within these populations may also lack maculae on the pronotal lobes and the tegulae. Clinal variation occurs uniformly from east to west, from north to south and with decreasing elevation. This clinal variation is manifested in two concordant characters, an increase in the tone and extent of the pale maculae and a decrease in the size and density of metasomal punctation, so that populations at opposite poles of the cline are very different in appearance. Specimens from

Turlock, California, for example have the face marks bright yellowish, the apical portion of the clypeus is strongly infused with reddish color and the pronotal lobes and collar and the tegulae are conspicuously maculate. The abdomen is smooth and shiny, with few or no distinct punctures. Such specimens contrast sharply with others from the New England area in which the maculae are dull yellowish-white, the clypeus is black and the thorax completely immaculate; such specimens may have the metasomal tergites with obvious fine scattered punctures. The same is true if one compares the Turlock specimens with samples from Revelstoke, British Columbia, or with others from Sonora Pass in the Sierra Nevada of California. In all cases the two extremes are connected, through the intervening portions of the range, by a series of specimens of intermediate character. These series of intermediates form, in their entirety, a well-defined cline for the characters noted.

Under these circumstances continued recognition of *H. pasadenae*, described from Pasadena, California, as a subspecies of *H. cressoni*, a status accorded this form in the past, is untenable. This bee does not possess any of the characteristics of a definable subspecies and I agree with Metz in placing *H. pasadenae* in the synonymy of *H. cressoni*. The subsequent continued recognition of *H. pasadenae* as a subspecies of *H. cressoni* seems to be traceable to Cockerell's refusal to accept the synonymy published by Metz. However persistent such a refusal has been, there appears to be no published indication why Metz's proposal should not be adopted.

Lovell's *H. teleporus* was proposed for *H. cressoni*-like males in which the lateral face marks terminate acutely at the level of the lower margin of the antennal sockets. These males seem to occur sporadically within the populations of *H. cressoni* in northern and montane areas. I have examined the terminalia of males of this form and find no distinctive characters which will serve to separate *H. teleporus* from *H. cressoni*. I believe that *H. teleporus* should be placed in the synonymy of *H. cressoni* until conclusive evidence for the specificity of this form can be advanced.

Cockerell and Sumner described *H. repolitus* from a single female taken at Ogden, Utah. Dr. Rozen sent the type to me and I find nothing in any of its characters to justify separating this bee from *H. cressoni*. The nearly smooth basal zone of the propodeum is exactly like that of many females of *H. cressoni* available to me which also show a strong reduction in the longitudinal rugulae of the basal zone. This characteristic cannot be correlated with other features nor is it geographically consistent.

Dr. Rozen has sent the type of *H. laciniatus*, and there is no doubt that this name, too, is a synonym of *H. cressoni cressoni*. Before I had the opportunity to study the type, I was puzzled by the peculiar shape of the seventh ventrite as figured by Cockerell and Sumner (1930:10, fig. 2). With the type slide before me, it is clear that the apical lobes of this ventrite have been broken off. The poor preparation of the slide, on which everything is badly

flattened and distorted, is also responsible for the seemingly expanded gonocoxites, as these were illustrated by Cockerell and Sumner.

Cockerell and Sumner cite the type as follows: "COLORADO—Boulder, May 24, 1913 (F. E. Lutz)." The labels on the specimens clearly read "Boulder, Colo., M. D. Ellis, May 24, 1913," and "*Salix*." Since the specimen and slides are in accord with the original description and figures, and the type is so marked in Cockerell's handwriting, I have no reason to doubt that this is the true type.

*Hylaeus (Hylaeus) cressoni mesillae* (Cockerell)

Figures 3C; 5C; 6.

*Prosopis subtilis* Cockerell, 1895. Trans. Amer. Ent. Soc., 22:295. ♀. Preoccupied by Förster, 1871.

*Prosopis mesillae* Cockerell, 1896. Canad. Ent., 28:42. new name for *P. subtilis* Cockerell, not *H. subtilis* Förster.

*Prosopis magniclavis* Swenk and Cockerell, 1910. Ent. News, 21:68. ♂ ♀. NEW SYNONYMY.

*Prosopis cressoni*, form *mesillae*, Metz, 1911. Trans. Amer. Ent. Soc., 37:107 (in part).

*Hylaeus cressoni*, var. *magniclavis*, Meade-Waldo, 1923. IN Wytzman, Gen. Insect., fasc. 181:30.

*Hylaeus mesillae*, Meade-Waldo, 1923. *Op. cit.* :30.

*Hylaeus (Hylaeus) magniclavis*. Linsley, 1951. IN Muesebeck, *et al.*, Hymen. Amer. N. Mex., Synoptic Cat., Monogr. 2, U.S.D.A., p. 1051.

*Hylaeus (Hylaeus) mesillae*, Linsley, 1951. *Op. cit.* :1051.

The status of *H. cressoni mesillae* has been confused. Proposed originally as a full species, it was reduced by Metz to status as a "form" of *H. cressoni*. Crawford, two years later, elevated the name to specific status based on differences in the shape of the eighth ventrite, and the bee has been recognized at this level since then. Unfortunately, while Crawford's conclusions were sound, they were based on misidentified specimens. I have examined the genitalia and associated ventrites of many males from New Mexico, Arizona, California and Sonora, Mexico. With the exception of the California specimens all exhibited characters typical of *H. cressoni*.

The California material, however, was represented by two very distinctly different types of terminalia. The first of these was typically *H. cressoni*, identical to those specimens from New Mexico and Arizona. The second type agreed closely with the figure published by Crawford under the name *H. mesillae*. Crawford dissected the terminalia from at least three males, which I have seen; all were from California. The type locality of *H. mesillae* is Mesilla, New Mexico, and the terminalia of males from this area are consistently of the *H. cressoni* type, and I am certain that the interpretation

offered here is the correct one: that *H. mesillae* is conspecific with *H. cressoni*, and that Crawford's specimens represent another species, described below as new.

I have reduced *H. mesillae* to subspecific rank under *H. cressoni*. The females of this subspecies are a little smaller, on the average, than those of

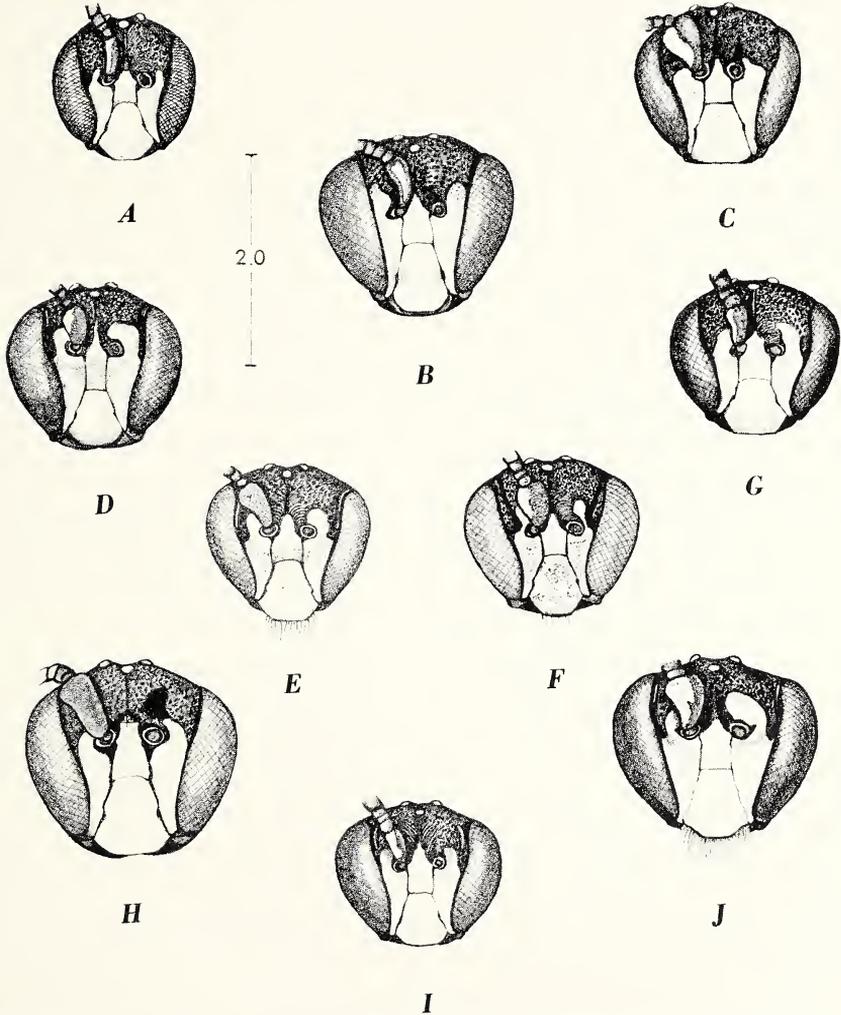


Figure 2. *Hylaesus* (*H.*) spp., male faces: A, *H. fedorica*; B, *H. stevensi*; C, *H. ellipticus*; D, *H. maritimus*; E, *H. granulatus*; F, *H. rudbeckiae*; G, *H. cressoni cressoni*; H, *H. verticalis*; I, *H. sejunctus*; J, *H. conspicuus*. Figures by Ruth A. DeNicola.

*H. cressoni*, and the integument of the body is less densely tessellate, hence more shiny. The punctation, too, differs, being distinctly finer and sparser on the mesoscutum and scutellum, as indicated in the key. Some western material, such as the synonymous form of *H. cressoni*, *H. pasadenae*, are as extensively maculate as *H. c. mesillae* but differ in that the maculae are bright yellow in these, while in *H. c. mesillae* they are whitish. These highly maculate specimens also possess large maculae on the pronotal collars, usually lacking in *H. c. mesillae*. When such maculae are present in the desert subspecies, they are small and inconspicuous.

Females from the desert areas commonly have the rugulae of the basal zone of the propodeum absent or restricted to the extreme anterior margin. In most material of *H. cressoni cressoni* the entire basal zone is distinctly longitudinally rugulose, except in some samples from Colorado and Utah. These appear to be intergrades between the two subspecies. This is somewhat puzzling, since such specimens do not seem to occur in other areas where the ranges of these two forms overlap.

Another intermediate form occurs in western Nebraska, eastern Wyoming and northeastern Colorado. This was described by Swenk and Cockerell as *H. magniclavis*. I have examined most of the type series of this bee and find no reason for its continued recognition. The males have the lateral face marks slightly expanded at their upper ends, but are otherwise similar to that sex of *H. c. mesillae*. I cannot find any differences to distinguish the females from those of *H. c. mesillae*. The male terminalia do not differ significantly from those of *H. c. cressoni* or *H. c. mesillae*, so there is no doubt that *H. magniclavis* is conspecific with these. Since the pale maculae and fine, sparse thoracic punctation are in accord with those characters in *H. c. mesillae*, I consider *H. magniclavis* a synonym of this subspecies.

In figure 6 I have shown the results of a series of cephalic measurements which reflect differences between *H. c. cressoni* and *H. c. mesillae*. In 6A two phenomena are apparent. First that there are two concentration points on the basis of head width. There is some overlap, but the existence of two centers of concentration remains clear. A similar, but more obscure, pattern exists based on head length. These measurements of head length and head width are usefully converted into a Cephalic Index ( $CI = \frac{HL}{HW} \times 100$ ) which demonstrates their relationship as a ratio, figure 6B. A CI value of 100, of course, indicates HL and HW being equal, values lower than 100 indicate increasing relative width. The CI values of each form have been plotted in 4C as a frequency indication. From this figure it is obvious that while both forms most commonly possess CI values ranging from 91 to 100, a much higher percentage (25%) of *H. c. mesillae* have the head longer than broad than is true of the nominate form (9%).

The second noteworthy feature in figure 6A is the displacement of the

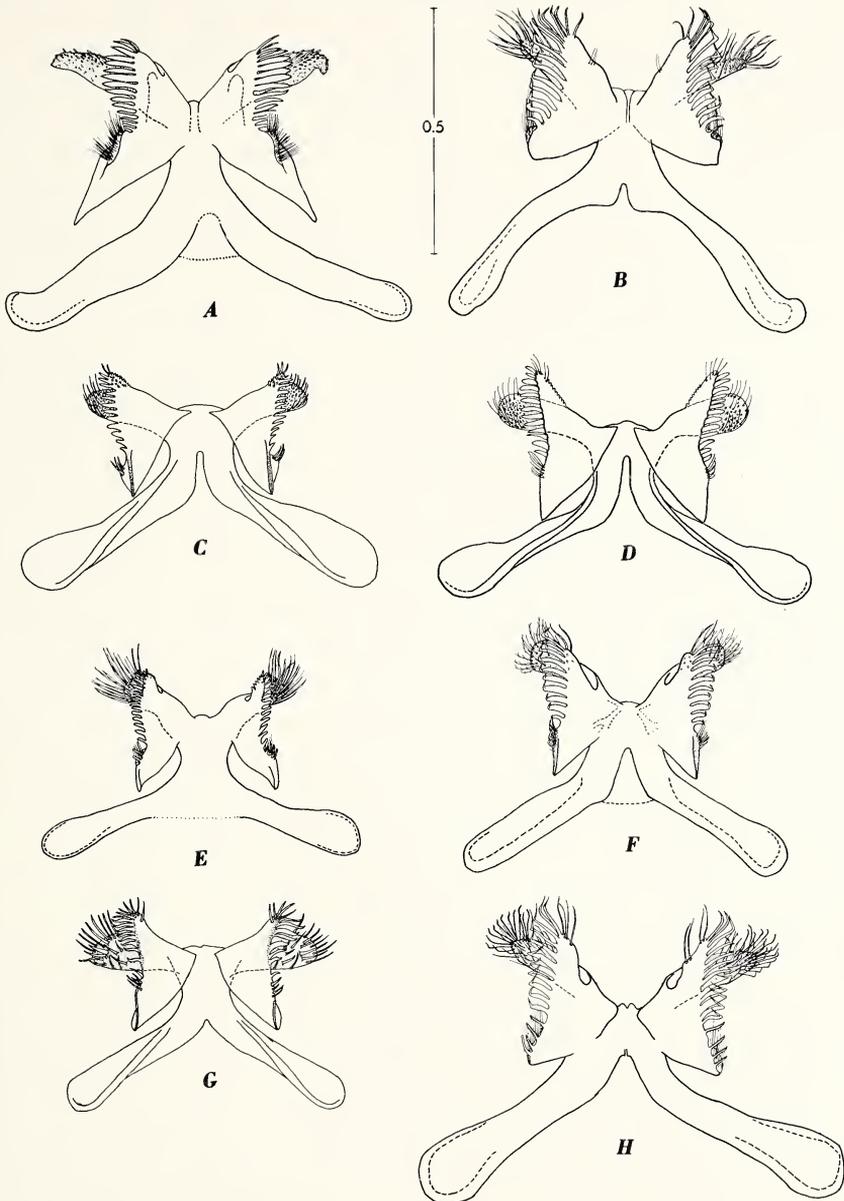


Figure 3. *Hylaues* (*H.*) spp., ventrite VIII of males: A, *H. ellipticus*; B, *H. verticalis*; C, *H. cressoni mesillae*; D, *H. sejunctus*; E, *H. saniculae*; F, *H. fedorica*; G, *H. maritimus*; H, *H. stevensi*.

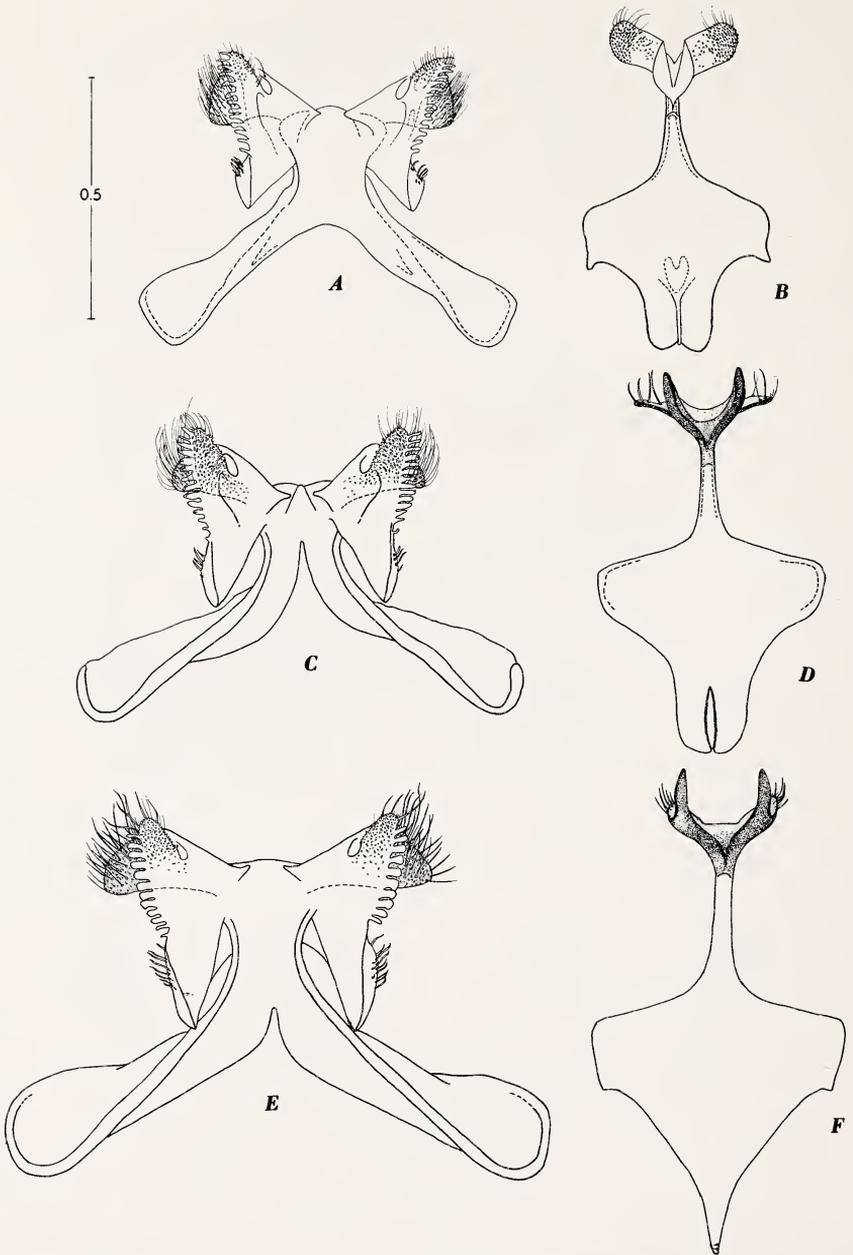


Figure 4. *Hylaenus* (*H.*) spp., ventrites VIII and IX, respectively, of males: A, D, *H. granulatus*; B, E, *H. rudbeckiae*; C, F, *H. conspicuus*.

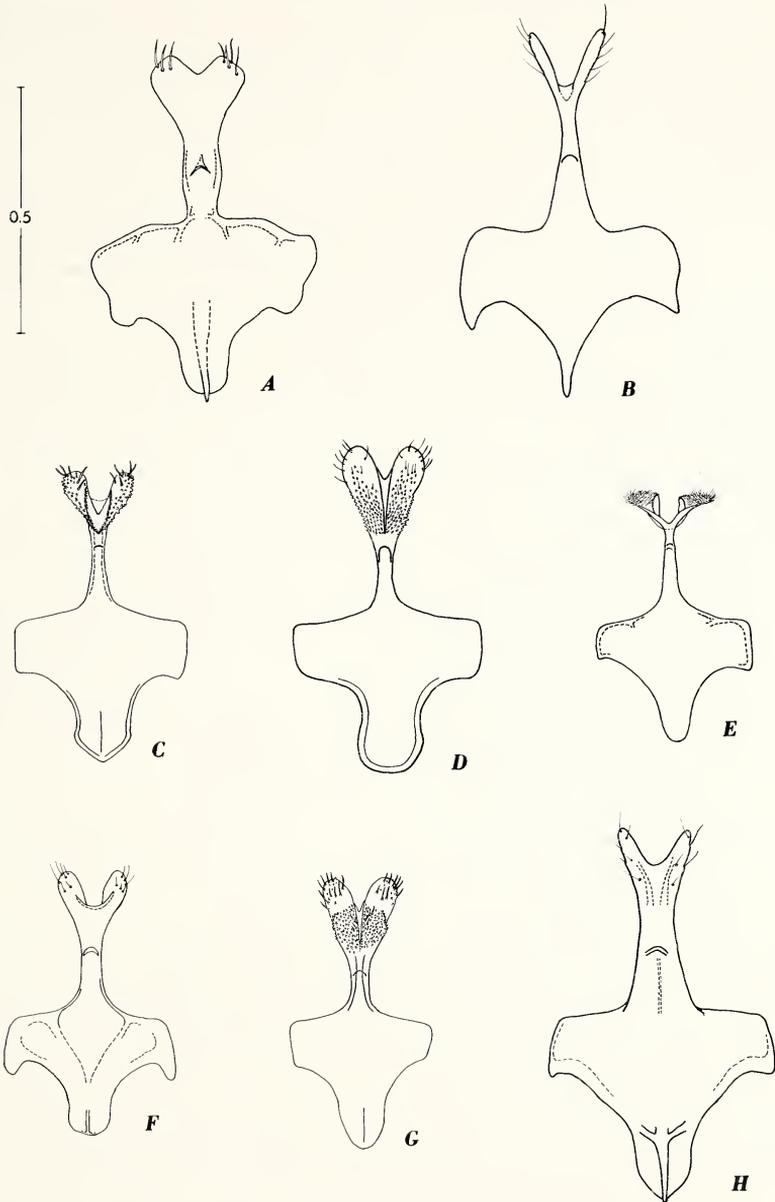


Figure 5. *Hylaeus* (*H.*) spp., ventrite IX of males: A, *H. ellipticus*; B, *H. verticalis*; C, *H. cressoni mesillae*; D, *H. sejunctus*; E, *H. saniculae*; F, *H. fedorica*; G, *H. maritimus*; H, *H. stevensi*.

skew-line of *H. c. mesillae* to a level below that of *H. c. cressoni*. There is also an apparent, though slight, reorientation of the skew-line angle to that of *H. c. cressoni*. These suggest that perhaps *H. c. mesillae* might be best regarded as a full species rather than as a subspecies. I am not inclined, at this time, to do so since specimens of an apparently intermediate nature do exist. These specimens come from those areas where they may be expected to occur if *H. c. mesillae* is truly a subspecies, *i.e.*, in the zones of sympatry. It is equally possible that these are hybrids of two incompletely separate species. However, since the male terminalia are, for practical purposes, so similar as to appear identical, I prefer to consider the desert form a subspecies of *H. cressoni*. This is also consistent with my treatment of other species.

This subspecies extends from western Nebraska, Kansas and Texas westward to Nevada, California and Baja California, Mexico. Southward it ranges into the Mexican States of Nuevo Leon, Coahuila, Chihuahua and Sonora. Populations in Colorado and Utah are largely sympatric with those of the nominate subspecies and hybridization occurs in these areas.

*Hylaeus (Hylaeus) sejunctus* Snelling, NEW SPECIES

Figures 1H; 2I; 3D; 5D.

*Prosopis cressoni* form *mesillae*, Metz, 1911, Trans. Amer. Ent. Soc. 37:107 (in part).

*Prosopis mesillae*, Crawford, 1913. Canad. Ent. 45:154-155. Not of Cockerell, 1896.

This is the species which Crawford called *P. mesillae* when he raised that name to specific level after Metz had reduced *mesillae* to a variety of *H. cressoni* (Cockerell).

*Diagnosis*: The male differs from that of *H. c. mesillae* in the less coarsely, closely punctate abdomen and in the shape of ventrite IX. The female differs in the much finer, sparser punctures of tergite II, the shorter, sparser pubescence of the abdomen, and the smaller size.

*Male*. Very similar structurally to that of *H. c. mesillae* but differs in having the punctures of the mesoscutum finer, sparser, usually separated by a puncture diameter or more; punctures of tergite I very fine, separated by two or more times a puncture diameter; discal pubescence of tergite III shorter than that of mesoscutum; apical lobes of ventrite IX broad, as long as, or longer than, basal pedicel.

*Female*. Very similar structurally to that of *H. c. mesillae* but differs as follows: punctures of median area of upper face of tergite I extremely fine, perceptible only under high magnification, very sparse; lateral areas of propodeum roughened, densely tessellate, with scattered, but distinct, punctures; erect discal pubescence of tergite III little, if any, more than two-thirds an ocellar diameter in length (a few widely scattered hairs may attain this length, but are outnumbered by shorter hairs).

Length, both sexes, to apex of tergite II, 3.2-3.7 mm.

*Holotype* male, allotype female (Los Angeles County Museum of Natural History), Winterhaven, Imperial Co., California, March 25, 1956 (R. R. Snelling), *Heliotropium curassavicum*.

*Paratypes*.—CALIF. *Imperial Co.*: 13 ♂♂, 10 ♀♀, same data as holotype (LACM); 1 ♀, 15.8 mi. NW Niland, April 11, 1963 (R. C. Dickson; UCR), on *Prosopis*; 1 ♂, 2 mi. S. Travertine Rock, March 29, 1936 (F. R. Platt; UCR), on *Prosopis*; 1 ♀, 5.2 mi. SE Kane Springs, April 15, 1949 (P. H. Timberlake; UCR), on *Tamarix gallica*; 1 ♂, 5 ♀♀, Coachella Canal, 20 mi. SE Hwy 195, April 2, 1960 (R. C. Dickson, P. H. Timberlake; UCR), on *Prosopis*; 2 ♀♀, U.S.D.A. Exp. Farm, May 31, 1912 (J. C. Bridwell; USNM); 1 ♂, 1 ♀, same locality, June, 1912 (J. C. Bridwell; USNM); 1 ♂, 1 ♀, El Centro, April, 1911 (J. C. Bridwell; USNM); 2 ♂♂, 1 ♀, Imperial Valley, April, 1911 (J. C. Bridwell; USNM). *San Diego Co.*: 1 ♂, 1 ♀, Borrego Valley, April 26, 1954 (J. G. Rozen; CIS); 1 ♂, Palm Cyn., Borrego Valley, March 29, 1936 (P. H. Timberlake; UCR), on *Prosopis*; 1 ♀, Borrego Valley, April 26, 1954 (M. Wasbauer; CIS); 1 ♀, same locality and collector, April 30, 1954 (CIS), on *Croton californica*; 11 ♂♂, 19 ♀♀, Coyote Cr., Borrego Valley, April 5, 1963 (F. D. Parker, R. M. Bohart, M. E. Irwin, A. Willink; UCD, IML); 2 ♂♂, Borrego Springs, April 2, 1960 (M. Wasbauer; CDA), on *Phacelia*; 2 ♂♂, Split Mt., Anza Desert State Park, April 1, 1955 (W. R. Richards; CNC); 1 ♀, Borrego Valley, April 20, 1961 (Rozen and Schrammel; AMNH), on *Prosopis*; 1 ♀, Borrego Valley, April 11, 1962 (R. M. Bohart; UCD). *Riverside Co.*: 10 ♂♂, 5 ♀♀, Andreas Cyn., March 26, 31, 1955 (W. R. M. Mason; CNC); 1 ♂, Willis Palms Oasis, April 9, 1955 (W. R. M. Mason; CNC); 2 ♂♂, Indio, March 30, 1955 (W. R. Richards; CNC); 1 ♀, Andreas Cyn., April 11, 1955 (W. R. M. Mason; CNC); 1 ♂, 1000 Palms Cyn., April 3, 1944 (P. H. Timberlake; UCR); on *Cryptantha barbiger*; 3 ♂♂, 5½ mi. NW Indio, April 9, 1936 (P. H. Timberlake; UCR), on *Prosopis*; 3 ♂♂, Andreas Cyn., April 2, 1955 (P. H. Timberlake; UCR), on *Hyptis emoryi*; 1 ♀, same locality and collector, April 11, 1936 (UCR), on *Prosopis*; 2 ♀♀, 1000 Palms Cyn., April 10, 1937 (P. H. Timberlake; UCR), on *Prosopis*; 1 ♀, 5 mi. W Indio, April 30, 1949 (E. G. Linsley, J. W. MacSwain, R. F. Smith; CIS), on *Melilotus*. *San Bernardino Co.*: 10 ♂♂, 7 ♀♀, Cronise Valley, April 29, 1956 (J. Powell, M. Wasbauer; CIS), on *Prosopis*; 5 ♂♂, 1 ♀, same locality, date, host (P. H. Timberlake; UCR), on *Salix*; 1 ♀, 29 Palms, April 13, 1935 (P. H. Timberlake; UCR), on *Isomeris arborea*; 7 ♂♂, 11 ♀♀, Needles, May 3, 1964 (P. Torchio & G. Bohart; USU), on *Tamarix* and *Prosopis*; 1 ♂, Needles, 20 mi. S., May 3, 1964 (P. Torchio & G. Bohart; USU). *Inyo Co.*: 1 ♂, Furnace Cr., Death Valley Natl. Mon., April 19, 1939 (E. G. Linsley; CIS), on *Prosopis*. NEVADA. 4 ♂♂, Searchlight, 30 mi. S., Clark Co., April 21, 1966 (Torchio, Rust, Yousef; USU). ARIZONA. 1 ♀, Yuma, 21 mi. N., Yuma Co., April 4, 1963 (A. Willink;

IML). MEXICO. 2 ♂ ♂, 2 ♀ ♀, Mexicali, 20 mi. W., Baja California del Norte, April, 1939 (C. D. Michener; CAS), on *Prosopis*.

*Hylaeus (Hylaeus) labiatifrons* (Cockerell)

*Prosopis labiatifrons* Cockerell, 1896. Psyche, 7 (suppl.): 437. ♂.

*Prosopis cressoni*, Metz, 1911. Trans. Amer. Ent. Soc., 37:105 (in part).

*Hylaeus (Hylaeus) labiatifrons*, Mitchell, 1960. No. Car. Agr. Exp. Sta. Tech. Bull. 141:62, 72. ♂.

The status of this form, described from a single male from Georgia, is enigmatical. It is known only from the unique type, which I have not examined. Metz (1911) considered it a synonym of *H. cressoni*, but Mitchell (1960) has elevated it to species level and briefly redescribed the type. Unfortunately, Mitchell's description contributes nothing new to permit the recognition of *H. labiatifrons*. In all features it seems to agree quite closely with males of *H. cressoni cressoni*, and seems to differ from that species only in the entirely yellow tibiae.

This difference seems to me to be of little value. Another Nearctic *Hylaeus*, *H. illinoisensis* (Robertson), is supposedly recognizable on the same basis. In that species, at least, males with entirely yellow tibiae are exceptional. Even those which have the tibiae wholly yellow show, under intense light, a slightly darker basal two-thirds which corresponds to the black basal area of most specimens. I suspect that the same is true in the case of *H. labiatifrons*, which I regard as a probable synonym of *H. cressoni cressoni*. The solution must wait until the type, especially ventrites eight and nine, can be examined and compared with those of the related species.

*Hylaeus (Hylaeus) fedorica* (Cockerell)

Figures 1A; 2A; 3F; 5F.

*Prosopis digitata* var. *fedorica* Cockerell, 1909. Ann. Mag. Nat. Hist. (ser. 8) 4:27. ♂.

*Prosopis grossicornis* Swenk and Cockerell, 1910. Entomol. News, 21:67. ♂. Metz, 1911. Trans. Amer. Ent. Soc., 37:118. NEW SYNONYMY.

*Hylaeus (Hylaeus) grossicornis*, Linsley, 1951. IN Muesebeck, et al., U.S.D.A. Monogr. 2:1050; Mitchell, 1960. N. Car. Agr. Expt. Sta., Tech. Bull., 141:71-72.

I have examined the type of *Prosopis digitata* var. *fedorica*, now in the American Museum of Natural History, and have compared it with homotypes of *H. grossicornis* and there can be no doubt that these are conspecific, as first suspected by Metz (1911). The type locality of *H. fedorica* is Fedor, Lee County, Texas; *H. fedorica* has priority by one year over *H. grossicornis*.

This species ranges from Michigan to Minnesota, then southward to Texas; an eastern extension exists through the southern United States to North Carolina. The male may be readily distinguished by the characters

A

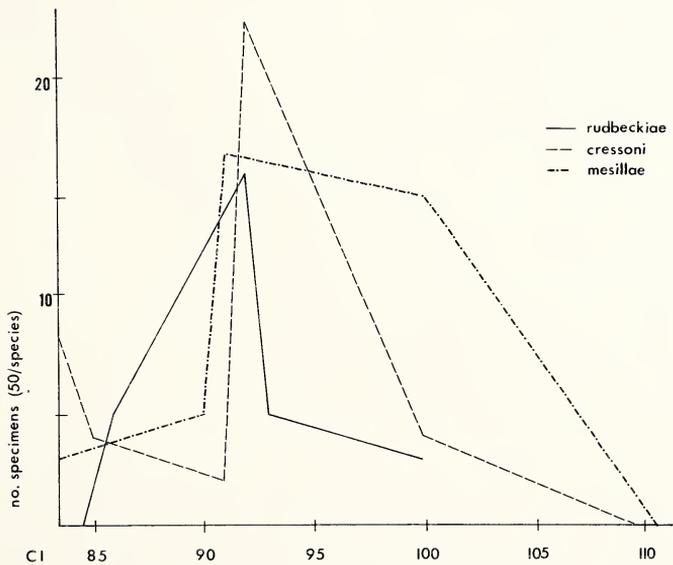
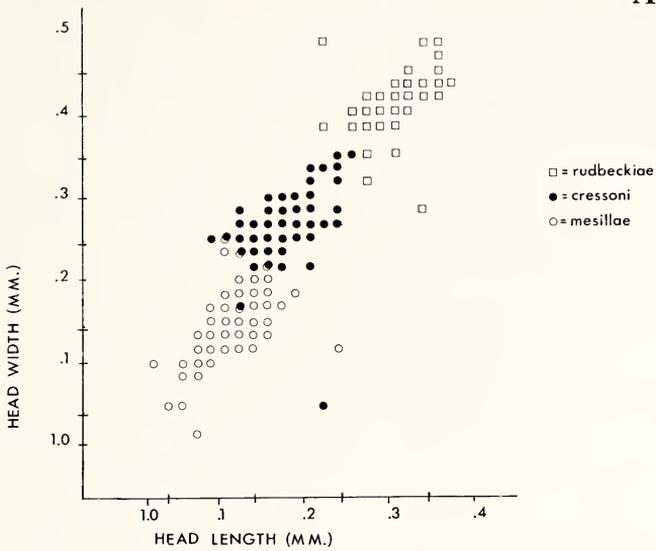


Figure 6. A, scatter diagram plotting Head Width and Head Length of *H. rudbeckiae* (squares), *H. cressoni cressoni* (solid circles) and *H. cressoni mesillae* (open circles); B, Cephalic Index frequency for *H. rudbeckiae* (solid line), *H. cressoni cressoni* (broken line) and *H. cressoni mesillae* (dot-dash line).

given in the key. The female, similar to that of *H. cressoni*, is best recognized by the shape of the head in full face view. In all other species of the *H. cressoni* group, the inner margins of the eyes are strongly divergent above, with the eyes rather strongly bulging. In these species the widest part of the head is somewhat above the level of the antennal sockets. In the female of *H. fedorica* the inner margins of the eyes are only slightly divergent above; the eyes are much less strongly bulging above and the widest part of the head is at, or below, the level of the antennal sockets. The head is always slightly longer than broad.

*Hylaeus (Hylaeus) saniculae* (Robertson)

Figures 3E; 5E.

*Prosopis saniculae* Robertson, 1896. Can. Entomol., 28:137. ♂ ♀.

*Prosopis cressoni* form *saniculae*, Metz, 1911. Trans. Amer. Ent. Soc., 37:106, 107. ♂ ♀.

*Hylaeus (Hylaeus) saniculae*, Linsley, 1951. IN Muesebeck, et al., U.S.D.A. Monogr. 2:1052. Mitchell, 1960. N. Car. Agr. Expt. Sta. Tech. Bull., 141:73-74.

This rare species, largely northern in distribution, is very poorly known. In the United States it extends from Minnesota to the New England states and southward, through the Appalachian Mountains, to Tennessee and Georgia. In Canada it is known from Ontario and Nova Scotia. Although the male may be readily recognized by the peculiar oval depressions on the sides of the face, the female appears to be indistinguishable from that of *H. cressoni* except for its more restricted maculae. Attempts to characterize the female of *H. saniculae* are futile at this time because I have seen no females which I can confidently consider to be this species. Reared series, including both sexes, would be extremely useful in solving this problem.

*Hylaeus (Hylaeus) rudbeckiae* (Cockerell & Casad)

Figures 1E; 2F; 3B; E; 6.

*Prosopis rudbeckiae* Cockerell and Casad, 1895. Trans. Amer. Ent. Soc., 22:380. ♂; Metz, 1911. Trans. Amer. Ent. Soc., 37:111-114.

*Prosopis bakeri* Cockerell, 1896. Psyche, 7 (suppl.): 26. ♂.

*Prosopis digitatus* Cockerell, 1896. *Op. cit.*, 30. ♂.

*Prosopis rudbeckiae ruidosensis* Cockerell, 1896. *Op. cit.*, 30. ♂.

*Prosopis rudbeckiae subdigitatus* Cockerell, 1896. *Op. cit.*, 31. ♂.

*Prosopis rudbeckiae* form *digitatus*, Metz, 1911. Trans. Amer. Ent. Soc., 37:111, 112.

*Prosopis rudbeckiae* var. *bakeri*, Metz, 1911. *Op. cit.*, 111, 112.

*Hylaeus rudbeckiae*, Cockerell and Sumner, 1931. Amer. Mus. Novit., 490:7, 15.

*Hylaeus (H.) rudbeckiae*, Linsley, 1951. IN Muesebeck, et al., U.S.D.A.

Monogr. 2:1052; Mitchell, 1960. N. Car. Agr. Expt. Sta. Tech. Bull., 141:73.

Although it is a simple matter to separate the males of this species from those of *H. cressoni*, I have found no reliable means to separate the females of the two species. There is a difference in the overall size of the females of these species which I have found most easily measured in terms of head width. However, the difference is a minute one and requires precise measurements. In figure 6A I have given the results of measurements of head width and head length of females of *H. rudbeckiae* compared with females of *H. cressoni* (represented by both subspecies). The range of head width is limited, varying from 1.31 mm to 1.50 mm, with the majority of the specimens having a head width in excess of 1.41 mm. In those specimens which have a head with less than 1.40 mm, the head length is 1.24 mm or more. In *H. cressoni* the total range of head width variation is much greater, extending from 1.12 mm to 1.37 mm. In those few specimens of *H. cressoni* which have a head width in excess of 1.34 mm the head length does not exceed 1.23 mm. These differences are slight but appear to be valid. They have been verified by checking against associated males and in reared series.

Figure 6B contrasts the cephalic index of *H. rudbeckiae* with that of the nominate form of *H. cressoni*. It may be noted that while both species most frequently possess a CI rating of 92, that is, with the head a little broader than long, a distinct tendency exists in *H. rudbeckiae* for the head to be broader still, and no specimens of this species seem to have a cephalic index over 100. While such high ratings are not common in *H. cressoni*, they do occur. In *H. rudbeckiae*, about 70% of the females examined had a cephalic index of 92 or less; in females of *H. cressoni*, only 33% have such a low rating.

In other morphological features the females are very similar and I have noted none that are sufficiently constant to be reliable. The two species are almost completely sympatric, *H. rudbeckiae* absent only from those areas inhabited by *H. c. mesillae*. In most areas *H. rudbeckiae* is slightly more brightly maculate, the maculae as a rule both more extensive and of a brighter, yellower tone. The integument of the mesoscutum and scutellum is more densely tessellate and less shiny.

*Hylaeus (Hylaeus) granulatus* (Metz)

Figures 2E; 4A; D.

*Prosopis rudbeckiae* var. *granulatus* Metz, 1911. Trans. Amer. Ent. Soc., 37:114. ♂.

Although this closely resembles *H. rudbeckiae*, it may be recognized by the features of the eighth and ninth ventrites (fig. 4A, D). External features do not appear to be reliable since both species are so variable. The following differences have been noted as tendencies which may be of value. The antennal and thoracic maculae of *H. granulatus* are less extensive than is usually true of *H. rudbeckiae*. In *H. granulatus* the scape may be black or with a small, basal

spot on the lower margin; the pronotal collar may be immaculate or with a pair of minute yellowish spots at the extreme sides; the pronotal lobes are one-half, or more, black; the tegulae may be either black or with a small median spot. In *H. rudbeckiae* these areas are usually conspicuously maculate, except in specimens from northern or high altitude sites. The metanotum of both species is dull, but in *H. granulatus* it is rugosopunctate, while in *H. rudbeckiae* it has fine sparse rugulae and a few distinct scattered punctures. In *H. rudbeckiae* the basal zone of the propodeum is coarsely rugose, with the rugae in the median portion basically parallel. The basal zone of *H. granulatus* may be coarsely and irregularly rugulose, or with fine rugulae only on the anterior half, the posterior half appearing granulose.

The status of this form is enigmatical. Metz described it from three males from Ormsby County, Nevada. No type was ever designated and so I am selecting a specimen from the original series, collected by Baker in July, as the lectotype. This specimen has been deposited in the American Museum of Natural History. Since the time of its description this bee has never been regarded as anything other than a variety of *H. rudbeckiae*, of which it has been considered a synonym. Its status here as a species is provisional, pending the acquisition of more material. This form may ultimately prove to be a hybrid resulting from a cross between *H. rudbeckiae* and *H. cressoni*. The extremes in variation in the sculpturing of the basal zone of the propodeum are suggestive of *H. cressoni* and the details of the eighth and ninth ventrites are intermediate between *H. cressoni* and *H. rudbeckiae*. If *H. granulatus* is a valid species, its female is currently unknown, but probably will be extremely similar to that of *H. rudbeckiae*.

In addition to the three males from Nevada I have seen others from scattered localities in the Sierra Nevada of California, from Lassen County to Tulare County, and from the San Gabriel Mountains in Los Angeles County. I also have a few males from Colorado which seem referable to this form; these differ slightly, however, in the shape of the ninth ventrite which is very similar to that of *H. cressoni*. In areas where these specimens were taken, both *H. cressoni* and *H. rudbeckiae* are common.

*Hylaeus (Hylaeus) maritimus* Bridwell

Figures 1D; 2D; 3G; 5G.

*Hylaeus maritimus* Bridwell, 1910. Proc. Haw. Ent. Soc. 4:159. ♀ ♂.

*Hylaeus (Hylaeus) maritimus*, Linsley, 1951. IN *Musesebeck, et al.*, U.S.D.A. Monogr. 2:1051.

This rare species appears to be largely restricted to the coastal sand dunes of central California. The two females taken by Timberlake at Mt. Pinos are the only exceptions, and it is difficult to explain the presence of *H. maritimus* in that area.

Both sexes of this species, which is closely related to *H. conspicuus*, may be readily recognized by the characters given in the key.

NEW RECORDS (all California): *Sonoma Co.*: 4 ♀ ♀, Wright's Beach, August 22, 1950 (J. Linsley; CIS), on *Eriogonum*. *Marin Co.*: 1 ♂, Pt. Reyes, April 11, 1959 (G. I. Stage; LACM); 9 ♂ ♂, 2 ♀ ♀, same locality, May 16, 1958 (D. D. Linsdale; CIS); 2 ♂ ♂, same locality and date (J. Powell; CIS); 1 ♀, same locality, May 15, 1937 (R. C. Dickson; UCR). *San Francisco Co.*: 1 ♂, San Francisco (Land's End), July, 1922 (F. X. Williams, UCR); 1 ♂, San Francisco, April 16, 1960 (G. I. Stage and R. R. Snelling; LACM); 1 ♂, San Francisco (Lobos Cr.), June 15, 1960 (G. I. Stage; GIS); 1 ♂, San Francisco (Lone Mtn.), July 4, 1920 (F. X. Williams; CAS); 1 ♂, 4 ♀ ♀, San Francisco (sand dunes), April 9 to August 22, 1926 (C. L. Fox; CAS); 1 ♀, Lake Merced, June 5, 1959 (R. Haig; UCD). *San Mateo Co.*: 1 ♂, Salada Beach, April 21, 1918 (E. P. Van Duzee; CAS). *Monterey Co.*: 1 ♂, Pacific Grove, July 3 (T. D. A. Cockerell; UCR); 5 ♂ ♂, 10 ♀ ♀, same locality, May 29, 31, 1954 (M. Wasbauer; CIS); 3 ♂ ♂, same locality, May 16, 1959 (G. I. Stage; GIS, LACM); 1 ♀, Carmel, July 21, 1923 (L. S. Slevin; CAS); 2 ♂ ♂, 2 ♀ ♀, Asilomar, May 10, 16, 1959 (D. J. Burdick; GIS, LACM); 1 ♀, Asilomar, 1 mi. S, May 17, 1959 (D. J. Burdick; LACM); 1 ♂, Asilomar, 2 mi. S, September 26, 1959 (C. W. O'Brien; LACM); 1 ♂, same locality, May 17, 1959 (G. I. Stage; GIS). *San Luis Obispo Co.*: 7 ♂ ♂, 9 ♀ ♀, Grover City, July 4, 1956 (E. G. Linsley, P. D. Hurd; CIS), "dunes Assoc." *Santa Barbara Co.*: 1 ♂, Refugio Cyn., July 4, 1959 (J. R. Russell; UCD). *Kern Co.*: 1 ♀, Mt. Pinos, August 17, 1935 (P. H. Timberlake; UCR), on *Hemizonia corymbosa* (var. *barclayi*); 1 ♀, same data, except, *Grindelia (robusta) platyphylla* (UCR).

*Hylaeus (Hylaeus) conspicuus* (Metz)

Figures 1I; 2J; 4C; F.

*Prosopis conspicua* Metz, 1911. Trans. Amer. Ent. Soc. 37:114. ♂ ♀.

*Hylaeus conspicuus*, Cockerell and Sumner, 1931. Amer. Mus. Nov. 490:9.

Cockerell and Sumner (1931) recorded a female from Jackson, Wyoming, July 15, 1920, presumably collected by F. E. Lutz. I have on hand two females collected at Jackson on July 13-17, 1920, presumably by Lutz. Although these authors were surprised at finding this species in Wyoming, it is a widely distributed species in the northwestern states. In addition to the considerable material from California, I have seen specimens of *H. conspicuus* from the following states: *Nevada* (Ormsby Co., Gardnerville, Sparks, Paradise V.; AMNH, USNM, UCD, *Oregon* (Medford, UCD), *Washington* (Pullman; UCD), UC, CAS), *Idaho* (Shoshone, Star, Murtaugh, Midvale, 5 mi. NE Mackay, Parma, Dixie, Boise, Moscow Mts., Sweet, Emery Can., Melba, 8 mi. N Twin Falls, 18 mi. S Moscow; UI), and *Wyoming* (Jackson; AMNH, CU).

*Hylaeus (Hylaeus) stевensі* (Crawford)

Figures 1; B; 2B; 3H; 5H.

*Prosopis stевensі* Crawford, 1913. Can. Ent., 45:155. ♂ ♀.*Hylaeus (Hylaeus) stевensі*, Linsley, 1951. IN Muesbeck, et al., U.S.D.A. Agr. Monogr. 2:1052. Mitchell, 1960. N. Car. Agr. Exp. Sta. Tech. Bul. 141:61, 62, 74-75; figs. 11, 12, 13, 14.

This species is not closely related to any other in the Nearctic fauna, but is very similar to the Palearctic *H. bisinuatus* Förster. The two are so closely related that I know of no reliable external features which will separate them. The male terminalia of the two are very similar to one another. More material must be studied, however, to determine whether they are conspecific or not.

This species has recently been introduced into Hawaii (Beardsley, 1959), and is evidently adventive in parts of its range where it is now quite common. I believe that this species has extended its range appreciably within the past 50 years. The earliest known capture of this species is in 1912 at Fargo, North Dakota; these specimens form the type series. The species has been collected in North Dakota on many occasions since then, but remained rare in *Hylaeus* samples taken until after 1925. After this date it became increasingly common, until it is now the species most frequently captured.

The earliest records outside of North Dakota are 1915 (Colorado) and 1916 (Alberta, Canada). Earliest records for other states, proceeding west from North Dakota to the Pacific coast, are: Wyoming and Idaho (1920), Utah (1922), British Columbia and Washington (1925) and California (1933). This species is found in eleven states east of the Mississippi River; the earliest date of capture which I have seen is 1927 in Massachusetts. In none of his numerous papers on eastern bees does Robertson mention this bee; this species is so distinctly different from the remaining eastern *Hylaeus* that he certainly would have recognized it as different from any previously described.

Within California the earliest record for this species is 1933 at Sacramento. There are few records in the 1930's and 1940's. But, beginning with 1950 there are abundant records, largely from the Central Valley area. My greatest field acquaintance with this species is in California, so the following observation must be considered with this point in mind. All of the California records are within, or on the periphery of, agricultural cultivated areas. I can affirm, further, that the bulk of my records from most of the area west of the Continental Divide come from similar situations, as nearly as I have been able to determine.

This bee is of further interest in that it alone of all the species of *Hylaeus*, s. str., exhibits a pronounced tendency toward oligolecty on flowers of the family Leguminosae. Of 87 specimens bearing floral data, 56 were taken on *Melilotus* species. These legumes are introduced from the Palearctic region. Of the remaining 31 records, 13 are from introduced Palearctic plants in other families (Amaranthaceae, Umbelliferae, Cruciferae, Tamaricaceae, Legu-

minosae) and eight of these are records of males. The remaining 18 records involve the families Polygonaceae, Asclepiadaceae, Salicaceae and Compositae, all belonging to genera represented in the Palearctic region: six of these records are of males.

The above data would seem to indicate the possibility that this species was introduced into the area around Fargo, North Dakota sometime prior to 1912. Once established there it began to extend its distribution both east and west and by 1925 apparently reached both coasts; subsequent distribution has been extended southward, so that this species now occurs in southern California, Oklahoma and Georgia. It is now a well-established part of our fauna and appears to be oligolectic on the legume genus *Melilotus*. If this is, in fact, an introduced species, it may well prove to be a synonym of a described Palearctic species. This, however, may not be decided for many years yet due to the extremely chaotic status of the taxonomy of European *Hylaeus*.

It is possible that this species is a native component which was, prior to the first quarter of the century, a very rare species. Subsequent to that time the increased abundance of a suitable food-source plant (the introduced genus *Melilotus*) and the conditions of an unbalanced ecology may have permitted this species first to thrive in its native region and then to spread out to other, similarly disturbed areas. Of numerous series of specimens reared from soda straw traps by A. R. Gittins in Idaho, many are referable to *H. stevensi*. This species, then, is strongly apt to exploit artificial nesting possibilities, such as exist in and around farm buildings.

#### EXCLUDED SPECIES

In 1966 I included *H. gagei* (Cockerell) in this subgenus largely on the conjectural statement of Mitchell (1960), who had seen the type, that it may prove to be the female of *H. rudbeckiae*. Since then I have examined the type, in the U.S. National Museum, and conclude that it was incorrectly associated by me with the subgenus *Hylaeus*. The type, a female, is a small, obscurely maculate individual. This species belongs to the subgenus *Prosopis* and may be a synonym of *H. modestus* Say.

#### PARAPROSOPIS

The subgenus *Paraprosopis* in America north of Mexico is exceeded in number of species only by the subgenus *Prosopis*. This group is largely western in distribution and seems to be centered in the southwest. Although Holarctic, few species extend into Canada, and none of these very far. Only one species may be considered truly boreal; species of *Paraprosopis* are most commonly encountered in the Transition and Sonoran zones.

This subgenus is a difficult one with which to work and this is particularly true of the females. The various species are very similar in appearance and structure and several of the most widely distributed species are quite variable.

Species groups are so poorly delimited that I see little point in attempting to define them except in very general terms.

The largest group is that of *H. wootoni* (Cockerell) which includes the following species: *H. coloradensis* (Cockerell), *H. cookii* (Metz), *H. floridanus* (Robertson) *H. lunicraterius*, n. sp., *H. nevadensis* (Cockerell), *H. personatellus* (Cockerell), *H. polifolii* (Cockerell) and *H. wootoni* (Cockerell). There is considerable variation within the group, but all the species are superficially very similar in the females. In these the first tergite is densely and distinctly punctate (excepting *H. floridanus*), the integument between the punctures usually smooth and somewhat shining, the transverse propodeal carina is absent (except in *H. cookii*), the lateral and oblique propodeal carinae often reduced or absent, the facial foveae ending one-third or less of the distance between the eyes and ocelli, the mesopleurae densely and closely punctate and the head as broad, or broader, than long. Although the clypeus is typically immaculate, some females of one species (*H. polifolii*) may possess a small preapical spot. The males are similar to their females except for the usual sexual differences.

Three groups include but a single species each. The *H. sonorensis* group contains only *H. sonorensis* Cockerell, a desert species recognizable by the head being longer than broad, the elongate pale macula on the female clypeus, the entire transverse macula on the pronotal collar and the extremely fine punctures of the second tergite. Another species in which the pronotal macula is entire is *H. asininus* (Cockerell and Casad), the sole member of the *H. asininus* group. In this group the facial foveae of the female end much nearer to the ocelli than the eyes, the transverse propodeal carina is present in both sexes, and the female mandibles are truncate apically. The only other species with an entire macula on the pronotal collar is *H. megalotis*. This unique member of the *H. megalotis* group may be easily separated from the other groups in the female by the elongate apical mandibular tooth, the absent or incomplete oblique propodeal carina and the broadly translucent apical margins of the first four tergites. The male differs from that of most others by the finely, sparsely punctate first tergite, the broadly translucent tergal margins and the longer flagellar segments.

All three of these groups, while apparently related to the *H. wootoni* group, seem not to be closely related to one another, although it is interesting that all occur in arid and semi-arid regions. Of the three, that of *H. sonorensis* seems farthest removed from the *H. wootoni* group as evidenced by the elongate face and the male apical sternites.

The last group, that of *H. calvus*, includes four species: *H. calvus* (Metz), *H. georgicus* (Cockerell) and *H. timberlakei*, n. sp., and the Palearctic species, *H. ater* Saunders. In these species the facial foveae of the female end closer to the ocelli than the eyes, the anterior coxae tend to be angulate or spinose laterobasally, the mesopleurae are shining and finely, sparsely punc-

tate, the female genae are broader than the eyes in profile, the female clypeus is usually distinctly maculate and the first tergite of the female is finely and sparsely punctate.

The females of several of the most common western species are very difficult to identify with certainty. The three most consistently difficult species are *H. coloradensis* (Cockerell), *H. polifolii* (Cockerell) and *H. wootoni* (Cockerell). Slight, but apparently consistent, differences in the shape of the eyes have been utilized. In the full frontal aspect the *Eye Length* (EL) is measured to the nearest tenth of a millimeter; the *Frontal Eye Width* (FEW) is measured across the eye to the inner margin at the level of the antennal sockets (fig. 10A). Similar measurements are made in lateral view. Here, however, *Lateral Eye Width* (LEW) is measured at its greatest point. Considerable use has been made of the presence or absence of the oblique propodeal carina as a supportive feature. This carina is best seen when the dorsal surface of the propodeum is viewed obliquely from above and cephalad of the propodeum.

The upper termination point of the facial foveae has also been frequently used in the key to the females. The position of termination is determined by viewing the top of the head from above. Measurement is made from the lateral ocellus to the nearest point of the inner eye margin and the position of the uppermost point of the fovea made on the basis of this line.

The method of determining the *Facial Width* (FW) used in previous papers on this genus (*i.e.*, the distance between the inner eye margins at the level of the antennal sockets) was found to be nearly useless within this subgenus. A different method for determining facial width has been used below. In full frontal view, the inner margins of the eyes are seen to be slightly sinuate at a point a little above the level of the antennal sockets, at the lower end of the foveae. This sinuation probably corresponds to the ocular sinuses of many wasps. The measurement for facial width is made at the center of the slight sinuation. The *Facial Length* (FL) is measured as in previous papers (*i.e.*, the distance from the anterior ocellus to the medio-apical clypeal margin). The *Upper Facial Distance* (UFD) is the maximal distance between the eye margins above, while the *Lower Facial Distance* (LFD) is the minimal distance between the eyes below. The *Clypeo-Ocular Distance* (COD) is measured from the laterobasal clypeal angle to the nearest point on the eye margin; the *Basal Clypeal Width* (BCW) is the maximal width of the clypeal base; the *Clypeo-Antennal Distance* (CAD) is measured from the laterobasal clypeal angle to the nearest point on the rim of the antennal sockets. The *Supraclypeal Quadrangel* (SCQ) is bounded below by the clypeal base, on the sides by the subantennal sutures and above by an imaginary line connecting the juncture of the subantennal sutures with the rims of the antennal sockets.

At several places in the key to the females reference has been made to punctures as being fine or coarse. The use of such poorly expressive terms has

been relegated to the role of supportive features, since such vague expressions are both subjective and relative. Punctures which appear to be fine on one bee may appear *relatively* coarse on another bee of smaller size. In a rough way, punctures which I refer to as "coarse" are those which exceed 0.025 mm in diameter and are usually about 0.03 mm in diameter. Fine punctures are usually less than 0.02 mm in diameter. Such measurements are nearly without value, however, since the punctures of the mesopleura may vary as much as 50% in diameter measurements. Statements relative to puncture size are to be interpreted as referring to the largest punctures on the pertinent sclerite. Examination of females of several different species will soon permit one to adequately interpret the usage of such terms.

The figures of the eighth and ninth sternites of the males require some comment. The eighth sternite consists of a complex arrangement of four membranous lobes, conveniently termed the lateral (or basal) and apical lobes, basad of which are the apodemal arms. The orientation on the plates places the apical lobes uppermost and the apodemal arms below; this is the same arrangement used in preceding papers and will be used in all subsequent papers on this genus.

The lateral lobes of the eighth sternite are simple and usually possess a number of simple setae along their lower margins and at the apices. Sometimes the apical portion of this lobe folds back upon itself and consequently assumes a shape very different from that which is considered normal. The apical lobes are much more apt to present difficulties because the membrane is much more delicate and complex, hence subject to more pronounced distortion. These lobes may fold either along the inner margin or transversely at the middle. A well defined crease line is evident from the apex of the lateral arms to the outer margin and the transverse fold usually occurs at this point. Such folds will, of course, greatly alter the contour of the apical lobes and, because the membrane is so thin, this fact may easily pass unnoticed. An example is the figure by Metz (1911; pl. 5, fig. 60) of the eighth sternite of *H. cookii*; the distal half of the apical lobe has folded back upon itself, a fact unsuspected by Metz.

The ninth sternite is a much simpler structure; it is elongate and apically bifurcate. The apical lobes are thin and are partially sclerotized. The normal plane of these lobes is more or less vertical, so that a true illustration of this segment in a normal position would show two thin, apically divergent processes. However, since such a view would tend to conceal some characters of use taxonomically, the figures are traditionally based on slide mounted, and somewhat flattened, specimens in which the apical lobes are even more divergent than is normal and the plane is angularly distorted. The alternative to such a procedure is to prepare two figures, one of the true ventral aspect and one of the lateral aspect. I have here abided by the traditional method of figuring this segment largely in order than a common ground for comparison between my

figures and similar figures by other authors may be established. Thus, when comparing these figures with specimens, important features to note are the width of the basal shaft, the relative length of the lobes and the number and arrangement of the plumose setae. The shape and degree of divergence of the apical lobes should be viewed with caution.

The key below includes all North American species described by previous authors, and recognized by me, as well as two new species described at this time. There exist a number of undescribed species from the western United States and Mexico but these are represented by too few specimens for me to wish to describe them at this time. If and when suitable series become available they will be described in a future part of this series, together with a new key.

KEY TO NEARCTIC SPECIES OF *PARAPROSOPIS*

- 1. Females; antennae twelve-segmented..... 2  
 Males; antennae thirteen-segmented.....15
- 2. Gaster without evident punctures, first tergite shining, polished; basal zone of propodeum as long as, or longer than, scutellum, much longer than metanotum; facial foveae ending much nearer ocelli than eyes ..... *georgicus* (Cockerell)  
 Gaster with distinct punctures, at least on first tergite, the tergite polished or not; basal zone of propodeum shorter than scutellum, little, if any, longer than metanotum; facial foveae variable..... 3
- 3. Apical mandibular tooth elongate, as long or longer than its basal width, extending much beyond the well-defined inner tooth, apex of mandible thus acute; oblique propodeal carina absent or incomplete; facial foveae ending slightly nearer ocelli than eyes; first tergite polished, shining, punctures fine, separated by a puncture diameter or more; apical margins of tergites 1-4 broadly translucent yellowish.....  
 .....*megalotis* Swenk and Cockerell  
 Apical mandibular tooth much shorter than basal width, hardly extending beyond the poorly defined inner tooth, apex of mandible thus truncate; oblique propodeal carina present or not; facial foveae variable; tergal surface variable; tergites usually without pallid apical margins ..... 4
- 4. Facial length 1.4 times facial width, oblique propodeal carina absent, lateral carina absent or obsolescent; facial foveae ending near mid-point between eyes and ocelli; punctures of first tergite very fine, separated by about a puncture diameter; second to fifth tergites duller, densely micropunctate and with fine appressed pubescence; clypeus with longitudinal macula; pronotal collar with complete transverse macula .....*sonorensis* Cockerell  
 Facial length 1.3 or less, times facial width; oblique and lateral propodeal carinae usually present; punctures of tergites variable, first tergite

- frequently coarsely punctate; clypeus usually immaculate; pronotal collar usually with macula, when present, interrupted in middle..... 5
5. Outer margin of fore coxae abruptly produced near base, forming a triangular to subspinose process; facial foveae ending nearer ocelli than eyes; mesopleura distinctly shining, with well-separated fine punctures; first tergite finely, sparsely punctate; clypeus with longitudinal macula ..... *calvus* (Metz)
- Outer margin of fore coxae not abruptly produced near base; remaining characters without the above combination..... 6
6. Basal zone of propodeum abruptly declivous behind, with distinct transverse carina separating the more or less horizontal anterior face from the vertical posterior face; metanotum densely tessellate, with scattered distinct punctures; wings pale whitish, veins yellowish to light brown ..... 7
- Without above combination of characters..... 8
7. Smaller species, facial length not over 1.2 mm.; second tergite sharply, closely punctate; facial foveae ending nearer eyes than ocelli, or midway between; macula on pronotal collar interrupted in middle..... *cookii* (Metz)
- Larger species, facial length 1.3 mm. or more; second tergite with very fine obscure punctures or nearly impunctate; facial foveae ending nearer ocelli than eyes; macula on pronotal collar usually entire..... *asininus* (Cockerell and Casad)
8. First tergite smooth, punctures extremely fine, sparse to scattered; second tergite without obvious discernible punctures; mesopleura dull to moderately shining, with fine punctures separated by a puncture diameter or more; metanotum dull, without evident punctures..... *floridanus* (Robertson)
- Without above combination of characters..... 9
9. Mesopleura moderately shining, with fine punctures separated by a puncture diameter or more; propodeal disc with coarse oblique rugae convergent toward mid-line, metanotum with coarse quadrate areolae at extreme base; clypeus with longitudinal median stripe *timberlakei* Snelling
- Mesopleura dull to slightly shining, punctures variable, usually separated by about one-half a puncture diameter; propodeal disc usually without rugae, when rugae are present they are irregular; metanotum either not areolate basally or areolae extremely fine, appearing as a band of quadrate punctures; clypeus immaculate or with small pre-apical spot ..... 10
10. Facial length 1.3 times facial width; oblique propodeal carina present, area above carina coarsely reticulate; transverse propodeal carina present..... *lunicraterius* Snelling
- Facial length no more than 1.2 times facial width; oblique propodeal

- carina present or absent, area above usually not coarsely reticulate; transverse propodeal carina usually absent.....11
11. Small species, facial length not exceeding 1.2 mm., usually about 1.1 mm.; facial length 1.1 times facial width; facial foveae ending about one-third of distance between eyes and ocelli; oblique propodeal carina usually present and area above coarsely reticulate..*nevadensis* (Cockerell)  
Larger species, facial length 1.3 mm. or more; facial length 1.2 times facial width; facial foveae ending about midway between eyes and ocelli; oblique propodeal carina and area above variable.....12
12. Metanotum flattened, densely tessellate, but with distinct punctures nearly as large as those of scutellum; scutellum distinctly flattened, shinier than mesoscutum, more finely punctate, the punctures separated by a puncture diameter or slightly more; lateral face marks reduced, frequently absent; erect hairs of mesoscutum sparse, short, less than half as long as those of scutellum.....*personatellus* (Cockerell)  
Metanotum at least slightly convex, roughened, without evident punctures; scutellum slightly convex, not much duller than mesoscutum, punctures dense, nearly as large as those of mesoscutum; lateral face marks usually filling most of area between eye and clypeus; erect hairs of mesoscutum variable.....13
13. Larger species, head width 1.6 mm. or more; oblique propodeal carina evanescent or absent; lateral propodeal carina usually evanescent above; clypeus always immaculate; EL 4.5-4.6 X FEW..*coloradensis* (Cockerell)  
Smaller species, head width 1.5 mm. or less; oblique and lateral propodeal carina variable, but often present; clypeus often maculate; EL 3.3-4.5 X FEW .....14
14. Oblique propodeal carina often absent, sometimes present but evanescent; clypeus immaculate.....*wootoni* (Cockerell)  
Oblique propodeal carina usually present and complete; clypeus often with preapical spot in middle.....*polifolii* (Cockerell)
15. Basal zone of propodeum twice as long as metanotum, as long or longer than scutellum; first tergite microtesselate, impunctate or with very fine scattered punctures; scape 1.2-1.3 times longer than greatest width .....*georgicus* (Cockerell)  
Basal zone of propodeum usually less than twice as long as metanotum, usually much shorter than scutellum; first tergite polished or tessellate, as a rule with abundant punctures, scape variable.....16
16. Head slightly longer than wide; FL 0.97 times HW, 1.17-1.20 times EL, 1.46-1.50 times UFW; oblique propodeal carina absent, lateral carina absent or evanescent; pronotal collar frequently with complete stripe; scape half as broad as long.....*sonorensis* Cockerell  
Head no longer than broad, usually broader than long; remaining characters not in above combination.....17

17. Eyes rather strongly converging below, UFW at least  $1.85 \times$  LFW.....18  
 Eyes less strongly convergent below, UFW no more than  $1.80 \times$  LFW,  
 usually  $1.75$  or less.....21
18. First two tergites with sparse, fine punctures, surface shining, with  
 strong bluish iridescence; FL  $2.6$ , or more, times LFW.....  
 .....*floridanus* (Robertson)  
 First two tergites with coarse, distinct punctures mostly separated by a  
 puncture diameter or less, surface variable, but never with bluish  
 iridescence; FL  $2.5$ , or less, times LFW.....19
19. Transverse propodeal carina absent, oblique carina poorly developed,  
 basal zone narrowly rounded onto declivious face; second submarginal  
 cell on marginal cell longer than adjacent portion of first submarginal  
 cell; FL no more than  $2.3 \times$  LFW.....*polifolii* (Cockerell)  
 Transverse and oblique propodeal carinae well-developed, basal zone  
 abruptly declivious behind transverse carina; second submarginal cell  
 on marginal cell shorter than adjacent portion of first submarginal cell;  
 FL at least  $2.50 \times$  LFW.....20
20. Smaller species, HW not exceeding  $1.0$  mm.; basal, horizontal portion  
 of propodeum nearly twice as long as metanotum, little shorter than  
 scutellum .....*cookii* (Metz)  
 Larger species HW  $1.28$  mm. or more; basal, horizontal portion of  
 propodeum little, if any, longer than metanotum, about half as long as  
 scutellum.....*asininus* (Cockerell and Casad)
21. First tergite finely, sparsely punctate, the punctures often obscured by  
 dense tessellation .....22  
 First tergite coarsely, closely punctate, surface usually shining, punctures  
 always clearly defined.....23
22. First tergite densely tessellate, rather dull, the punctures very obscure;  
 lateral face marks ending abruptly at level of upper margin of antennal  
 sockets (fig. 8K) or narrowly extended along inner orbits; labrum  
 black or with median macula; flagellar segments beyond second slightly  
 longer than broad.....*calvus* (Metz)  
 First tergite shining, the punctures distinct; lateral face marks slightly  
 expanded above, and ending well above level of upper margin of  
 antennal sockets (fig. 9F); labrum wholly yellowish; flagellar segment  
 beyond second at least as broad as long ..*megalotis* (Swenk and Cockerell)
23. COD  $0.85 \times$  BCW; supraclypeal quadrangle distinctly wider than long;  
 lateral face marks short, ending at or below upper margin of antennal  
 sockets; supraclypeal area usually immaculate, but sometimes with an  
 obscure, irregular macula.....*nevadensis* (Cockerell)  
 COD at least equal to BCW; supraclypeal quadrangle often as long as  
 wide; lateral face marks usually ending well above level of upper margin  
 of antennal sockets; supraclypeal area usually with a large, quadrate

- macula .....24
24. COD 1.45 x BCW or less; HW less than 1.2 mm.; BCW 1.20-1.25 x  
CAD .....*wootoni* (Cockerell)  
COD :: BCW variable; HW more than 1.3 mm.; BCW :: CAD  
variable .....25
25. BCW less than CAD; COD more than BCW; sides of face usually  
strongly depressed below (fig. 8F).....*coloradensis* (Cockerell)  
BCW equal to or exceeding CAD; COD = BCW; sides of face never  
depressed below.....26
26. CAD more than BCW; supraclypeal mark always present distinctly  
quadrate; lateral face marks narrowed toward inner eye margin (fig.  
8J) .....*timberlakei* Snelling  
CAD = BCW; supraclypeal mark often reduced or absent; lateral face  
marks ending broadly above (fig. 8I).....*lunicraterius* Snelling

*Hylaeus (Paraprosopis) wootoni* (Cockerell)

Figures 7A; 8A; 10B; 11E.

*Prosopis wootoni* Cockerell, 1896. Psyche 7 (sup.): 26. ♂.

*Prosopis divergens* Cockerell, 1896. *Op. cit.*: 29. ♂. NEW SYNONYM.

*Prosopis wootoni*, Metz, 1911. Tarns. Amer. Ent. Soc. 37:144.

*Prosopis cookii* Metz, 1911. Trans. Amer. Ent. Soc. 37:139-141. ♀, not

♂.

*Hylaeus wootoni*, Cockerell and Sumner. Amer. Mus. Nov. 490:6.

*Hylaeus divergens*, Cockerell and Sumner. *Op. cit.*: 7-8.

*Hylaeus perparvus* Cockerell and Sumner, 1931. *Op. cit.*: 10-12. ♂.

NEW SYNONYM.

This is one of the more widely distributed species of the subgenus *Paraprosopis*. Throughout its range it varies considerably in both size and structure; one of these variants was named by Cockerell (*H. divergens*). Metz reduced the name to the synonymy of *H. wootoni*, but twenty years later Cockerell and Sumner resurrected it on the basis of supposed genitalic differences as well as a slight difference in the shape of the lateral face marks. These claimed differences will not hold up when one considers the range of variation in a long series of specimens from many localities. Thus, one finds specimens with the genitalic characters of *H. wootoni* and the face marks of *H. divergens*, and vice versa. Furthermore, these varying combinations are usually found to occur together in a single area. The differences noted are therefore considered merely to be due to variation in the range exhibited by a single species, *H. wootoni*. Unless there are other, more stable, characters which I have not discovered, there seems to be no reason for the continued recognition of *H. divergens*.

I have examined the types of *H. cookii*, which are in the collection of

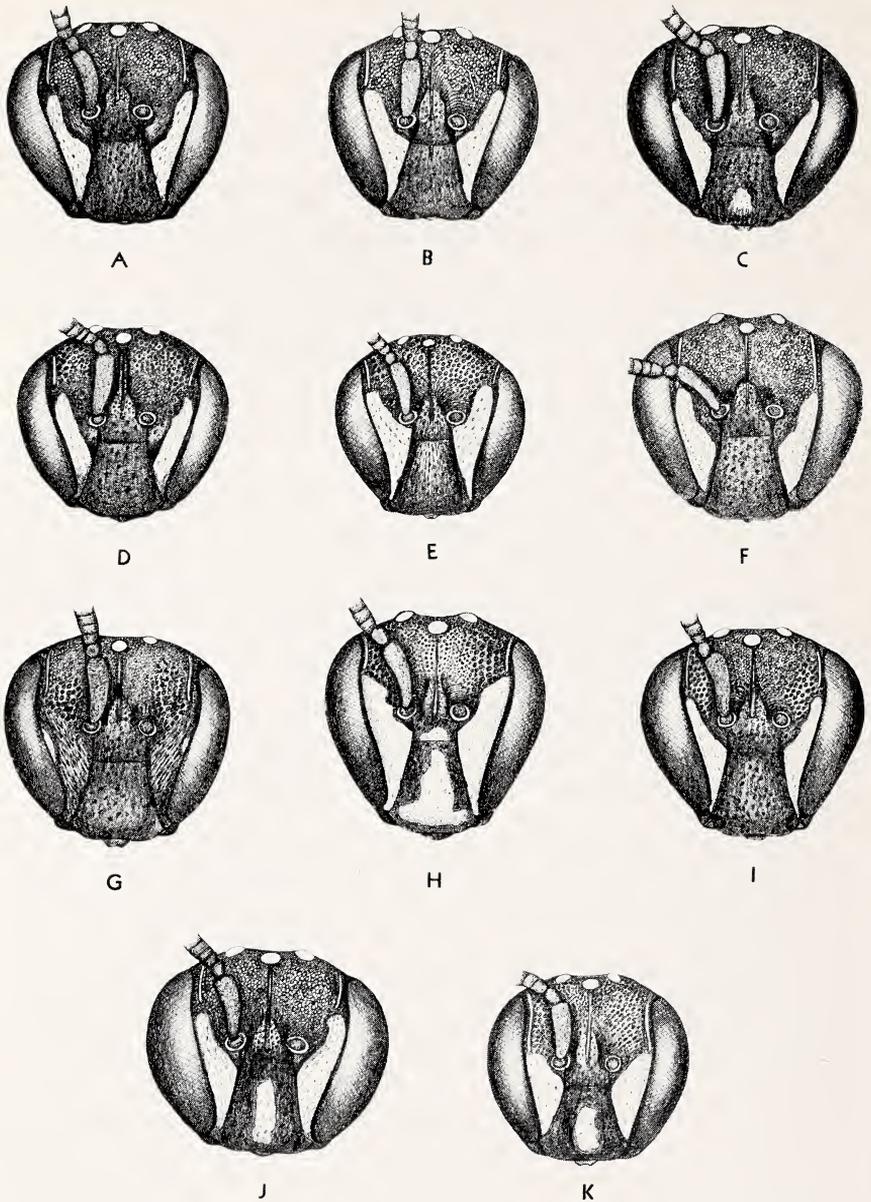


Figure 7. *Hylaes* (*Paraprosopis*) spp., female faces: A, *H. wootoni*; B, *H. floridanus*; C, *H. polifolii*; D, *H. nevadensis*; E, *H. cookii*; F, *H. coloradensis*; G, *H. personatellus*; H, *H. sonorensis*; I, *H. lunicraterius*; J, *H. timberlakei*; K, *H. calvus*. Figures by Ruth A. DeNicola.

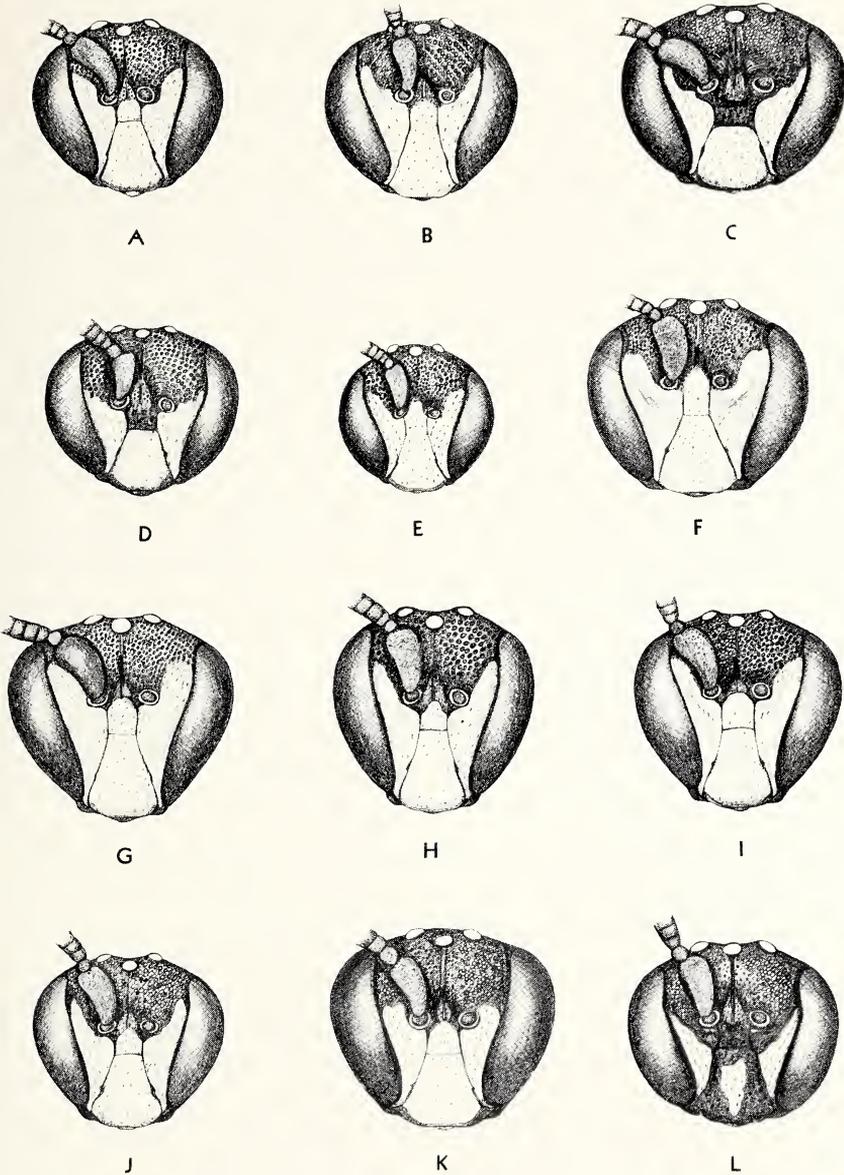


Figure 8. *Hylaeus* (*Paraprosopis*) spp., male faces: A, *H. wootoni*; B, *H. floridanus*; C, *H. polifolii*; D, *H. nevadensis*; E, *H. cookii*; F, *H. coloradensis*; G, *H. personatellus*; H, *H. sonorensis*; I, *H. lunicraterius*; J, *H. timberlakei*; K, *H. calvus*; L, *H. polifolii*, melanic form. Figures by Ruth A. DeNicola.

P. H. Timberlake, and find that the female allotype cannot be separated from that sex of *H. wootoni*, although the type male represents a valid species (see below).

The holotype male of *H. perparvus* Cockerell and Sumner has been examined. This specimen is a typical male of *H. wootoni*. The supposed differences in the genitalia are due to distortion which resulted from extreme flattening during the preparation of the slide. The distal portions of the lateral wings of the eighth ventrite are curled upward on the mount; this segment is at the edge of the balsam and difficult to see clearly. The ninth ventrite falls well within the range of variation attributed to *H. wootoni*.

Specimens have been examined from the following localities: *UNITED STATES*. *Nebraska* (Monroe Can. in Sioux Co.; UN), *Colorado*, *New Mexico*, *Arizona*, *Utah* (Emigration Can. and Big Cottonwood Can. in Salt Lake Co., Ogden; UCD), *Nevada*, *California*, *Oregon* (Tumalo Res. and Sisters in Deschutes Co.; UCD, CIS), *Idaho* (Craters of the Moon, Moscow Mts., Starkey, Ahsahke, 8 mi. E., Whitebird, 7 mi. N., Rock Cr., 12 mi. S., in Twin Falls Co., Twin Spr., 2.5 mi. W., Emery Can. in Cassia Co.; UCD, UI), *Wyoming* (Little Goose Can. near Sheridan; AMNH, CU). *MEXICO*. *Chihuahua* (Madera, San Jose de Babicora; AMNH). *CANADA*. *British Columbia* (Revelstoke; CU).

*Hylaeus (Paraprosopis) floridanus* (Robertson)

Figures 7B; 8B; 10C; 11F.

*Prosopis floridanus* Robertson, 1893. Trans. Amer. Ent. Soc., 20:273. ♀.

*Prosopis eulophi* Robertson, 1905. Canad. Ent., 37:236. ♀ ♂.

*Prosopis modestus*, Metz, 1911. Trans. Amer. Ent. Soc., 37:121. (in part)

*Hylaeus (Paraprosopis) packardi* Mitchell, 1951. Jour. E. Mitchell Sci. Soc., 67:244. ♂; Mitchell, 1960. N. Car. Agr. Exp. Sta. Tech. Bul., 141:62, 77. **NEW SYNONYMY.**

*Hylaeus (Paraprosopis) floridanus*, Mitchell, 1960. *Op. cit.*, 61, 62, 77-78; figs. 11, 12, 14. ♂ ♀.

I have examined the paratype of *H. packardi* and find that, aside from the immaculate pronotal collar and tegulae, it does not differ sufficiently from *H. floridanus* to justify specific status. Since such maculations are highly variable within this subgenus I do not feel that this form can be considered a subspecies either. While I have seen no other specimens with the immaculate pronotal collar, I have seen some with the tegular spot absent; it is commonly greatly reduced.

This species is so far known from the eastern United States, from Maine to Florida. A westward extension occurs along the Great Lakes as far as Minnesota.

*Hylaeus (Paraprosopis) nevadensis* (Cockerell)

Figures 7D; 8D; 10D; 11H.

*Prosopis nevadensis* Cockerell, 1896. Psyche 7 (sup.): 32. ♂.*Prosopis nevadensis*, Metz, 1911. Trans. Amer. Ent. Soc. 37:148.*Hylaeus oregonensis* Bridwell, 1919. Proc. Haw. Ent. Soc. 4:160-161.

♂ ♀. NEW SYNONYMY.

Bridwell based *H. oregonensis* on the lack of hairs on the eighth ventrite of the male, which he stated was like that of *H. calvus* (Metz). I have examined the holotype specimen, which is in the United States National Museum, and the paratype male. An examination of the eighth ventrites of these specimens convinces me that there is no justification for continued recognition of this form. The presence or absence of hairs on this segment appears to be a variable feature in *H. nevadensis* and I have seen many degrees of expression in specimens from widely scattered areas. In all other features *H. oregonensis* agrees with material of a more typical nature. The paratype female is inseparable from *H. nevadensis*.

This species occurs at moderate elevations in *California, Nevada, Oregon* (Mt. Jefferson, Grayback Camp in Josephine Co., Union Cr. in Jackson Co.; USNM, UCD), *Washington* (Seattle; UC), *Idaho* (Troy, Craters of the Moon, Whitebird, 7 mi. N., Athol, Granite, Nampa; UCD, UI), and *British Columbia* (Lilleoet, Robson, Summerland; CU, CNC).

*Hylaeus (Paraprosopis) coloradensis* (Cockerell)

Figures 7F; 8F; 10F; 11J.

*Prosopis coloradensis* Cockerell, 1896. Psyche 7 (sup.): 7. ♂.*Prosopis coloradensis*, Metz, 1911. Trans. Amer. Ent. Soc. 37:141. ♂ ♀.*Hylaeus coloradensis*, Cockerell and Sumner, 1931. Amer. Mus. Nov. 490:6. ♀ (in part).

Specimens examined are from the following states and Canadian provinces: *UNITED STATES*. *Wyoming* (Yellowstone Natl. Park; AMNH), *Colorado, Utah, New Mexico, Arizona, Nevada, California, Idaho* (Whitebird, 7 mi. N., Leadore; UI), *Washington* (Mt. Constitution, Pullman, Colfax; CAS, UC). *CANADA*. *British Columbia* (Revelstoke; CU).

*Hylaeus (Paraprosopis) personatellus* (Cockerell)

Figures 7G; 8G; 10I; 11K.

*Prosopis personatella* Cockerell, 1915. Annals and Magazine of Natural History (ser. 8) 16:485. ♀.

This species was described from a single female from Corona, Colorado, a locality which I have been unable to locate. Cockerell remarked, however, that the collection was made above timber-line which suggests a high altitude. The species has remained virtually unknown since that time although (Linsley, 1951) added California to the distribution. During this study I have seen few

specimens which I can assign to this species, the type of which I have examined at the U.S. National Museum.

The females which I assign to this species all agree more or less closely with Cockerell's original description and with the type. The lateral face marks are commonly absent; when present they are greatly reduced, restricted to an irregular stripe or blotch along the lower inner orbits. Since females of other species of *Paraprosopis* taken in the same area frequently also have reduced face marks, this character alone is of little value. The pronotal collar seems always to be immaculate; the pronotal lobes and tegulae are maculate or not. As a rule, only the hind tibiae have a yellow basal spot, although some have such a mark on the fore tibiae.

The females most closely resemble those of *H. coloradensis*, to which this species appears to be related. They may be separated from that species by the distinctly flattened scutellum which is distinctly more shining than the mesoscutum and with fine, well-separated punctures. The metanotum, too, is flattened. As in *H. coloradensis*, it is dull and densely tessellate, but has distinct, well-separated punctures about equal to those of the scutellum. Females from areas where this species occurs together with *H. coloradensis* differ from that species also in having the erect hairs of the mesoscutum very sparse and short, so that they are hardly distinguishable from the reclinate hairs. These erect hairs are much shorter, usually no more than one-third as long, than those of the scutellum. In the sympatric females of *H. coloradensis* the erect mesoscutal hairs are abundant, and are usually as long, or nearly so, as those of the scutellum.

The presumed male of this species is similar to that of *H. coloradensis* but the sides of the face are not depressed as in that species. There are tangible differences in head shape as may be seen upon comparing figures 8F and 8G. Although the eyes are apparently more strongly convergent below in *H. personatellus* this is not actually the case, as the ratios are very nearly identical in the two species. The greater eye length of *H. personatellus* may be used as a convenient factor. In this species the eye is 3.4 times its greatest width but twice as long as the lower interorbital distance. In *H. coloradensis* the eye is 3.8 times longer than its greatest width, but only about 1.7 times longer than the lower interorbital width. The few males of *H. personatellus* which I have seen are all more densely pubescent on the thoracic dorsum than is true of *H. coloradensis*. The difference, however, is a matter of degree, and I do not attribute much significance to this character. Otherwise, the males are very similar externally and no reliable differences between them have been discovered.

In addition to the type I have seen the following additional specimens: COLORADO. 1 ♀, Ouray, 7500-8000', 1-15 July 1897 (H. F. Wickham; LACM). CALIFORNIA. 1 ♀, Strawberry Valley, El Dorado Co., 16 Aug. 1912 (E. C. Van Dyke; CAS); 1 ♀, Sonora Pass, Tuolumne Co., 4 Aug. 1948

(P. D. Hurd & J. W. MacSwain; CIS); 1 ♀, Blue Canyon, Sonora Pass, Tuolumne Co., 10 Aug. 1960 (J. W. MacSwain; CIS); 1 ♀, same locality, 30 Aug. 1960 (P. D. Hurd; CIS); 9 ♂♂, Tioga Pass, 7 mi. E., Mono Co., 15 July 1961 (H. V. Daly, G. I. Stage; CIS); 1 ♂, Tom's Place, 1 mi. W., Mono Co., 13 Aug. 1957 (D. D. Linsdale; CIS), on *Eriogonum elatum*; 4 ♂♂, 1 ♀, near Mono Pass, 12,000', Inyo Co., 15 Aug. 1957 (C. D. MacNeill; CAS); 5 ♀♀, Mono Pass, Inyo Co., 13 Aug. 1957 (J. Powell, D. D. Linsdale; CIS), one on *Pentstemon newberryi*.

*Hylaeus (Paraprosopis) polifolii* (Cockerell)

Figures 7C; 8C; 8L; 10G; 11G.

*Prosopis polifolii* Cockerell, 1901. *Canad. Ent.*, 33:281. ♂. Metz, 1911. *Trans. Amer. Ent. Soc.*, 37:146-148.

*Hylaeus polifolii catalinensis* Cockerell, 1938. *Annals and Magazine of Natural History*, ser. 11, 2:150. ♂♀. NEW SYNONYMY.

This common California species is closely related to *H. wootoni* and females are apt to be very difficult to separate in the absence of males. The two species are largely allopatric with overlaps occurring only in some areas of southern California and along the western portions of the Sierra Nevada. Females of *H. polifolii* which possess the preapical clypeal macula are easily recognized; I have never seen specimens of *H. wootoni* so maculated. The population of *H. polifolii* present on Santa Catalina Island, Los Angeles Co., Calif., was given a varietal name by Cockerell; in the females of this population, the clypeal macula seems always to be present. Populations from mainland California may or may not have a maculate clypeus, but this feature is subject to much variation within a given sample and is, moreover, not correlated with distribution. I see nothing to be gained by recognition of this insular form and have synonymized it under the nominate form.

The facial maculae of the males, too, are subject to considerable variation. In what I consider to be the basic or "typical" pattern, the clypeus is entirely yellow, the supraclypeal area is black, and the lateral face marks terminate above at a point about equal to a socket diameter above the antennal sockets. One variant form, very rare, exhibits an obscure maculation of variable size on the supraclypeal area. In the second variant form, which is fairly common, the clypeus becomes darkened along the lateral margins; this infuscation frequently encroaches so extensively onto the clypeus that the maculation is reduced to an erect median stripe.

*Hylaeus (Paraprosopis) cookii* (Metz)

Figures 7E; 8E; 10E; 11I.

*Prosopis cookii* Metz, 1910. *Trans. Amer. Ent. Soc.* 37:139-141. ♂, not ♀.

As indicated above, the female assigned by Metz to this species is *H.*

*wootoni*; the male type, now in the collection of the University of California at Riverside, is from Filmore Canyon, New Mexico, collected on Aug. 27 by T. D. A. Cockerell. Another male, with identical data is in the collections of the Los Angeles County Museum.

Until the present study was undertaken *H. cookii* was known only from the type. It is doubtful if this species could have been recognized from the original description, or the figures of the genitalia and hidden ventrites as illustrated by Metz. When I was able to examine the type, I found it to be identical with a species which P. H. Timberlake and I had independently assumed to be undescribed. Because of the inadequacies of the original description, the species is redescribed and the hidden ventrites illustrated.

*Diagnosis*.—Male: Small species, head width not exceeding 1 mm.; scape less than half as wide as long; lateral face marks ending well above level of antennal sockets; frontal punctures coarse, distinct; mesoscutal punctures distinctly finer than those of frons; punctures of tergite I as coarse as those of mesoscutum, those of tergite II finer, dense on both segments. Female: Small, head width not exceeding 1.3 mm.; frontal punctures coarse, distinct; mesoscutal punctures equal to those of frons; metanotum not rugulose, with distinct punctures; abdominal punctation similar to that of male, but punctures finer, tergite III distinctly, though finely, punctate.

Male.—Integument black, except the following pale creamy-white: clypeus; supraclypeal mark; lateral face marks, ending acutely on eye margin well above level of antennal sockets; medially interrupted stripe on pronotal collar; pronotal lobe; spot on anterior half of tegula; small apical spot on all femora; stripe on anterior tibiae; elongate basal and small apical spots on middle and hind tibiae; basitarsal and mediotarsal segments. Apical tarsal segments light ferruginous; tibial spurs whitish. Wings whitish-hyaline, veins and stigma light ferruginous. Erect pubescence whitish.

*Head*: UFD 0.76 x FL; LFD 0.52 x UFD; OCD 1.06-1.21 x TFD; basal width of clypeus 0.77 x distance from laterobasal angle to eye margin; distance between antennal sockets about equal to a socket diameter, distance from sockets to eye margin about 0.85 x a socket diameter. Maximum scape width about 0.42 x maximum length; minimum length of first flagellar segment about one-half length of second. Maculate portions of face slightly shining, finely punctate, those of clypeus separated by one-half to a full puncture diameter, those of lateral part of face somewhat elongate, linearly arranged, spacing variable; frons coarsely, contiguously punctate, the punctures distinct, the frons somewhat bulging on either side of midline. Vertex sharply raised above tops of eyes, coarsely punctate, the punctures crowded and less sharply defined than on frons.

*Thorax*: Mesoscutum dull, closely coarsely punctate, the punctures slightly larger than those of frons, separated by one-third to one-half a puncture diameter; mesoscutellum slightly shining, punctures about equal to those

of mesoscutum, separated by one-half to a full puncture diameter; metanotum dull, densely tessellate, with punctures finer than those of mesoscutum, separated by about a puncture diameter; mesopleurae dull, tessellate, punctures about equal to those of mesoscutum, separated by about one-third to one-half a puncture diameter. Basal area of propodeum areolate; lateral areas coarsely punctate, the punctures poorly defined; transverse carina poorly developed, oblique carina absent; disc densely tessellate, with coarse punctures.

*Abdomen*: Tergite I shining, smooth, densely punctate, the punctures smaller than those of mesoscutum, separated by one-half to a full puncture diameter; tergite II more finely closely punctate, apical one-third (approximately), depressed, with scattered micropunctures, apical margin slightly reflexed; tergite III more finely, sparsely punctate; apical ventrites as illustrated.

Length, to apex of second tergite, 3.0-3.4 mm.; of forewings, 2.45-2.9 mm.

Female.—Similar to male in essential features, except as follows: clypeus and supraclypeal area dark, lateral face marks more rounded above; UFD 0.72-0.80 x FL; LFD 0.55-0.61 x UFD; OCD 1.02-1.07 x TFD; basal width of clypeus equal to distance from laterobasal angle to eye margin; distance between antennal sockets about 1.5 x a socket diameter; distance from sockets to eye margin slightly exceeding a socket diameter.

Length, to apex of second tergite, 4.0-4.3 mm.; of forewings, 3.2-3.5 mm.

New records.—*Arizona*: 1 ♀, Rincon Mtn., IX-16-1937 (E. D. Ball); 11 ♂♂, Stockton Peak, Pinaleño Mts., V-20-1954 (F. Werner), on *Fallugia*; 6 ♀♀, Madera Can., Sta. Rita Mts., IX-28-1956 (F. Werner), swept from *Aplopappus* and *Eriogonum*; 2 ♂♂, Sta. Catalina Mts., V-15-1955 (G. D. Butler); 1 ♀, Ramsey Can., Huachuca Mts., IX-8-1955 (F. G. Werner and G. D. Butler), on *Petalostemum candidum*; 1 ♀, west slope Patagonia Mts., V-21-1955 (G. D. Butler), on *Prosopis*; 3 ♂♂, 15 ♀♀, same locality, IX-7-1955 (G. D. Butler and F. G. Werner; all UA), on *Erigeron canadensis*; 7 ♀♀, Sycamore Can., Santa Cruz Co., IX-7, 8-1961 (G. I. Stage); 5 ♀♀, Southwest Research Station, IX-3, 4-1959 (G. I. Stage; all LACM); 1 ♂, same locality, V-14-1956, 1 ♀, same locality, VI-14-1956, 1 ♀, same locality, VII-19-1956 (all M. Statham); 6 ♀♀, Paradise, 4 mi. W., IX-9-1950 (W. Gertsch and M. Cazier; all AMNH); 1 ♀, 7 mi. W. Onion Saddle, Chiricahua Mts., Cochise Co., IV-10-1954, on *Haplopappus gracilis*; 2 ♀♀, Cave Cr., 5400 ft., Chiricahua Mts., Cochise Co., IX-8-1958, on *Solidago*; 4 ♀♀, Prescott, VI-27-1932, on *Asclepias tuberosa*; 1 ♂, 5 ♀♀, same locality, VIII-30-1930, on *Eriogonum*; 1 ♂, 1 ♀, same locality and host, VII-31-1930 (all P. H. Timberlake; all UCR); 1 ♂, Painted Desert, Apache Co., VIII-18-1958 (G. I. Stage; UCR), on *Eriogonum aureum*. *Nevada*: 1 ♂, Eastgate, 1 mi. W., Churchill Co., VIII-11-1958 (E. G. Linsley; CIS), at honeydew on *Chrysothamnus* sp. *California*: 12 ♂♂, 2 ♀♀, Paradise Camp,

Mono Co., V-7-1960 (A. E. Menke; UCD); 1 ♂, 1 ♀, same locality and date (F. D. Parker; UCD); 1 ♂, Cottonwood Spr., Riverside Co., IV-12-1950 (W. F. Barr; UI); 10 ♂♂, Apple Valley, San Bernardino Co., V-10, 12-1955 (W. R. M. Mason; CNC); 5 ♂♂, 3 ♀♀, Ivanpah, 12 mi. SE., San Bernardino Co., V-1-1956 (M. Wasbauer); 1 ♂, same data, on *Salvia*; 1 ♂, same locality and date (B. J. Adelson), on *Salvia*; 4 ♂♂, same locality and date (P. D. Hurd; all CIS), 2 on *Sphaeralcea*; 2 ♂♂, same locality and date, on *Rhus trilobata*; 1 ♂, same locality and date, on *Salvia vitosa*; 2 ♀♀, same locality and date, on *Sphaeralcea ambigua*; 1 ♂, 3 ♀♀, Cactus Flat, 6000 ft., San Bernardino Mts., IX-1-1936, on *Chrysothamnus stenophyllus*; 1 ♀, Morongo Valley, San Bernardino Co., IX-29-1944, on *Eriogonum plumatella*; 3 ♀♀, same locality, X-5-1934, on *Gutierrezia lucida*; 1 ♀, same locality, X-14-1934, on *G. lucida*; 2 ♀♀, Yucca Valley, San Bernardino Co., IX-28-1944, on *G. lucida*; 1 ♀, same locality and host, IX-30-1944; 1 ♀, Mt. Home Cr., San Bernardino Mts., 5000 ft., VIII-14-1934, on *Phacelia ramosissima*; 2 ♀♀, Andreas Cyn., Riverside Co., X-27-1934, on *Solidago californica*; 1 ♀, Piñon Flat, San Jacinto Mts., VI-4-1934, on *Nolina perryi*; 1 ♀, same data except, on *Eriogonum fasciculatum*; 1 ♂, Whitewater, Riverside Co., IV-22-1928, on *E. fasciculatum*; 7 ♀♀, Whitewater Cyn., Riverside Co., X-14-1951, on *Lepidospartum*; 8 ♀♀, Lone Pine Cyn., 6000 ft., San Gabriel Mts., VII-21-1936, on *Tetradymia canescens*; 1 ♀, same locality and date, on *E. fasciculatum*; 1 ♂, Surprise Cyn., Panamint Mts., Inyo Co., IV-25-1957 (all P. H. Timberlake; all UCR), on *Eriogonum inflatum*.

*Hylaeus (Paraprosopis) sonorensis* Cockerell

Figures 7H; 8H; 10K; 11L.

*Hylaeus sonorensis* Cockerell, 1924. Proc. Calif. Acad. Sci. (4) 12:530-531. ♀.

*Hylaeus sonorensis* var. *melanorhinus* Cockerell, 1924. *Op. cit.* :531. ♀.  
NEW SYNONYMY.

*Diagnosis*: Although the superficial appearance of this species is quite similar to that of *H. asininus* (Cockerell & Casad), the shape of ventrites VIII and IX of the male ally it to *H. wootoni* (Cockerell). Both sexes differ from *H. asininus* in the more elongate face, denser and finer thoracic punctures and microscopic punctures of tergite II. From *H. wootoni* this species differs in the longer, narrower face, more finely punctate abdomen and more extensive maculae.

*Male*.—Integument black, except the following pale creamy-white; elongate spot at base of mandibles; labrum, clypeus; elongate supraclypeal mark; paraocular areas and along inner orbits, ending acutely on level midway between anterior ocellus and antennal sockets; entire transverse stripe on pronotal collar; pronotal tubercles; anterior half of tegulae; apical spot on all femora; entire fore tibiae except irregular blotch on inner surface; basal half

of middle tibiae; basal three-fifths of hind tibiae; all basitarsi and first hind mediotarsal segment. Underside of flagellum yellowish-ferruginous. Medio- and distitarsal segments brownish; wings clear hyaline, veins and stigma brownish. Pubescence all pale whitish, on abdomen suberect and obscure.

*Head*: UFD 0.64-0.65 x FL; LFD 0.59-0.60 x UFD; OCD 1.19-1.21 x TFD; clypeus distinctly narrower basally than distance from latero-basal angle to eye margin; distance between antennal sockets less than socket diameter, distance from sockets to eye margins equal to socket diameter; clypeus, supra-clypeal area and maculate facial area dull, densely tessellate, with scattered obscure punctures; nonmaculate areas with large, subcontiguous punctures, the densely tessellate interstices slightly shining; genae shining, punctures small, separated; minimum length of first flagellar segment about one-half length of second.

*Thorax*: Outer margin of fore coxae slightly convex; mesopleural punctures about equal to those of frons, mostly separated by about one-half a puncture diameter, the tessellate interstices more shining than frons; mesoscutal punctures equal to those of frons, subcontiguous, interstices slightly shining; mesoscutellar punctures larger than mesoscutal, spacing variable, but denser medially; metanotum not at all shining, very densely tessellate, with a few, coarse, deep punctures. Basal area of propodeum with a few irregular striae, the lateral ones transverse; latero-basal area roughened, shining, impunctate; lateral area slightly shining, with coarse, close punctures; oblique carina absent; lateral carina feebly developed, absent above lower half of disc.

*Abdomen*: Tergite I micro-tessellate, slightly shining, with fine punctures mostly separated by about a puncture diameter; tergite II more distinctly tessellate, punctures very fine, obscure, separated by about a puncture diameter; remaining tergites tessellate, slightly shining, with a few, scattered, obscure punctures; ventrites VIII and IX as in figures 10K and 11L.

*Measurements*: Body length (front of vertex to apex of second tergite), 3.5 to 3.8 mm.; forewing length, 2.9 to 3.1 mm.

*Female*.—Similar to male in sculpture and color, except as follows: mandibles and labrum entirely dark; clypeus with  $\perp$ -shaped macula; supra-clypeal area with small irregular mark; lateral face marks more rounded above; facial foveae ending about one-third of distance between eyes and lateral ocelli; UFD 0.69-0.70 x FL; LFD 0.68-0.70 x UFD; OCD 0.94-0.96 x TFD; distance between latero-basal clypeal angle and inner eye margin 0.75 times basal width of clypeus; distance between antennal sockets equal to a socket diameter and to distance between sockets and eyes. Fore basitarsus concolorous with medio- and distitarsi, hind basitarsus dark at apex. Punctures of tergite I a little finer and more separated than in male.

*Measurements*: Body length (front of vertex to apex of second tergite), 4.5 to 4.7 mm.; forewing length, 3.4 to 3.7 mm.

Both forms of *H. sonorensis* were described by Cockerell from single

females from Guaymas, Sonora, Mexico; I have examined the types of both at the California Academy of Sciences and can affirm that they are conspecific. Although Cockerell claimed this species to be related to those of tropical Mexico, this is not true. On the basis of currently available specimens *H. sonorensis* ranges from the Death Valley region of California and Nevada into southern Arizona, thence south into Sonora, Mexico at least as far as Guaymas. Another extension intrudes into Baja California at least as far as Bahia de Los Angeles.

The variety *melanorhinus* was distinguished by the lack of a supraclypeal mark and the reduction of the clypeal macula to a transverse apical band with a median upward extension. In the "typical" form the apical third of the clypeus was pale yellowish with a broad, cuneate upward extension. Such variants are common in the series of females available and there seems to be no good reason for the recognition of these variant forms, since the variations are not correlated with distribution.

Distribution.—*MEXICO. Baja California del Norte*: 2 ♂♂, Bahia de los Angeles, May 14, 15, 1949 (R. C. Dickson; UCR), one on *Prosopis glandulosa*. *Sonora*: 1 ♀, Guaymas, April 8, 1921 (E. P. Van Duzee; CAS, type of *H. s. melanorhinus*); 1 ♀, Guaymas, April 10, 1921 (E. P. VanDuzee; CAS, type of *H. sonorensis*). *UNITED STATES. Arizona*: 4 ♂♂, 2 ♀♀, Alamo Cyn., Organ Pipe Cactus Natl. Mon., April 15, 1955 (G. D. Butler and F. G. Werner; UA), on mesquite; 1 ♀, same data, except on *Encelia* (UA); 1 ♀, Sabino Cyn., Santa Catalina Mts., May 26, 1962 (F. D. Parker and L. A. Stange; UCD). *Nevada*: 1 ♂, Aurora, 7500', Mineral Co., August 9, 1939 (W. D. Pierce; LACM), on *Scrophularia californica*. *California*: 3 ♂♂, 6 ♀♀, Surprise Cyn., Panamint Mts., Inyo Co., April 22, 1957, on *Eriogonum inflatum*; 2 ♂♂, 9 ♀♀, same locality and host, April 23, 1957; 1 ♂, same locality, April 23, 1957, on *Stanleya pinnata*; 3 ♂♂, 16 ♀♀, same locality, April 25, 1957, on *E. inflatum*; 1 ♂, same locality, April 25, 1957, on *Prosopis*; 2 ♂♂, same locality, April 25, 1957, on *S. pinnata*; 2 ♂♂ same locality, April 28, 1957, on *S. pinnata*; 2 ♂♂, same locality, April 29, 1957, on *S. pinnata* (all P. H. Timberlake; UCR); 14 ♀♀, 9 ♂♂, same locality, April 24, 1957 (P. D. Hurd and G. I. Stage), on *E. inflatum*; 2 ♂♂, same locality, April 28, 1953 (P. D. Hurd); 3 ♂♂, same locality and date (G. A. Marsh), one on *Eucnide urens*, two on *Eriogonum* sp.; 1 ♀, Furnace Cr., Death Valley, Inyo Co., March 3, 1953 (J. W. MacSwain); 1 ♀, Cronise Valley, San Bernardino Co., April 29, 1956 (M. Wasbauer), on *Prosopis*; 2 ♂♂, Plaster City, 15 mi. N., Imperial Co., March 27, 1961 (C. A. Toschi; all CIS).

*Hylaeus (Paraprosopis) lunicraterius*, new species

Figures 7I; 8I; 10H; 12A.

This species is very closely related to the following species. The males

are especially similar in details of the hidden ventrites and genitalia.

*Diagnosis:* Female with head as broad as long; clypeus immaculate; facial foveae ending about one-third of distance between eyes and ocelli; mesopleural punctures separated by less than one-third a puncture diameter, uniform in size; propodeal disc roughened and with scattered oblique rugulae; punctures of first tergite dense, coarser than those of second. Male with head as broad as long; lateral face marks ending abruptly a little above level of antennal sockets; supraclypeal mark present; lower part of face coarsely punctate; apical portion of tergites II-VI broadly impressed, margins slightly reflexed.

*Male.*—Integument black, with pure white maculae as follows: clypeus; quadrate supraclypeal mark; lateral marks to a point ending about an antennal socket diameter above upper margin of antennal sockets; medially interrupted stripe on pronotal collar; pronotal lobe; anterior tegular spot; minute apical spot on all femora; complete stripe on anterior tibiae; basal and apical spots on mid and hind tibiae; all basitarsi, except small ferruginous apical spot; tibial spurs. Wings hyaline, veins and stigma brown. Scape entirely dark, flagellum light ferruginous beneath. Erect pubescence whitish.

*Head:* UFD 0.71-0.79 x FL; LFD 0.58-0.61 x UFD; OCD 1.05-1.17 x TFD. Distance from laterobasal clypeal angle to eye margin 1.3 times basal clypeal width; distance between antennal sockets slightly less than a socket diameter, distance from sockets to eye margins about equal to a socket diameter. Facial integument somewhat shining, maculate areas moderately coarsely punctate, punctures separated by one-third to three-fourths a puncture diameter on sides of face, the punctures somewhat elongate, linearly arranged; clypeal punctures more rounded, separated by about one-half a puncture diameter; frontal area slightly swollen, coarsely, closely punctate, the punctures for the most part clearly defined; vertex coarsely punctate laterally, the punctures a little larger than those of frons; ocellar triangle and occiput in middle dull, densely tessellate, contiguously punctate. Scape distinctly flattened, greatest width about one-half its length, median flagellar segments about as long as broad.

*Thorax:* Mesoscutal punctures a little smaller than those of clypeus, separated by half a puncture diameter or less; mesoscutellar punctures a little coarser, separated by about half a puncture diameter; metanotum densely tessellate and roughened, with a few obscure punctures; mesopleural punctures about equal to those of mesoscutellum, separated by about one-fourth a puncture diameter. Basal area of propodeum coarsely areolate, the areolae finer laterally; transverse and oblique carinae obsolescent; lateral area roughened, with some indistinct punctures, a few fine rugae below at the sides.

*Abdomen:* Tergite I shining, coarsely punctate, punctures separated by about a puncture diameter, with scattered micropunctures; tergite II more finely punctate, duller, punctures separated by one-half to three-fourths a

puncture diameter; apical one-third depressed, very finely and sparsely punctate, apical margin slightly reflexed; ventrites VIII and IX as illustrated (figures 10H and 12A).

Length, to apex of second tergite, 3.8-4.3 mm.; of forewings, 3.15-3.50 mm.

Female.—Integument black, except yellowish-white maculae as follows: lateral face marks, ending slightly above level of antennal sockets; interrupted stripe on pronotal collar; pronotal lobe; spot anteriorly on tegulae; minute apical spot on femora; basal spot on all tibiae; tibial spurs. Underside of flagellum light ferruginous. Erect pubescence whitish. Wings hyaline, veins and stigma brown. A very minute ferruginous to yellowish preapical spot sometimes present on clypeus.

*Head*: UFD 0.71-0.78 x FL; LFD 0.62-0.69 x UFD; OCD 0.81-0.92 x TFD. Basal margin of clypeus about 1.8 times as wide as distance from laterobasal angle to eye margin; distance between antennal sockets about 1.4 times a socket diameter; distance between sockets and eye margin slightly exceeding a socket diameter. Clypeus reticulate-lineolate, with fine punctures separated by a puncture diameter or more; supraclypeal area lineolate, with punctures separated by about a puncture diameter; maculate portions of face finely punctate, punctures somewhat elongate, linearly arranged; frontal punctures coarse, contiguous, becoming finer toward midline; occiput and ocellar triangle densely tessellate between coarse, close punctures; genae striatopunctate. Median flagellar segments broader than long.

*Thorax*: Mesoscutum dull, finely tessellate with punctures subequal to those of clypeus, separated by one-third a puncture diameter or less; mesoscutellar punctures about equal to those of mesoscutum, separated by about one-half a puncture diameter; metanotum somewhat granulose, punctures subequal to those of mesoscutum, separated by a puncture diameter or more; mesopleural punctures finer than those of clypeus, separated by about one-half a puncture diameter; propodeal basal area coarsely areolate, the areolae finer laterad; transverse carina present by poorly indicated, oblique carina barely evident; lateral areas strongly roughened; disc obliquely striolate.

*Abdomen*: Tergite I smooth, shining, finely punctate, punctures separated by a puncture diameter or more; tergite II smooth, shining, very finely punctate, punctures separated by one and one-half to two times a puncture diameter.

Length, to apex of second tergite, 3.95-4.35 mm., of forewings, 3.70-3.95 mm.

*Holotype* male, allotype female (Los Angeles County Museum of Natural History); Craters of the Moon National Monument, Idaho, Aug. 21, 1964 (D. S. Horning, Jr.), on *Chrysothamnus nauseosus*.

*Paratypes*, all from the type locality, collected by D. S. Horning, Jr., dates ranging from July 3 to Sept. 5: 23 ♂♂, 12 ♀♀. Host associations: *Chryso-*

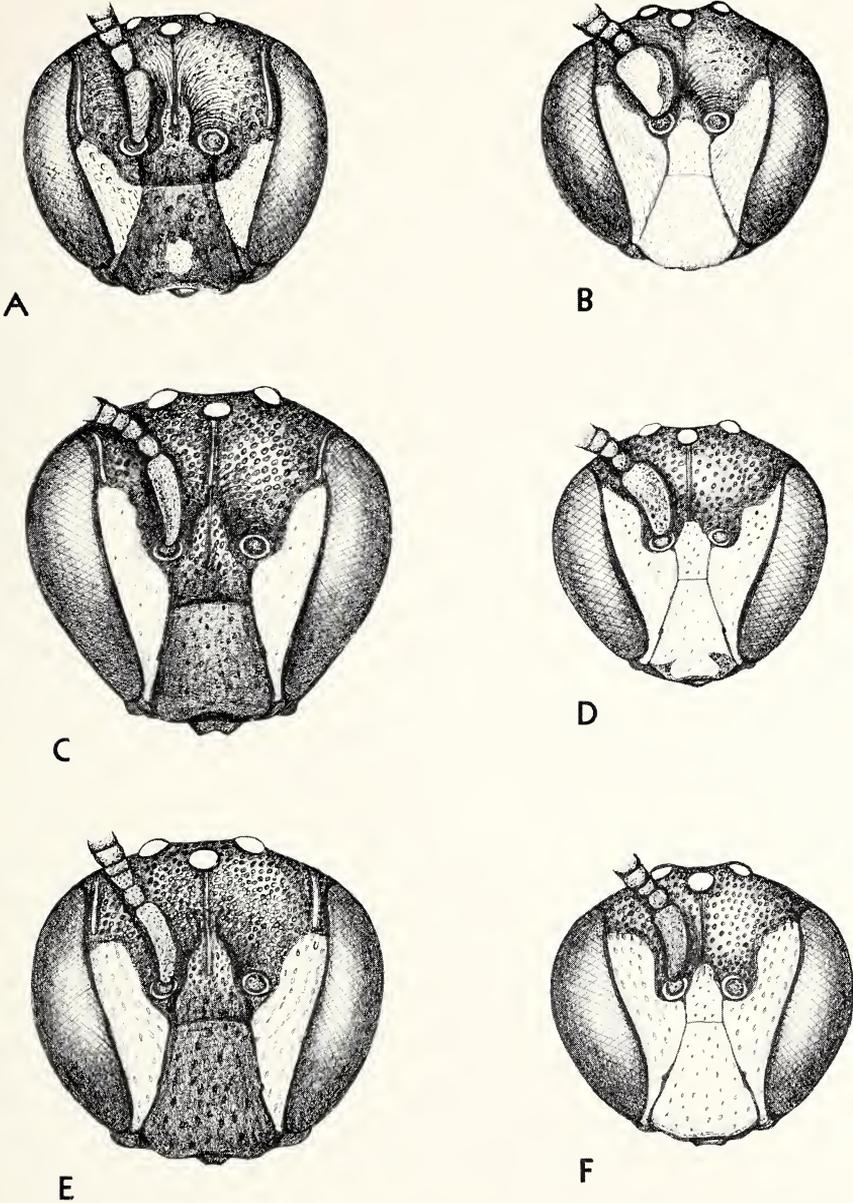


Figure 9. *Hylaeus* (*Paraprosopis*) spp., faces: A, *H. georgicus*, female; B, same, male; C, *H. asininus*, female; D, same, male; E, *H. megalotis*, female; F, same, male. Figures by Ruth A. DeNicola.

*thamnus viscidiflorus*, *C. nauseosus*, *Chamaebatiaria millefolium*, *Senecio serra*, *Eriogonum ovalifolium*, *Phacelia leucophylla* and *Populus tremuloides*; two males taken on Aug. 17, 1965 are marked "prey of Ph-2." Paratypes in United States National Museum, University of Idaho and the Los Angeles County Museum of Natural History.

The specific name for this species is derived from the type locality.

*Hylaeus (Paraprosopis) timberlakei* Snelling, NEW SPECIES

Figures 7J; 8J; 10J; 12B.

This species bears a strong resemblance to *H. calvus* in most features. The male differs from that of *H. calvus* externally in having the punctures on the dorsal surface of the first tergite sharply defined, the interspaces smooth and shining, while in *H. calvus* the punctures are obscured due to the strongly tessellated and roughened interspaces. The female of *H. timberlakei* has the declivity of the propodeum with coarse, oblique rugulae (absent or poorly defined in *H. calvus*) and the punctures of the first tergite are moderately dense and distinctly larger than those of the second tergite (sparse, finer than those of second tergite in *H. calvus*).

*Diagnosis:* Female with head broader than long; clypeus maculate; facial foveae ending slightly less than halfway between eyes and ocelli; punctures of mesopleura separated by more than a puncture diameter, uniform in size; rugulae of propodeal declivity coarse, obliquely directed toward mid-line; punctures of first tergite dense, distinctly larger than those of second tergite. Male with head slightly broader than long; lateral face marks ending rather broadly on eye margin about midway between level of antennae sockets and median ocellus; supraclypeal mark present; punctures on lower part of face coarse; apical margin of second tergite broadly impressed, very finely and sparsely punctate.

*Male.*—Integument black, with creamy-white maculae as follows: clypeus; triangular supraclypeal mark; lateral face marks, ending broadly on inner eye margins, about midway between level of antennal sockets and middle ocellus; pronotal collar, interrupted medially; spot on pronotal lobe; anterior spot on tegulae; small apical spot on all femora; complete outer stripe on anterior tibiae; basal and apical spots on middle and hind tibiae; all basitarsi (usually with distinct apical infuscation). Anterior medio- and distitarsi ferruginous, middle and hind medio- and distitarsi fuscous to black. Tibial spurs yellowish. Wings, hyaline, veins and stigma brownish. Scape all black; pedicel with reddish-yellow apical spot beneath; flagellum yellowish beneath, reddish-brown above. Erect pubescence whitish.

*Head:* UFD 0.70-0.77 x FL; LFD 0.50-0.61 x UFD; OCD 1.00-1.11 x TFD. Distance from latero-basal clypeal angle to eye margin 1.3 times basal clypeal width; distance between antennal sockets slightly more than a socket diameter, distance from sockets to eyes slightly more than a socket diameter.

Facial integument dull, maculate areas coarsely punctate, punctures separated by a puncture diameter or less; frontal area slightly swollen, coarsely rugosopunctate; vertex and genae coarsely contiguously punctate. Scape somewhat distinctly flattened, greatest width about one-half its length; median flagellar segments about as long as broad, or slightly longer.

*Thorax:* Mesoscutal punctures finer than those of vertex, separated by half a puncture diameter or less, interspaces tessellate and dull; punctures of mesoscutellum coarser than those of mesoscutum, about equal to those of vertex, separated by about half a puncture diameter on disc, apical one-fifth of the segment dull, densely rugosopunctate; metanotum dull, rugosopunctate; mesopleural punctures about equal to those of mesoscutellum, separated by one-fourth a puncture diameter or less. Basal area of propodeum areolate, the ridges sharply defined by very irregular; lateral area rugulose; disc rugulose laterally, with a few poorly defined oblique rugae medially; transverse carina present across basal area, oblique carina poorly defined. Outer margin of fore coxa subangulate basally to evenly convex.

*Abdomen:* Tergite I shining, densely punctate, punctures a little smaller than those of mesoscutum, separated by one-half to three-fourths a puncture diameter; punctures of tergite II a little finer, separated by about one-half a puncture diameter or less; apical one-third to one-fourth of tergite II depressed, brownish, transversely lineolate, with scattered very fine punctures; ventrites VIII and IX as illustrated (figures 10J and 12B).

Length, to apex of second tergite, 3.8 to 4.3 mm.; of forewings, 2.6 to 3.0 mm.

Female.—Integument black, except for yellow maculae as follows: median clypeal macula, varying from small preapical spot to broad vertical stripe, broad lateral face marks, ending slightly above antennal sockets; medially interrupted stripe on pronotal collar; large spot on pronotal lobe; triangular spot anteriorly on tegulae; basal spot on all tibiae. Underside of flagellum light reddish. Erect pubescence whitish. Wings hyaline, veins and stigma brownish.

*Head:* UFD 0.77-0.84 x FL; LFD 0.61-0.66 x UFD; OCD 0.81-0.91 x TFD. Basal margin of clypeus 1.5 times as wide as distance from laterobasal angle to inner margin; distance between antennal sockets 1.5 times a socket diameter; distance from socket to eye margin 1.3 times a socket diameter. Clypeus finely reticulate, with small punctures over most of the disc separated by about a puncture diameter, becoming denser, coarser, more elongate toward apical margin; supra-clypeal area lineolate, somewhat roughened above, with scattered obscure punctures; maculate portions of sides of face lineolate, with fine punctures separated by one-half to a full puncture diameter; frons coarsely, contiguously punctate, becoming finely, but very densely punctate on vertex, especially in ocellar triangle and behind; genal punctures obscure, a little larger than those of clypeus. Flagellar segments broader than long.

*Thorax*: Mesoscutum dull, finely tessellate with punctures finer than those of frons, separated by about one-half a puncture diameter on disc; mesoscutellum a little shinier, punctures variable, but mostly about same size as those of mesoscutum, some a little larger, mostly separated by about a puncture diameter; metanotum dull, rugulose; mesopleura bipunctate, *i.e.*, with punctures of two sizes, the larger ones equal to those of mesoscutum, punctures variably spaced, but most separated by about a puncture diameter. Basal zone of propodeum coarsely areolate; transverse, oblique and lateral carinae distinct; disc finely rugulose above, the rugulae becoming coarser, oblique, below. Outer margin of fore coxa evenly convex, without basal angulation or spine.

*Abdomen*: Tergite I shining, smooth, finely punctate, the punctures separated by a puncture diameter or more; tergite II shining, very finely reticulate, punctures finer than those of tergite I, separated by from one to one and one-half times a puncture diameter; remaining tergites increasingly more distinctly reticulate, with scattered micropunctures.

Length, to apex of second tergite, 4.5-5.1 mm.; of forewings, 3.5-4.0 mm.

*Holotype*: Male (Los Angeles County Museum of Natural History); Forest Hill, 12 mi. E., Placer Co., Calif., June 24, 1962 (R. R. Snelling), on *Ceanothus*. Allotype: Female (University of California, Riverside); Tyler, 4.5 mi. W., Nevada Co., Calif., Sept. 27, 1956 (P. H. Timberlake), on *Haplopappus*.

*Paratypes* (all California): 8 ♀ ♀, same data as allotype (UCR); 1 ♀, Goodyear's Bar, Sierra Co., Calif., Aug. 11, 1963 (E. J. Montgomery; UCD); 1 ♀, Buckhorn, Amador Co., July 25, 1955 (E. I. Schlinger; UCD); 8 ♂ ♂, Boca, Nevada Co., June 25, 1961 (F. D. Parker; UCD); 1 ♂, same locality, June 26, 1960 (F. D. Parker; UCD); 1 ♂, same locality, June 26, 1960 (A. S. Menke; UCD); 1 ♂, Pollock Pines, Eldorado Co., Aug. 9, 1957 (E. I. Schlinger; UCD); 1 ♂, Long Barn, 2.5 mi. W., Tuolumne Co., July 29, 1960 (G. I. Stage; GIS); 1 ♀, Camp Bob MacBride, 5400', near Pinecrest, Tuolumne Co., Aug. 1, 1952 (R. R. Snelling; LACM), on *Solidago californica*; 10 ♂ ♂, Shasta Co., May 2, 1913 (F. W. Nunenmacher; CIS, LACM); 1 ♂, 1 ♀, Eagle Creek, Trinity Co., Aug. 12, 1952 (H. L. Hansen; CIS).

This species is dedicated to Professor P. H. Timberlake, in recognition of his eminence in apoid systematics, and of the generous assistance he has given to me over many years. Professor Timberlake had recognized this species as new and with characteristic generosity permitted me to describe it.

VARIATION: In the females, the clypeal maculation varies a great deal. Some have the spot so minute as to be barely perceptible and other have it so developed as to occupy as much as 75% of the total area. The Eagle Creek female has the rugulae of the propodeal declivity confined to the lower one-third. The males of this species are remarkably uniform structurally. They do possess a melanic form which strongly resembles that of such species as

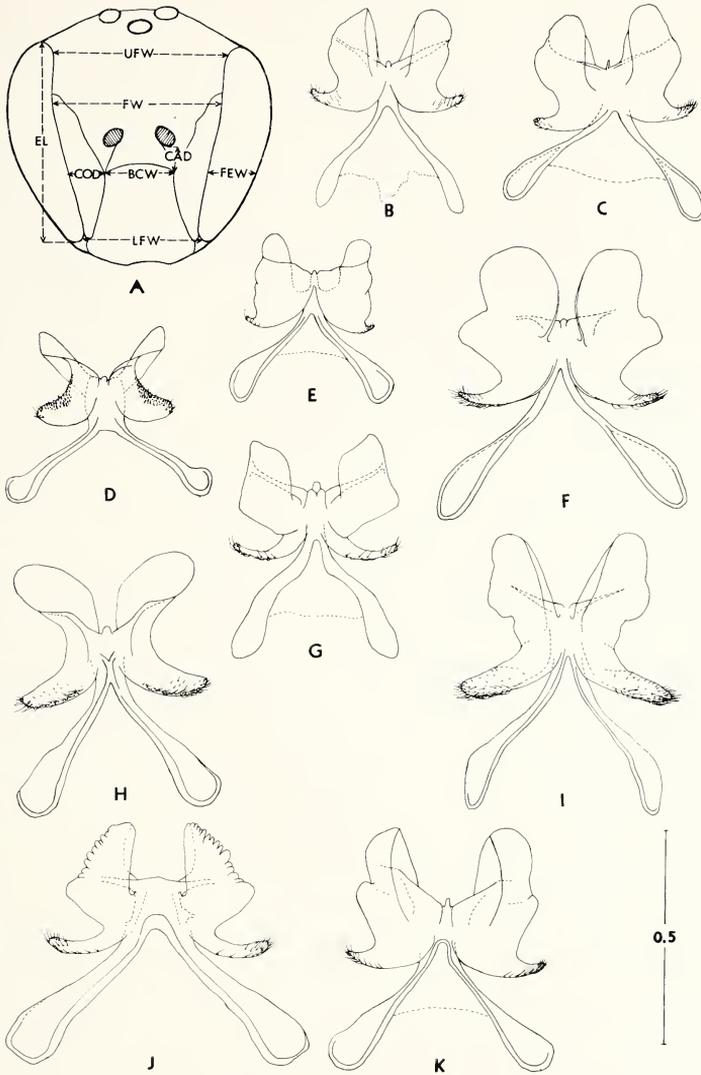


Figure 10. *Hylaeus* (*Paraprosopis*) spp. A, female face, illustrating methods of obtaining measurements used in text: BCW=Basal Clypeal Width; CAD=Clypeo-Antennal Distance; COD=Clypeo-Ocular Distance; EL=Eye Length; FL=Facial Length; FW=Facial Width; FEW=Frontal Eye Width; LFW=Lower Facial Width; SCQ=Supra-clypeal Quadrangle; UFW=Upper Facial Width. B-K, sternite VIII of males: B, *H. wootoni*; C, *H. floridanus*; D, *H. nevadensis*; E, *H. cookii*; F, *H. coloradensis*; G, *H. polifolii*; H, *H. lunicraterius*; I, *H. personatellus*; J, *H. timberlakei*; K, *H. sonorensis*.

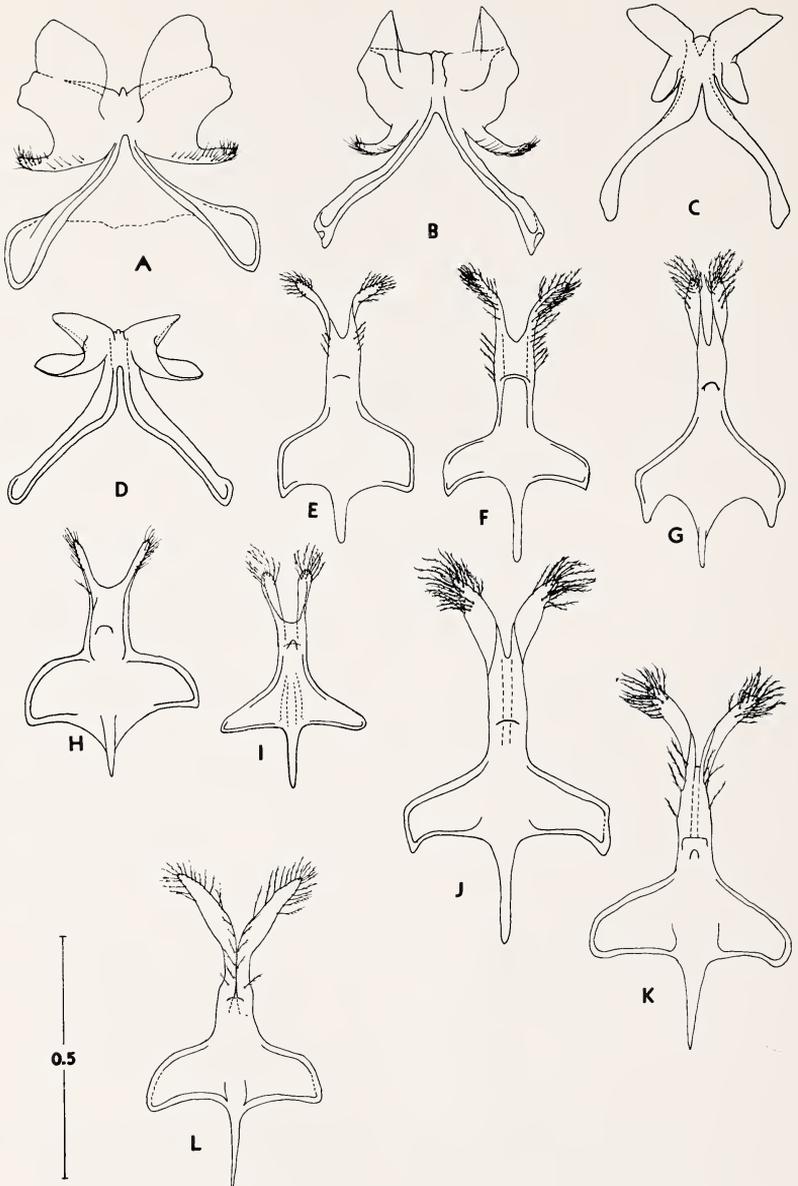


Figure 11. *Hyla* (*Paraprosopis*) spp., sternite VIII of males: A, *H. megalotis*; B, *H. asininus*; C, *H. calvus*; D, *H. georgicus*. E-L, sternite IX of males: E, *H. wootoni*; F, *H. floridanus*; G, *H. polifolii*; H, *H. nevadensis*; I, *H. cookii*; J, *H. coloradensis*; K, *H. personatellus*; L, *H. sonorensis*.

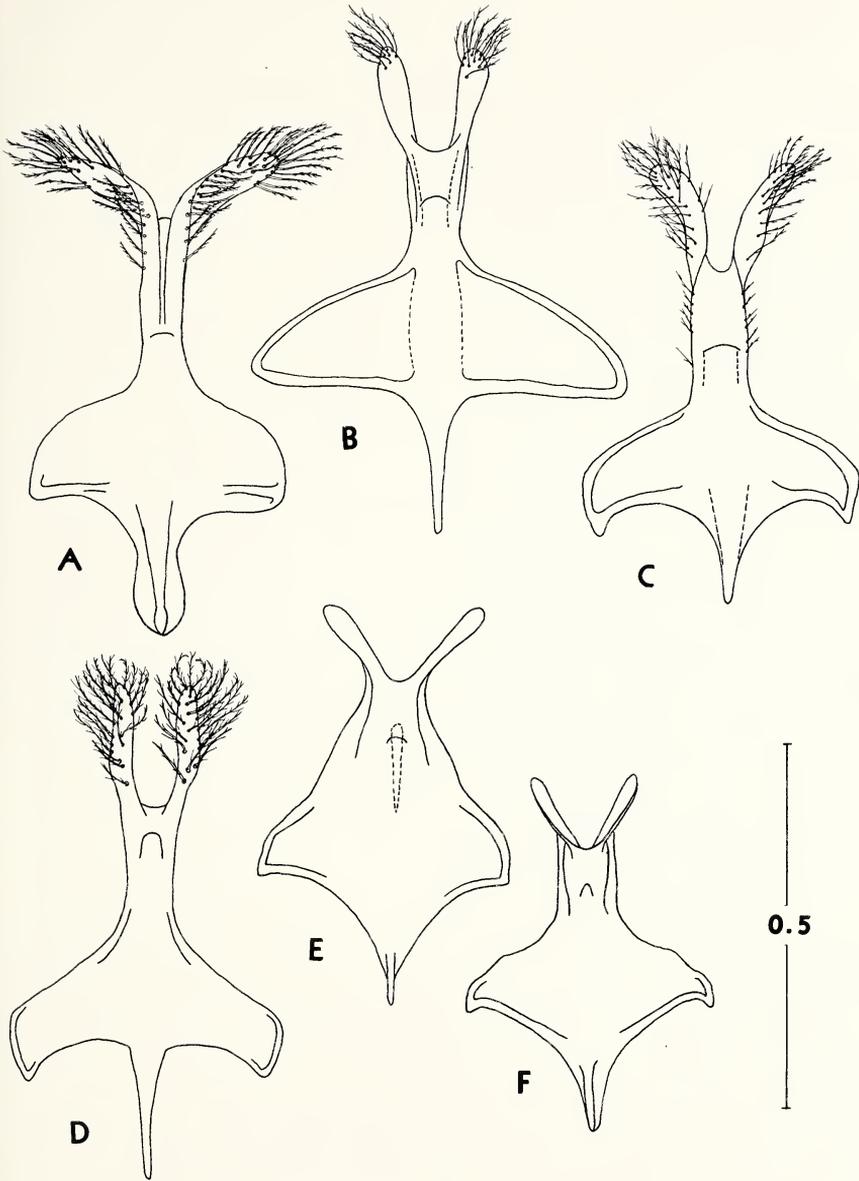


Figure 12. *Hylaeus* (*Paraprosopis*) spp., sternite IX of males: A, *H. lunicraterius*; B, *H. timberlakei*; C, *H. megalotis*; D, *H. asininus*; E, *H. calvus*; F, *H. georgicus*.

*H. calvus* and *H. polifolii*, but may be separated from these by the characters in the key.

*Hylaeus (Paraprosopis) calvus* (Metz)

Figures 7K; 8K; 11C; 12E.

*Prosopis rudbeckiae*, Metz, 1911. Trans. Amer. Ent. Soc., 37:111-114. ♀ (in part).

*Prosopis calvus* Metz, 1911. *Op. cit.* :143-144. ♂.

This common species ranges from southern Oregon to northern Baja California. A disjunct population exists in north central Arizona. In California *H. calvus* occurs through much of the Upper Sonoran area, along the coast ranges and the eastern foothills of the Sierra Nevada. Although in flight from early April until the middle of July it is most abundant during May and June. The females are often taken in large numbers at flowers of various chaparral shrubs such as *Rhamnus*, *Eriodictyon*, *Rhus* and *Ceanothus*.

The following are the marginal localities known to me for *H. calvus*: MEXICO. *Baja California del Norte*: 1 ♀, Encinas, 4 mi. S., Sierra San Pedro Martir, VI-2-1958 (J. Powell; CIS). UNITED STATES. *Oregon*: 2 ♂ ♂, Griffin Creek, Jackson Co., VI-6-1957 (C. Fitch; UCD). *Nevada*: 1 ♂, 1 ♀, Verdi, Washoe Co., VI-25-1961 (F. D. Parker; UCD). *Arizona*: 1 ♂, Parker Creek, Sierra Ancha, V-4-1947 (H. and M. Townes); 4 ♂ ♂, 1 ♀, Oak Creek Canyon, Coconino Co., V-16-1947 (H. and M. Townes); 1 ♂, same locality and collectors, V-19-1947; 1 ♂, 2 ♀ ♀, same locality and collectors, V-20-1947; 1 ♀, same locality, VI-26-1950 (L. D. Beamer; all UK).

This is one of the least variable of our species of *Paraprosopis* and one of the most easily recognized. In the female the combination of maculate clypeus, angularly produced laterobasal angle of the anterior coxae, shining, sparsely punctate mesopleurae and sparsely punctate abdomen are diagnostic. Typical males may be recognized by the lateral face marks truncate at the level of the antennal sockets, the finely, sparsely punctate shining mesopleurae and dull, densely tessellate abdomen. Males of this species, as well as those of *H. nevadensis* and *H. polifolii*, may have the clypeal borders broadly infuscated and the lateral face marks strongly narrowed above, ending acutely on the eye margin. Such males of this species may be recognized by the shining mesopleurae and dull abdomen with the punctures obscured by the dense tessellation.

*Hylaeus (Paraprosopis) georgicus* (Cockerell)

Figures 9A; 9B; 11D; 12F.

*Prosopis georgica* Cockerell, 1898. *Psyche*, 7 (suppl.): 438. ♂.

*Prosopis georgica* var. *leana* Cockerell, 1909. *Annals and Magazine of Natural History*, (ser. 8) 4:27. ♂.

*Hylaeus (Metziella) hydrangeae* Mitchell, 1951. *Jour. E. Mitchell Sci.*

Soc., 67:244. ♀; Mitchell, 1960. N. Car. Agr. Exp. Sta. Tech. Bul. 141:60, 79; Snelling, 1968. L. A. Co. Mus. Nat. Hist., Contrib. Sci., 144:3, 4. NEW SYNONYMY.

A careful reappraisal of the characters of *H. (Metziella) hydrangeae* has convinced me that this is actually the previously unrecognized female of *H. georgicus*. Both sexes were associated by me on the basis of a series of specimens from Texas before I realized that the females were conspecific with *H. hydrangeae*. In the Texas material two characteristics are outstanding; the greatly elongated basal zone of the propodeum and the extremely fine abdominal punctation. The angulate laterobasal angle of the fore coxa is much more pronounced in the female than in the male, but this is true also of these sexes of *H. calvus*. The propodeal structure of the female, while aberrant for a *Paraprosopis* is much more similar to that of other *Paraprosopis* than it is to that of the subgenus *Metziella*. In my paper on that subgenus (Snelling; 1968) I included *H. hydrangeae* because at that time there seemed no good reason not to do so. This is now obviously incorrect inasmuch as the male of this species is, aside from propodeal structure, a perfectly typical *Paraprosopis*.

The distribution of this species is limited. From New York it extends south to Florida and west to south central Texas. Mitchell (1960) recorded males from Ithaca, New York and Raleigh and Wake Co., North Carolina. The female was recorded (as *H. hydrangeae*) from Cruso, North Carolina. Snelling (1968) recorded a female (as *H. hydrangeae*) from Ft. Gordon, Georgia. Cockerell described *H. georgicus leana* from males taken by Birkmann in Lee County, Texas. Additional specimens, including both sexes, have been examined which were collected in Lee County by Birkmann. In addition to the above I have examined the following: 1 ♂, Augusta, Richmond Co., Georgia, 11-IV-1959 (R. R. Snelling; LACM), on *Crataegus*; 1 ♀, Gadsden Co., Florida, 11-IV-1960 (H. V. Weems; FPB), on *Crataegus*; 1 ♀, Hwy. 269, 8 mi. S. Chattahoochee, Gadsden Co., 6-IV-1955 (D. C. L. Gosling & party; MSU); 1 ♀, Torreya State Park, Liberty Co., Florida, 12-IV-1960 (H. A. Denmark; FPB), on *Crataegus*; 1 ♂, Lexington, Lee Co., Texas, 24-III-1951 (C. D. Michener; KU), on *Salix*; 2 ♂♂, Luling, Caldwell Co., Texas, 30-III-1951 (L. D. Beamer; KU), on *Salix*.

*Hylaeus (Paraprosopis) megalotis* (Swenk and Cockerell)

Figures 9E; F; 11A; 12C.

*Prosopis megalotis* Swenk and Cockerell, 1910. Ent. News, 21:69-70.  
♂ ♀.

This very distinctive species was originally described from a series of specimens from Glen, Sioux County, NEBRASKA and a single female from Fort Garland, COLORADO. The types were taken on *Cleome serrulata*. In addition to the types I have seen specimens of both sexes taken at the type locality on Aug. 28, 1959 (W. E. LaBerge and O. W. Isakson; UN) on

*Solidago*. The following are new records for this species. MONTANA: 13 ♀ ♀, Whitehall, Aug. 13, 1931 (J. Nottingham; KU). COLORADO: 1 ♀, Blue Mtn., Moffatt Co., Aug. 14, 1966 (G. F. Knowlton; USU). UTAH: 1 ♀, Castle Dale, Emery Co., Aug. 10, 1957 (C. D. Michener; KU), on *Cleome serrulata*; 2 ♂ ♂, 7 ♀ ♀, Clear Creek Canyon, Box Elder Co., June 11, 1954 (G. F. Knowlton; KU); 1 ♂, Hanksville, Wayne Co., Sept. 11, 1938 (G. F. Knowlton, F. C. Harmston; USU); 1 ♀, Eureka, Juab Co., Aug. 6, 1958 (G. E. Bohart; USU), on *Chrysothamnus*; 8 ♀ ♀, Manila, Daggett Co., Aug. 11, 1962 (G. E. Bohart; USU). ARIZONA: 1 ♀, Painted Desert, Apache Co., Aug. 18, 1958 (G. I. Stage; LACM), on *Eriogonum aureus*.

The female of this species is easily recognized by its complete pronotal macula and the elongate apical mandibular tooth. This tooth is subject to wear, however, and in older individuals may not be noticeably elongate. The male is very similar to that of *H. asininus* but may be separated by the finely and sparsely punctate first tergite, the head about as broad as long (broader than long in *H. asininus*) and by the gradually, rather than abruptly, depressed apico-lateral portion of the second tergite.

#### SPECIES OF UNCERTAIN POSITION

##### *Hylaeus (Paraprosopis) suffusus* (Cockerell)

*Prosopis suffusus* Cockerell, 1896. Psyche, 7 (supl.): 32 ♂.

This name is based on a single male from an unknown locality in Nevada. Although the type should be in the collections of the Academy of Natural Sciences, Philadelphia, it is apparently lost or destroyed. If the type cannot be found, it seems best to drop the name altogether since the species cannot be determined from the original description alone. The present assignment to the subgenus *Paraprosopis* is also tentative.

##### *Hylaeus (Paraprosopis) tuertonis* (Cockerell)

*Prosopis tuertonis* Cockerell, 1906. Bul. Amer. Mus. Nat. Hist., 22: 423-424. ♀.

This species was described from two females, one from Tuerto Mountain, near Santa Fe, New Mexico, and one from Florissant, Colorado. I have not seen these specimens, and the original description offers little information of use in identifying the species. It is probably correctly assigned to *Paraprosopis* and seems nearest to *H. wootoni*, of which it may be a synonym. The description applies equally well, however, to *H. cookii*. Until the types can be studied, the status of this name must remain uncertain.

#### ACKNOWLEDGMENTS

The material used during the preparation of this paper has been made available to me through the kindness of many individuals who have contributed specimens from the collections in their care. I wish to thank each of

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# CONTRIBUTIONS IN SCIENCE

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TYPE SPECIMENS OF FOSSIL INVERTEBRATA IN THE  
LOS ANGELES COUNTY MUSEUM OF NATURAL HISTORY,  
EXCLUSIVE OF PALEOENTOMOLOGY

By EDWARD C. WILSON AND DONALD E. BING



LOS ANGELES COUNTY MUSEUM OF NATURAL HISTORY • EXPOSITION PARK  
LOS ANGELES, CALIFORNIA 90007

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*Managing Editor*

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# TYPE SPECIMENS OF FOSSIL INVERTEBRATA IN THE LOS ANGELES COUNTY MUSEUM OF NATURAL HISTORY, EXCLUSIVE OF PALEOENTOMOLOGY

By EDWARD C. WILSON<sup>1</sup> AND DONALD E. BING<sup>2</sup>

**ABSTRACT:** Type specimens of fossil Porifera, Coelenterata, Brachiopoda, Bryozoa, Mollusca, Arthropoda, and Echinodermata in the Los Angeles County Museum of Natural History are listed by the original published names. Paleoentomological types are not included. The original reference, the museum type number, the age, the formation, and the locality are given for each specimen. Figured specimens not of the holotype or paratype groups are included.

## INTRODUCTION

This catalogue is published in compliance with Recommendation 72D of the International Commission on Zoological Nomenclature (1964, p. 75). It includes all the type and figured specimens, as defined below, of fossil invertebrates in the Los Angeles County Museum of Natural History, except for the paleoentomological types of W. D. Pierce and Georg Statz. A list of these will be published separately.

The catalogue is arranged systematically by phyla and classes. Within these, the genus and species group names, as originally published, are listed alphabetically. Each entry also contains the author and bibliographic reference for the lowest species-group name, the type category and number, the age assignment, the formation (if known), and the locality. We assign a separate number to every type specimen, unless it is not feasible to distinguish individuals, as in a rock containing many specimens, in which case the number refers to a lot. Figure references are included only if our specimen was figured. A question mark after the figure citation indicates some doubt that the figure was made from the specimen in our collections. "Missing" means that the specimen cannot now be found.

Definitions of type categories by Schenk, McMasters, Keen, and Muller (1956: 5-9) and the International Commission on Zoological Nomenclature (1964) are followed. In this list, hypotype refers to a specimen figured later than the original description of the species to which it is referred, or figured without a species designation. Casts of type specimens are classified like the originals from which they were made, with the prefix "plasto." Figured references for these refer to the original specimens.

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## CATALOGUE

## PORIFERA: HYALOSPONGEA

*Chancelloria eros* Walcott, 1920

MASON, 1935, p. 100, pl. 15, fig. 1.

Hypotype 1290; Cambrian, Cadiz Formation; Marble Mountains, San Bernardino County, California.

## COELENTERATA: ANTHOZOA

*Astrangia* cf. *A. insignifica* Nomland, 1916

HERTLEIN and GRANT, 1960, p. 79, pl. 19, figs. 1-4, 7.

Hypotypes 1731 (figs. 1, 7), 1732 (figs. 2-4); Pliocene, San Diego Formation; hills south of Tia Juana River, San Diego County, California.

*Balanophyllia elegans* Verrill, 1864

HERTLEIN and GRANT, 1960, p. 84, pl. 19, figs. 14, 19-21; pl. 24, figs. 4, 5, 8, 13, 15-17.

Hypotypes 1738 (fig. 14), 1739 (fig. 19), 1740 (fig. 20), 1741 (fig. 21), 1742 (fig. 4), 1743 (fig. 5), 1744 (fig. 8), 1745 (fig. 13), 1746 (fig. 15), 1747 (fig. 16), 1748 (fig. 17); Pliocene, San Diego Formation; hills south of Tia Juana River, San Diego County, California.

*Bergaueria* sp.

ARAI and McGUGAN, 1969, p. 93, pl. 18.

Hypotype 1232 (fig. 1), 1233 (figs. 2, 7), 1234 (figs. 3, 6), 1235 (fig. 4), 1236 (fig. 5); Cambrian; near Goldfield, Esmeralda County, Nevada.

*Dendrophyllia* cf. *D. oldroydi* Faustino, in Oldroyd, 1925

HERTLEIN and GRANT, 1960, p. 82, pl. 19, figs. 5, 6, 15.

Hypotype 1737; Pliocene, San Diego Formation; hills south of Tia Juana River, San Diego County, California.

*Paracyathus stearnsii* Verrill, 1869

HERTLEIN and GRANT, 1960, p. 80, pl. 19, figs. 8-13.

Hypotypes 1733 (figs. 8, 9), 1734 (figs. 10, 11), 1735 (fig. 12), 1736 (fig. 13); Pliocene, San Diego Formation; hills south of Tia Juana River, San Diego County, California.

## BRACHIOPODA: INARTICULATA

*Glottidia albida* (Hinds, 1844)

HERTLEIN and GRANT, 1960, p. 89, pl. 19, figs. 18, 24, 25.

Hypotypes 1749 (fig. 18), 1750 (fig. 24), 1751 (fig. 25); Pliocene, San Diego Formation; hills south of Tia Juana River (1749); quarry at end of Arroyo Drive, San Diego (1750, 1751), all San Diego County, California.

## BRACHIOPODA: ARTICULATA

- Laqueus californianus* (Koch), in Kuster, 1844  
HERTLEIN and GRANT, 1960, p. 96, pl. 20, figs. 1-3, 5-7.  
Hypotypes 1753 (figs. 1-3), 1754 (figs. 5-7); Pliocene, San Diego Formation; quarry at end of Arroyo Drive, San Diego, San Diego County, California.
- Laqueus vancouveriensis diegensis* Hertlein and Grant  
HERTLEIN and GRANT, 1960, p. 97, pl. 20, figs. 4, 8, 12.  
Paratypes 1755 (figs. 4, 8, 12), 1756; Pliocene, San Diego Formation; end of Loring Street (1755), 0.2 miles north of Harbor Boulevard and Tourmaline Street (1756), both San Diego, San Diego County, California.
- Orthis decipiens* Phleger  
PHLEGER, 1933, p. 17, pl. 1, fig. 2.  
Holotype 1258; Ordovician, Barrel Spring Formation; Barrel Spring Canyon, Inyo County, California.
- Orthis minusculus* Phleger  
PHLEGER, 1933, p. 7, pl. 2, figs. 6, 7.  
Syntypes 1239 (fig. 6?), 1240 (fig. 7); Ordovician, Mazourka Formation; Mazourka Canyon, Inyo County, California.
- Plectambonites angulatus* Phleger  
PHLEGER, 1933, p. 18, pl. 1, fig. 1.  
Syntypes 1259 (fig. 1), 1260; Ordovician Barrel Spring Formation; Barrel Spring Canyon, Inyo County, California.
- Plectorthis mazourkaensis* Phleger  
PHLEGER, 1933, p. 9, pl. 2, figs. 3-5.  
Syntypes 1244 (fig. 3), 1245 (fig. 5), 1246, 1247 (fig. 4), 1248; Ordovician, Mazourka Formation; Mazourka Canyon, Inyo County, California.
- Plectorthis patulus* Phleger  
PHLEGER, 1933, p. 10, pl. 2, figs. 1, 2.  
Syntypes 1241 (fig. 1), 1242 (fig. 2), 1243; Ordovician, Mazourka Formation; Mazourka Canyon, Inyo County, California.
- Terebratalia hemphilli* Dall, 1902  
HERTLEIN and GRANT, 1960, p. 93, pl. 19, fig. 26.  
Hypotype 1752; Pliocene, San Diego Formation; end of Loring Street, San Diego, San Diego County, California.

## BRYOZOA: GYMNOLAEMATA

- Ceriocava eastoni* Woollacott  
WOOLLACOTT, 1966, p. 226, figs. 1a-1c.  
Syntypes 1148; Cretaceous, Ladd Formation; Williams Canyon Road, 0.5 mile east of Santiago Canyon Road, Santa Ana Mountains, Orange County, California.

## MOLLUSCA: PELECYPODA

*Anatina* (?) sp.

PACKARD, 1922, p. 423, pl. 31, fig. 5.

Plastohypotype 2425; Cretaceous; west side of Baker Creek, Orange County, California.

*B.[arbatia] Morsei* Gabb

GABB, 1864, p. 216, pl. 32, fig. 286.

Plastoholotype 2421; Cretaceous [Eocene]; San Diego, San Diego County, California.

*Bornia cooki* Willett

WILLETT, 1937b, p. 389, pl. 25, figs. 2, 3.

Holotype 1047; Pleistocene; Baldwin Hills, Los Angeles, Los Angeles County, California.

*Cardita hilli* Willett

WILLETT, 1944, p. 19, pl. 7.

Holotype 1067; Pleistocene, Palos Verdes Sand; Newport Bay mesa, Orange County, California.

*Cardium (Protocardium) marysvillensis* Dickerson, 1916

CLARK and WOODFORD, 1927, p. 94, pl. 15, fig. 12.

Plastoparatype 2433; Eocene, Meganos Formation; north side of Mt. Diablo, Contra Costa County, California.

*Cardium sorrentoensis* Hanna

HANNA, 1927, p. 285, pl. 41, fig. 10.

Plastoholotype 2430; Eocene, La Jolla Formation; east side of Rose Canyon, 2 miles east of La Jolla, San Diego County, California.

*Chione picta* Willett

WILLETT, 1944, p. 21, pl. 8, figs. B.

Paratypes 1068 (pl. 8, figs. B, destroyed, *see* SPHON, 1962, p. 57), 1954-1975, 2313-2414; Pleistocene, Palos Verdes Sand; Newport Bay mesa, Orange County, California.

*Exputens llajasensis* Clark

CLARK, 1934, p. 270, pl. 37, fig. 14.

Plastoparatype 2432; Eocene; branch of Llajas Canyon, Ventura County, California.

*Leda rosa* Hanna

HANNA, 1927, p. 271, pl. 25, fig. 9.

Plastoholotype 2428; Eocene, La Jolla Formation; Rose Creek, San Diego County, California.

*Lucina packi* Dickerson

DICKERSON, 1916, p. 484, pl. 36, fig. 12.

Plastoholotype 2422; Eocene; Parson's Peak, Fresno County, California.

*Lucina packi* Dickerson, 1916

TURNER, 1938, p. 52, pl. 9, fig. 11.

Plastohypotype 2423; Eocene; Simi Valley, Ventura County, California.

*Nucula (Acila) semirostrata* Grant and Gale

GRANT and GALE, 1931, p. 113.

Paratype 1976; Pliocene; 1¼ miles west of San Martinez Grande Canyon, boundary of Los Angeles and Ventura Counties, California.

*Perna goniglensis* Hanna

HANNA, 1927, p. 275, pl. 27, fig. 13 (?).

Plastoholotype 2429; Eocene, La Jolla Formation; sec. 12, La Jolla Quadrangle, San Diego County, California.

*Rochefortia reyana* Willett

WILLETT, 1937b, p. 388, pl. 25, figs. 1.

Syntypes 1046 (fig. 1, left), 1703 (fig. 1, right), 1704-1728; Pleistocene; Baldwin Hills, Los Angeles, Los Angeles County, California.

*T.[ellina] ooides* Gabb

GABB, 1864, p. 157, pl. 22, fig. 135.

Plastolectotype 2420; Cretaceous; west of Martinez, Contra Costa County, California.

*Tellina santana* Packard

PACKARD, 1922, p. 426, pl. 33, fig. 4.

Plastoholotype 2424; Cretaceous; crest of Santiago-Aliso divide, Orange County, California.

## MOLLUSCA: GASTROPODA

*Acmaea mitchelli* Lipps

LIPPS, 1963, p. 3, figs. 2a-d, 3a-z, 3aa-kk, 4a-z, 4aa-kk.

Holotype 1126 (figs. 2a-d, 3a, 4a), paratypes 1127 (figs. 3b, 4b), 1781 (figs. 3c, 4c), 1782 (figs. 3d, 4d), 1783 (figs. 3e, 4e), 1784 (figs. 3f, 4f), 1785 (figs. 3g, 4g), 1786 (figs. 3h, 4h), 1787 (figs. 3i, 4i), 1788 (figs. 3j, 4j), 1789 (figs. 3k, 4k), 1790 (figs. 3l, 4l), 1791 (figs. 3m, 4m), 1792 (figs. 3n, 4n), 1793 (figs. 3o, 4o), 1794 (figs. 3p, 4p), 1795 (figs. 3q, 4q), 1796 (figs. 3r, 4r), 1797 (figs. 3s, 4s), 1798 (figs. 3t, 4t), 1799 (figs. 3u, 4u), 1800 (figs. 3v, 4v), 1801 (figs. 3w, 4w), 1802 (figs. 3x, 4x), 1803 (figs. 3y, 4y), 1804 (figs. 3z, 4z), 1805 (figs. 3aa, 4aa), 1806 (figs. 3bb, 4bb), 1807 (figs. 3cc, 4cc), 1808 (figs. 3dd, 4dd), 1809 (figs. 3ee, 4ee), 1810 (figs. 3ff, 4ff), 1811 (figs. 3gg, 4gg), 1812 (figs. 3hh, 4hh), 1813 (figs. 3ii, 4ii), 1814 (figs. 3jj, 4jj), 1815 (figs. 3kk, 4kk), 1816-1861; Pleistocene; San Nicolas Island, Ventura County, California.

*Aceteocina anomala* Willett

WILLETT, 1945, p. 29.

Holotype 1082, paratypes 1083, 2179-2181; Pleistocene (?); near shore of Salton Sea, Imperial County, California.

*Alabina effiae* Willett

WILLETT, 1939, p. 202, pl. 54.

Holotype 1061 (pl. 54), paratypes 1729, 1730; Pleistocene, San Pedro Formation; Hilltop Quarry, San Pedro (holotype); Pleistocene, Timms Point Formation; Timms Point (paratypes), both Los Angeles County, California.

*Architectonica llajasensis* Sutherland

SUTHERLAND, 1966, p. 1, figs. 1, 2.

Holotype 1140; Eocene, Llajas Formation; Las Llajas Canyon, Santa Susana Mountains, Ventura County, California.

*Balcis (Balcis) tersa* Berry

BERRY, 1954, p. 261.

Paratype 2182; Pleistocene, Lomita Formation; Hilltop Quarry, San Pedro, Los Angeles County, California.

*Balcis (Vitreolina) ebriconus* Berry

BERRY, 1954, p. 265.

Paratype 2188; Pleistocene, Lomita Formation; Hilltop Quarry, San Pedro, Los Angeles County, California.

*Balcis (Vitreolina) incallida* Berry

BERRY, 1954, p. 264.

Paratypes 2186, 2187; Pleistocene, Lomita Formation; Hilltop Quarry, San Pedro, Los Angeles County, California.

*Balcis (Vitreolina) obstipa* Berry

BERRY, 1954, p. 262.

Paratypes 2183-2185; Pleistocene, Lomita Formation; Hilltop Quarry, San Pedro, Los Angeles County, California.

*Boetica hertleini* Kanakoff

KANAKOFF, 1966, p. 3, fig. 1.

Holotype 1145 (fig. 1), paratypes 1146, 2176-2178; Pliocene, Pico Formation; ½ mile south of Humphreys railroad station, Los Angeles County, California.

*Calyptraea calabasensis* Nelson

NELSON, 1925, p. 419, pl. 54, figs. 8a, 8b.

Plastoholotype 2437; Eocene, Martinez Formation; Simi Hills, Ventura County, California.

*Caly[p]traea filosa* (Gabb, 1866)

CLARK, 1915, p. 560, pl. 65, figs. 23, 24.

Plastohypotype 2438; Miocene, San Pablo Group; Mt. Diablo quadrangle, Contra Costa County, California.

*Chedvillia stewarti* Clark

CLARK, 1942, p. 117, pl. 19, fig. 8.

Plastoparatype 2439; Eocene, Llajas Formation; Ventura County, California.

*Diodora constantiae* Kanakoff

KANAKOFF, 1953, p. 67, pls. 12, 13.

Holotype 1089 (pl. 12), paratypes 1094 (pl. 13, missing?), 2191-2312; Pleistocene, Palos Verdes Sand; Vermont Avenue, south of Sepulveda Boulevard, Wilmington, Los Angeles County, California.

*Exilia taliaferroi* Vokes

VOKES, 1939, p. 125, pl. 17, fig. 21.

Plastoholotype 2435; Eocene, Arroyo Hondo Formation; north side of Domengine Creek, Fresno County, California.

*Fusinus (Exilia) lincolnensis* (Weaver, 1916)

CLARK, 1918, p. 178, pl. 23, fig. 10.

Plastohypotype 2440; Oligocene, Kreyenhagen Shale; 15 miles north of Coalinga, Fresno County, California.

*Fusinus ucalius* Vokes

VOKES, 1939, p. 137, pl. 18, fig. 15.

Plastoholotype 2436; Eocene, Domengine Formation; first large canyon south of Big Tar Canyon, Kings County, California.

*Homalopoma berryi* McLean

McLEAN, 1964, p. 132, pl. 24, figs. 7-8.

Holotype 1138 (figs. 7-8), paratypes 1139, 1657-1702; Pleistocene, Timms Point Formation; Timms Point, Los Angeles County, California.

*Kelletia vladimiri* Kanakoff

KANAKOFF, 1954, p. 114, pls. 29-31.

Holotype 1097 (pl. 29), paratypes 1098 (pl. 30), 1099 (pl. 31); Pliocene, Pico Formation; ½ mile south of Humphreys railroad station, Los Angeles County, California.

*Leptothyra suboboleta* Willett

WILLETT, 1937a, p. 63, pl. 25.

Holotype 1054; Pleistocene, Timms Point Silt; San Pedro, Los Angeles County, California.

*Macrarena diegensis* McLean

McLEAN, 1964, p. 131, pl. 24, figs. 9-14.

Holotype 1136 (figs. 9, 10), paratypes 1137 (fig. 11), 1300 (figs. 12-14)—1656; Pliocene, San Diego Formation; hills south of Tia Juana River, San Diego County, California.

*Marginella jewettii nanella* Oldroyd

OLDROYD, 1925, p. 24.

Paratypes 2152-2154; Pleistocene, San Pedro Formation; Nob Hill, San Pedro, Los Angeles County, California.

*Mediargo mediocris* (Dall, 1909)

TERRY, 1968, pl. 4, fig. 2.

Hypotype 1190; reworked Pliocene in Pleistocene Lomita Marl; Western Avenue cut, Palos Verdes Hills, Los Angeles County, California.

*Megistostoma caminoensis* Hanna

HANNA, 1927, p. 330, pl. 57, figs. 9, 10.

Plastoholotype 2431; Eocene, La Jolla Formation; 0.4 mile south of Sorrento Station, San Diego County, California.

*Micrarionta (Xerarionta) agnesae* Kanakoff

KANAKOFF, 1950, p. 85, pl. 27.

Holotype 1088 (pl. 27), paratypes 1864-1953; Pleistocene (?); China Point, San Clemente Island, Los Angeles County, California.

*Mitromorpha galeana* Berry

BERRY, 1941, p. 12.

Paratypes 2189, 2190; Pleistocene, Lomita Formation; Hilltop Quarry, San Pedro, Los Angeles County, California.

*Nassarius (Caesia) fossatus* forma *coiloterus* (Woodring), in Woodring, Bramlette, and Kew, 1946

ADDICOTT, 1965, p. 8, pl. 2, figs. 30, 31.

Hypotypes 1129 (fig. 30), 1130 (fig. 31); Pleistocene, Palos Verdes Sand; Playa del Rey, Los Angeles County, California.

*Nassarius (Catilon) hildegardae* Kanakoff, 1956

ADDICOTT, 1965, p. 16, pl. 3, figs. 11, 12.

Hypotypes 1131 (fig. 11), 1132 (fig. 12); Pliocene, Pico Formation (Towsley Formation); ½ mile south of Humphreys railroad station, Los Angeles County, California.

*Nassarius hildegardae* Kanakoff

KANAKOFF, 1956, p. 113, pl. 31.

Holotype 1110 (pl. 31), paratypes 2097-2151; Pliocene, Pico Formation; ½ mile south of Humphreys railroad station, Los Angeles County, California.

*Nassarius stocki* Kanakoff

KANAKOFF, 1956, p. 110, pl. 30A-C.

Holotype 1109 (pl. 30A, C), paratypes 1977 (pl. 30B)—2096; Pliocene, Pico Formation; ½ mile south of Humphreys railroad station, Los Angeles County, California.

*Neadmete schwartzi* Mount

MOUNT, 1970, p. 3, fig. 1.

Holotype 1779 (fig. 1), paratype 1780; Pliocene, Fernando Formation; Newport Bay mesa, Orange County, California.

*Neadmete sutherlandi* Kanakoff and McLean

KANAKOFF and McLEAN, 1966, p. 4, figs. 1, 2.

Holotype 1150 (figs. 1, 2), paratypes 1151, 1862, 1863; Pleistocene, Lomita Marl; San Pedro, Los Angeles County, California.

*Odostomia (Amaura) menzola* Oldroyd

OLDROYD, 1925, p. 33.

Paratype 2173; Pleistocene, San Pedro Formation; Nob Hill, San Pedro, Los Angeles County, California.

*Odostomia (Amaura) timesa* Oldroyd

OLDROYD, 1925, p. 35.

Paratypes 2174, 2175; Pleistocene, San Pedro Formation; Nob Hill, San Pedro, Los Angeles County, California.

*Odostomia (Chrysallida) elsiae* Willett

WILLETT, 1948, p. 19, pl. 4, fig. 3.

Holotype 1071 (fig. 3), paratype 2415; Pleistocene, Palos Verdes Sand; Newport Bay mesa, Orange County, California.

*Odostomia (Evalea) manca* Oldroyd

OLDROYD, 1925, p. 32.

Paratypes 2170-2172; Pleistocene, San Pedro Formation; Nob Hill, San Pedro, Los Angeles County, California.

*Odostomia (Menestho) effiae* Willett

WILLETT, 1948, p. 19, pl. 4, fig. 4.

Holotype 1070 (fig. 4), paratypes 2416-2419; Pleistocene; Palos Verdes Sand; Newport Bay mesa, Orange County, California.

*Surcula (Surculites) andersoni* Dickerson

DICKERSON, 1914, p. 149, pl. 16, fig. 11.

Plastoholotype 2434; Eocene, Martinez Group; southeast of Muir Station, Contra Costa County, California.

*Triphora fossilis* Willett

WILLETT, 1937a, p. 62, pl. 24.

Holotype 1053; Pleistocene, Timms Point Silt; San Pedro, Los Angeles County, California.

*Triphora kanakoffi* Willett

WILLETT, 1948, p. 20, pl. 4, fig. 2.

Holotype 1072; Pleistocene, Palos Verdes Sand; Newport Bay mesa, Orange County, California.

*Turbonilla (Mormula) epiphanea* Oldroyd

OLDROYD, 1925, p. 28.

Paratype 2169; Pleistocene, San Pedro Formation; Nob Hill, San Pedro, Los Angeles County, California.

*Turbonilla (Pyrgolanpros) collisella* Oldroyd

OLDROYD, 1925, p. 25.

Paratypes 2157, 2158; Pleistocene, San Pedro Formation; Nob Hill, San Pedro, Los Angeles County, California.

*Turbonilla (Pyrgolanpros) idae* Oldroyd

OLDROYD, 1925, p. 26.

Paratypes 2159-2168; Pleistocene, San Pedro Formation; Nob Hill, San Pedro, Los Angeles County, California.

- Turbonilla (Strioturbonilla) pecora* Oldroyd  
OLDROYD, 1925, p. 24.  
Paratypes 2155, 2156; Pleistocene, San Pedro Formation; Nob Hill, San Pedro, Los Angeles County, California.
- Turbonilla (Turbonilla) grouardi* Willett  
WILLETT, 1948, p. 17, pl. 4, fig. 1.  
Holotype 1069; Pleistocene, Palos Verdes Sand; Newport Bay mesa, Orange County, California.
- Turritella andersoni* subsp. *lawsoni* Dickerson, 1916  
MERRIAM, 1941, p. 77, pl. 12, fig. 4.  
Plastohypotypes 2427; Eocene, Llajas Formation; Las Llajas Canyon, Simi Valley, Ventura County, California.
- Turritella schencki* Merriam  
MERRIAM, 1941, p. 81, pl. 10, fig. 10.  
Plastoholotype 2425 (fig. 10), plastoparatype 2426; Eocene, Tejon Formation; Tecuya Creek, Kern County, California.

## ARTHROPODA: TRILOBITA

- Acrocephalites ? trifossatus* Mason  
MASON, 1935, p. 102, pl. 15, figs. 2, 3.  
Syntypes 1279 (fig. 2), 1280 (fig. 3); Cambrian, Cadiz Formation; Marble Mountains, San Bernardino County, California.
- Alokistocare linnarssoni* (Walcott, 1884)  
MASON, 1935, p. 104, pl. 15, fig. 4.  
Hypotype 1281; Cambrian, Cadiz Formation; Marble Mountains, San Bernardino County, California.
- Amecephalus piochensis* (Walcott, 1886)  
MASON, 1935, p. 105, pl. 15, figs. 5-7.  
Hypotypes 1282 (fig. 5), 1283 (fig. 6), 1284 (fig. 7?); Cambrian, Cadiz Formation; Marble Mountains, San Bernardino County, California.
- Amecephalus strangulatus* Mason  
MASON, 1935, p. 106, pl. 15, figs. 8, 9.  
Holotype 1285 (fig. 8), paratype 1286 (fig. 9); Cambrian, Cadiz Formation; Marble Mountains, San Bernardino County, California.
- Anomocarella ? spatha* Mason  
MASON, 1935, p. 107, pl. 15, fig. 10.  
Holotype 1287; Cambrian, Cadiz Formation; Marble Mountains, San Bernardino County, California.
- Anoria lodensis* (Clark, 1921)  
MASON, 1935, p. 109, pl. 15, fig. 11.  
Hypotype 1288 (fig. 11), 2442 (fig. 12, missing); Cambrian, Cadiz Formation; Marble Mountains, San Bernardino County, California.

- Bathyuriscus howelli* Walcott, 1886  
MASON, 1935, p. 110, pl. 15, fig. 13.  
Hypotype 1289; Cambrian, Cadiz Formation; Marble Mountains, San Bernardino County, California.
- Bathyuriscus maximus* Mason  
MASON, 1935, p. 111, pl. 15, figs. 14-16.  
Syntypes 1291 (fig. 14), 1292 (fig. 15), 1293 (fig. 16); Cambrian, Cadiz Formation; Marble Mountains, San Bernardino County, California.
- Bumastus billingsi* Raymond and Narraway  
RAYMOND and NARRAWAY, 1908, p. 250, pl. 62, figs. 1, 2.  
Plastoholotype 2441; Ordovician, Trenton Limestone; Hull, Quebec, Canada.
- Ceraurus infrequens* Phleger  
PHLEGER, 1933, p. 15, pl. 2, fig. 12.  
Holotype 1255; Ordovician, Mazourka Formation; Mazourka Canyon, Inyo County, California.
- Corynexochus* ? sp.  
MASON, 1935, p. 113, pl. 15, fig. 17.  
Hypotype 1294; Cambrian, Cadiz Formation; Marble Mountains, San Bernardino County, California.
- Cybeloides calliteles* Phleger  
PHLEGER, 1933, p. 14, pl. 2, fig. 8.  
Holotype 1254; Ordovician, Mazourka Formation; Mazourka Canyon, Inyo County, California.
- Dorypyge quadriceps* (Hall and Whitfield, 1877)  
MASON, 1935, p. 116, pl. 15, figs. 18-22.  
Hypotypes 1295 (fig. 18), 1296 (fig. 19), 1297 (fig. 20), 1298 (fig. 21), 1299 (fig. 22); Cambrian, Cadiz Formation; Marble Mountains, San Bernardino County, California.
- Encrinurus hastula* Phleger  
PHLEGER, 1933, p. 12, pl. 2, figs. 13, 14.  
Syntypes 1251 (fig. 13), 1252 (fig. 14); Ordovician, Mazourka Formation; Mazourka Canyon, Inyo County, California.
- Encrinurus octonarius* Phleger  
PHLEGER, 1933, p. 13, pl. 2, fig. 9.  
Holotype 1253; Ordovician, Mazourka Formation; Mazourka Canyon, Inyo County, California.
- Isotelus gigas* Dekay, 1824  
PHLEGER, 1933, p. 3, pl. 1, figs. 5, 6.  
Hypotypes 1277 (fig. 5), 1278 (fig. 6); Ordovician, Barrel Spring Formation; Barrel Spring Canyon, Inyo County, California.
- Isotelus spurius* Phleger  
PHLEGER, 1933, p. 20, pl. 1, fig. 7.

Syntypes 1275 (fig. 7), 1276; Ordovician, Barrel Spring Formation; Barrel Spring Canyon, Inyo County, California.

*Lloydia obsoletus* Phleger

PHLEGER, 1933, p. 11, pl. 2, fig. 15.

Syntypes 1249 (fig. 15, left), 1250 (fig. 15, right); Ordovician, Mazourka Formation; Mazourka Canyon, Inyo County, California.

*Pliomerops barrandei* (Billings, 1865)

PHLEGER, 1933, p. 16, pl. 2, figs. 10, 11.

Hypotypes 1256 (fig. 10), 1257 (fig. 11); Ordovician, Mazourka Formation; Mazourka Canyon, Inyo County, California.

*Remopleurides occidens* Phleger

PHLEGER, 1933, p. 18, pl. 1, figs. 3, 4.

Syntypes 1261 (fig. 3?), 1262 (fig. 4), 1263-1274; Ordovician, Barrel Spring Formation; Barrel Spring Canyon, Inyo County, California.

#### ARTHROPODA: CRUSTACEA

*Balanus gregarius* (Conrad, 1856)

ZULLO, 1969, p. 6, figs. 3-7, 45.

Hypotypes 1197 (fig. 3, missing), 1198 (fig. 4, missing), 1199 (fig. 5), 1200 (fig. 6), 1201 (fig. 7, missing), 1202 (fig. 45); Pliocene, San Diego Formation; Market Street, east of Euclid Avenue, San Diego, San Diego County, California.

*Balanus kanakoffi* Zullo

ZULLO, 1969, p. 7, figs. 11-12, 15-17, 19-20, 22.

Holotype 1209 (fig. 19), paratypes 1205 (fig. 11), 1206 (fig. 12), 1207 (fig. 15), 1208 (figs. 16-17), 1210 (fig. 20), 1211 (fig. 22); Pliocene, San Diego Formation; hills south of Tia Juana River, San Diego County, California.

*Balanus nubilus* Darwin, 1854

ZULLO, 1969, p. 8, figs. 8-10.

Hypotype 1203 (figs. 8-9), 1204 (fig. 10); Pliocene, San Diego Formation; hills south of Tia Juana River, San Diego County, California.

*Balanus proinus* Woodring, in Woodring and Bramlette, 1950

ZULLO, 1969, p. 16, figs. 26-28, 30-32.

Hypotypes 1214 (figs. 26, 27), 1215 (fig. 28), 1216 (figs. 30-32); Pliocene, San Diego Formation; hills south of Tia Juana River, San Diego County, California.

*Balanus* sp., cf. *B. pacificus* Pilsbry, 1916

ZULLO, 1969, p. 10, figs. 23, 25.

Hypotypes 1212 (fig. 23), 1213 (fig. 25); Pliocene, San Diego Formation; hills south of Tia Juana River, San Diego County, California.

*Balanus wilsoni* Zullo

ZULLO, 1969, p. 10, figs. 33-34, 36, 38-39, 43-45.

Holotype 1224 (fig. 45), paratypes 1217 (fig. 33), 1218 (fig. 34), 1219 (fig. 36), 1220 (fig. 38), 1221 (fig. 39), 1222 (fig. 43), 1223 (fig. 44); Pleistocene (?), end of Loring Street (1222); Pliocene, San Diego Formation; Market Street, east of Euclid Avenue (1217-1221, 1223, 1224), both San Diego, San Diego County, California.

*Cancer branneri* Rathbun, 1926

MENZIES, 1951, p. 170, figs. 2a-2d.

Hypotypes 2448 (figs. 2a, 2b), 2449 (figs. 2c, 2d); Pleistocene, Timm's Point Formation; Timm's Point, Los Angeles County, California.

*Cancer jordani* Rathbun, 1900

MENZIES, 1951, p. 169, figs. 5a-5d.

Hypotypes 2446 (figs. 5a, 5b), 2447 (figs. 5c, 5d); Pleistocene; San Pedro, Los Angeles County, California.

*Cancer productus* Randall, 1839

MENZIES, 1951, p. 168, figs. 4a-4d.

Hypotypes 2444 (figs. 4a, 4b, missing), 2445 (figs. 4c, 4d, missing); Pleistocene, San Pedro Formation; San Pedro, Los Angeles County, California.

*Cetolepas hertleini* Zullo

ZULLO, 1969, p. 17, figs. 47, 49-50, 53, 55, 58-59, 61-63, 66, 68, 71-72. Holotype 1230 (figs. 49, 61-62), paratypes 1225 (figs. 47, 59), 1226 (figs. 58, 71-72), 1227 (figs. 50, 63), 1228 (figs. 53, 66), 1229 (figs. 55, 68); Pliocene, San Diego Formation; hills south of Tia Juana River, San Diego County, California.

*Coronula barbara* Darwin, 1854 (?)

ZULLO, 1969, p. 21, figs. 73-75.

Hypotype 1231; Pliocene, San Diego Formation; hills south of Tia Juana River, San Diego County, California.

*Lepas* sp.

ZULLO, 1969, p. 4, figs. 1, 2.

Hypotype 1196; Pliocene, San Diego Formation; hills south of Tia Juana River, San Diego County, California.

## ECHINODERMATA: STELLEROIDEA

*Inyoaster bradleyi* Phleger

PHLEGER, 1936, p. 82.

Paratypes 1237, 1238; Ordovician, Barrel Spring Formation; Barrel Spring Canyon, Inyo County, California.

## ECHINODERMATA: ECHINOIDEA

*Briaster townsendi woynari* Hertlein and Grant

HERTLEIN and GRANT, 1960, p. 132, pl. 25, fig. 5; pl. 26, figs. 1-3. Holotype 1778 (figs. 1-3), paratype 1777 (fig. 5); Pliocene, San Diego Formation; quarry at end of Arroyo Drive, San Diego, San Diego County, California.

*Dendraster ashleyi* (Arnold), in Arnold and Anderson, 1907

HERTLEIN and GRANT, 1960, p. 117, pl. 21, figs. 2, 6; pl. 22, fig. 1; pl. 26, fig. 9.

Hypotypes 1762 (fig. 2), 1763 (figs. 6, 9), 1764 (fig. 1); Euclid Avenue between Federal Boulevard and Home Avenue (1762, 1764); 2400 block of Euclid Avenue (1763), both San Diego, San Diego County, California.

*Dendraster ashleyi ynezensis* Kew, 1919

HERTLEIN and GRANT, 1960, p. 118, pl. 21, figs. 4, 5; pl. 22, fig. 2; pl. 26, fig. 7.

Hypotypes 1765 (fig. 4), 1766 (figs. 5, 7), 1767 (fig. 2); Pliocene, San Diego Formation; quarry at end of Arroyo Drive (1765); Market Street, ¼ mile south of Euclid Avenue (1766); 3550 Dove Street (1767), all San Diego, San Diego County, California.

*Dendraster casseli* Grant and Hertlein, 1938

HERTLEIN and GRANT, 1960, p. 120, pl. 22, fig. 7.

Hypotype 1768; Pliocene, San Diego Formation; quarry at end of Arroyo Drive, San Diego, San Diego County, California.

*Encope tenuis* Kew, 1914

HERTLEIN and GRANT, 1960, p. 126, pl. 23, figs. 7, 13; pl. 24, fig. 11.

Hypotype 1775; Pliocene, San Diego Formation; quarry at end of Arroyo Drive, San Diego, San Diego County, California.

*Eucidaris* cf. *E. thoursii* (Valenciennes), in Agassiz and Desor, 1846

HERTLEIN and GRANT, 1960, p. 103, pl. 24, figs. 19-22.

Hypotypes 1757 (fig. 19), 1758 (fig. 20), 1759 (fig. 21), 1760 (fig. 22); Pliocene, San Diego Formation; hills south of Tia Juana River, San Diego County, California.

*Lovenia hemphilli* Israelsky, 1923

HERTLEIN and GRANT, 1960, p. 130, pl. 24, fig. 18.

Hypotype 1776; Pliocene, San Diego Formation; end of Loring Street, San Diego, San Diego County, California.

*Mellita kanakoffi* Durham

DURHAM, 1961, p. 5, pl. 2, fig. 2; text-fig. 1D.

Holotype 1121 (fig. 2, text-fig. 1D), paratype 1122 (missing); Pleistocene, Palos Verdes Sand; Newport Bay mesa, Orange County, California (1121); Lomita Boulevard and Main Street, Wilmington, Los Angeles County, California (1122).

*Merriamaster* cf. *M. israelskyi* (Jordan and Hertlein, 1926)

HERTLEIN and GRANT, 1960, p. 122, pl. 23, figs. 12, 14.

Hypotypes 1769 (fig. 12), 1770 (fig. 14); Pliocene, San Diego Formation; under Snyder Continuation School, San Diego, San Diego County, California.

*Merriamaster pacificus* (Kew, 1920)

HERTLEIN and GRANT, 1960, p. 124, pl. 23, figs. 2-4, 6, 11; pl. 25, fig. 6; pl. 26, fig. 11.

Hypotypes 1771 (pl. 23, figs. 2, 3, 11), 1772 (pl. 23, fig. 4), 1773 (pl. 23, fig. 6), 1774 (pl. 25, fig. 6; pl. 26, fig. 11); Pliocene, San Diego Formation; 0.2 mile north of Harbor Boulevard and Tourmaline Street (1771, 1772); end of Loring Street (1773, 1774), both San Diego, San Diego County, California.

*Strongylocentrotus purpuratus* (Stimpson, 1857)

HERTLEIN and GRANT, 1960, p. 112, pl. 19, fig. 29.

Hypotype 1761; Pliocene, San Diego Formation; Pacific Beach, San Diego, San Diego County, California.

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# CONTRIBUTIONS IN SCIENCE

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AQUATIC ADAPTATIONS OF THE WATER MOUSE,  
*RHEOMYS UNDERWOODI*

By ANDREW STARRETT AND GEORGE F. FISLER



LOS ANGELES COUNTY MUSEUM OF NATURAL HISTORY • EXPOSITION PARK  
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# AQUATIC ADAPTATIONS OF THE WATER MOUSE, *RHEOMYS UNDERWOODI*

By ANDREW STARRETT AND GEORGE F. FISLER<sup>1</sup>

**ABSTRACT:** An adult male *Rheomys underwoodi* caught alive along the Río Poasito, at 2000 m on Volcán Poás, Alajuela Province, Costa Rica, in April, 1966, was maintained in captivity for a short time. Limited observations on maintenance behavior and locomotion of this animal are presented. In addition, morphological features (body form, tail shape and foot structure) related to the high degree of specialization for aquatic locomotion shown by this rodent are described, and some ideas concerning the evolution of the semi-aquatic habit are discussed in relation to *Rheomys* and other small mammals.

## INTRODUCTION

Information available on the biology of the genus *Rheomys* is quite limited. These animals live primarily in and around swift flowing streams of the Neotropics. Howell (1930) described certain aquatic features of *Rheomys* but did not give a full account of the high degree of adaptation to a semi-aquatic existence which the species *R. underwoodi*, in particular, exhibits. Hooper (1968) briefly mentioned some of the aquatic characteristics of *Rheomys* in a comparison of *R. underwoodi* and *R. hartmanni*, the two species which occur in Costa Rica, and also included ecological information and stomach analyses for both. Our capture of a living animal has prompted us to record some observations on the behavior and morphology of the water mouse with additional comments on aquatic adaptations in this and other species.

On the basis of information and materials provided for us by Emmet T. Hooper, we set 31 traps (18 museum specials, 13 National single door live traps) along the banks of the Río Poasito, 2000 m, Volcán Poás, in Alajuela Province, Costa Rica, on the evening of 9 April 1966. This same area was trapped on 6 and 7 April 1966 by Hooper and James H. Brown and is described by Hooper (1968). Instead of using the method of trapping *Rheomys* described by Stirton (1944), we set seven live traps along relatively quiet eddy pools just outside white-water areas. Our *Rheomys* was taken near such a pool in a trap which was placed on rocks about 7.5 cm above the water line. The mouth of the trap was about 20 cm from the pool, one meter from any white water, and 15-20 meters below a small waterfall. Bait used was peanut butter with sardine meat and oil spread over it, placed on the treadle inside of the trap. Some sardine oil was smeared on the trap entrance but no bait was placed outside of the trap. No other mammals were taken in the live traps

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but three *Reithrodontomys creper* and one *Peromyscus nudipes* were caught in the snap traps. About half of the snap traps were placed next to the water. The water mouse was an adult male having abdominal testes (10 x 18 mm) with epididymides well developed and caudae protruding into the inguinal passages. The standard measurements are 300-158-39-7 (mm).

#### GENERAL BEHAVIOR

The actions of the *Rheomys* when first observed were slow and deliberate, as if it had been in the trap for some time and was weakened, but later it became more active. It darted about the trap hurriedly, in the manner of a shrew, yet when quiet, it sat mostly hunched over like a muskrat (*Ondatra zibethicus*). Stirton (1944) described it as a miniature model of a beaver (*Castor canadensis*). When seated, its hind feet were spread out at an angle of some 30-40 degrees from the body with its fore feet usually tucked along its chest. A striking, and probably adaptively significant reaction, was its tendency to bite at objects with which it came into contact. Even while being carried in the trap, it nipped at fingers whenever it encountered them at the edges of the trap as it dashed about. When handled, however, it was docile and did not bite, and attempts to induce it to nibble fingers were successful only if the animal blundered into them, as it did not seem to seek out such prey. The biting reaction on contact with moving objects was also later shown when the animal was observed swimming. In the capture of prey under water, where vision and olfaction may be of minimal use, it would be of great advantage for an animal to be adapted to biting at any moving object with which it came in contact. The eyes of this rodent are very small and presumably are of little use, particularly under water, and especially in fast moving, turbulent streams. The face is rather well endowed with vibrissae, probably advantageous in hunting and orientation, but it was difficult to tell if they were used as sensors.

When the trap was first observed, all of the bait had been eaten, or, less likely, washed away. Our captive animal was fed small pieces of sardines which it ate from the container rather than manipulating the food while sitting up as do many of the more familiar rodents. It occasionally manipulated larger chunks of sardine (10-12 mm) with its fore feet, so perhaps the size and consistency of the food determines the manner of feeding. It probably handles insect larvae with its fore feet. In general, the animal would eat for a minute or so, pause for 15-20 seconds, and then resume eating. It was first fed about thirty minutes after the trap was picked up and it ate roughly a small thimbleful of sardines in the succeeding hour. Attempts at feeding it green vegetation (leaves and herbs from its habitat) while it was still hungry were unsuccessful. Stirton (1944) found no evidence that *Rheomys* was piscivorous but thought that it was omnivorous and even cannibalistic. Goldman (1920) suggested that one species may feed on snails. Hooper's (1968) analysis of contents from six stomachs of *Rheomys* from Costa Rica and Guatemala (one stomach

empty) shows a diet of primarily aquatic insect larvae. Fish are present in the Río Poasito but are not native. Our captive was observed drinking sparingly. It lapped with its tongue in the familiar manner of many small rodents, directly off the water surface.

When first seen in the trap, the *Rheomys* was dry except for its tail, underparts, feet and muzzle. After removal from the stream area, it dried quickly. Grooming was accomplished in the manner of many rodents, except that the enlarged hind feet serve as very effective combs for the body fur. When wet or grooming, or both, as grooming is evidently an important part of the drying process, the animal moved the skin of the back in a peculiar fashion, appearing to erect the guard hairs, a grooming as well as a drying aid. This movement appeared to pass in waves over the hunched back antero-posteriorly and the reverse. All of the time the animal sat much like a muskrat. After leaving the water, the animal groomed extensively.

Limited swimming observations of the captive *Rheomys* were made in a small 27 x 36 cm wash basin. The water was about 8 cm deep and for part of the time the trap was used as an island although the basin could barely accommodate it. The small size of the container restricted the movement of the animal. It tried to climb the sides, violently treading water with its hind feet, maintaining its body about half to two-thirds out of the water. The large hind feet made tremendous splashes as it attempted to escape, very strikingly pointing out their propulsive power. Observations of diving were limited but the process was extremely quick. While swimming on the surface, the mouse had its head out of the water, the rump under, while the tail was curved concavely with the tip at the water surface. Most of the swimming motion was with the hind feet with little body undulation except when sculling (noted only 2 or 3 times). These latter motions seemed to give the animal added impetus for quick acceleration or turning. The fore feet could not be seen while swimming, indicating that they are not used other than to hold on to objects when landing, or perhaps to fend off objects while swimming. In all swimming motions, the animal was extremely quick, presumably an adaptive feature for feeding under water as well as for swimming in swift moving streams. Hooper (1968) has reported on the swiftness in movement and swimming of an animal, undoubtedly *Rheomys underwoodi*, observed in the wild.

While in captivity, the animal lived in the trap. Soft tissue and newspaper given to the *Rheomys* was slightly shredded but no real nest building occurred. Excelsior was ignored. Rather, the animal slept mostly on its side rolled in the typical rodent ball, under the paper. Stirton (1944) mentioned that water mice probably nest in dead brush and logs lodged in the stream or under large boulders or other rocks.

After the swimming session on the evening of capture, the animal appeared to be drying rather slowly. However, by the following morning (11 April) it was dry and appeared to be in good health. It ate readily (sardines). It was placed in a light cloth sack for transport to Los Angeles, California,

but it died in transit. The specimen was preserved as a skin and skull with the body preserved in fluid and is now in the collection of the Los Angeles County Museum of Natural History (LACM 28260).

#### MORPHOLOGY

Because of the absence of such information from the literature, and in order to lay the background for a discussion of the adaptations of this animal to a semi-aquatic existence, a detailed account of pertinent morphological characters is here provided. The body is streamlined to a high degree with essentially no projections other than the hind feet and tail when in the water. The head is somewhat depressed and the mouth opening is small. The eyes are also reduced in size. The snout is truncated in dorsal view and the rhinarium is prominent. The nostrils are situated laterally and open posteriorly behind flaplike valves. The numerous vibrissae are situated dorsally and laterally on the snout and cheeks posterior to the rhinarium and around the mouth. They reach maximum lengths of 32 to 34 mm, although most are 14 to 26 mm long. The ear pinnae are reduced essentially to small, pointed posterior lobes, about 4 mm in length, which do not extend above the surface of the fur.

The pelage is generally dense and soft, the type characteristically associated with the smaller aquatic mammals. In the mid-dorsal region the underfur is dense with fine hairs which range from 5 to 7 mm in length. Abundant but less dense and grosser hairs, about 12 to 14 mm long, form an outer layer. The ventral pelage is similar to that of the dorsum, but the underfur is shorter.

The fore limbs are relatively short and do not project much from the body, even when walking. The proximal portions of the hind limbs blend similarly into the body contours, leaving the remarkable hind feet as the only limb segments which project obviously from the furred outline of the body. The tail also is flared into the body outline over the proximal 15 mm of its length. The front feet are much smaller than the hind feet with long, curved, sharply pointed claws. On the hind feet, digit I is the shortest, then in order of increasing length, digits V, II, III, and IV. The greatest differences in length are between digits I and II and, to a lesser degree, between digits V and IV. The first and, to a lesser extent, the fifth digits appear to have the greatest amount of independent movement.

The hind feet have laterally compressed digits interconnected by webbing. The sides of the feet and toes are lined with single rows of closely spaced stiff hairs which reach maximum lengths of three and four mm on the medial and lateral sides of the feet, respectively, and two to three mm on the toes and webbing, with the shortest hairs being those near the middle of each web. The claws are deep and essentially as broad as the tip of the terminal phalanx, that on digit I being the deepest and the claw on digit II the broadest. The tips are pointed in lateral profile, but somewhat rounded and scooplike in ventral aspect. The massive appearance of the hind claws is very striking when they

are compared with those of other rodents of similar size such as *Neotoma*, *Nelsonia*, *Xenomys*, *Tylomys*, *Nyctomys*, and *Rattus*.

When the digits are abducted, the webbing reaches the level of the penultimate interphalangeal joint between digits II, III, IV, and V, but is less extensive between digits I and II. Each web originates at the base of the claw and extends, as a widening flap, to the levels just mentioned. There the margin turns and a similar but narrower flap continues to about the same claw level on the next toe. On the lateral (post-axial) side of each digit, the webbing arises along the dorsolateral surface, whereas on the medial side of the succeeding digit it connects along the medial surface. When the foot is extended, the digits rotate so that their ventral surfaces turn mediad. The metatarsophalangeal joints are somewhat loose, apparently allowing the digits to rotate even more than do the metatarsals. The metatarsals (except III and IV) and free digits abduct and, since they are rotated, the latter also extend at the metatarsophalangeal joints in a more or less horizontal plane. These actions spread the foot and toes while turning the digits so that they present their broad compressed surfaces and spread the webbing to its greatest extent. Part of the rotation of the digits may be passively effected by the tension of the webbing.

When fully expanded, the hind foot of our specimen measured 14 mm across the plantar surface at the level of the distal ends of the metatarsals, and the expanded hair fringes added another six mm at that level, resulting in greatest dimensions of 20 x 39 mm. Planimetric measurements of the best of a number of inkpad prints of the right hind foot, including hair fringes, showed areas of 3.8 to 4.0 cm<sup>2</sup>. The two hind feet, then, form impressive propulsive surfaces during extension in the backward stroke while swimming. In the recovery stroke, it is probable that the foot is flexed and the digits flexed, abducted, and possibly rotated somewhat laterad again so that the compressed toes are curled slightly and lie close together in a staggered sequence (cross sectional), with digit I leading, and the hair fringes flattened against the sides of the foot and toes. Thus the pes becomes narrowed with the digit alignment presenting a laterally compressed, rather than an anteroposteriorly flattened unit, approaching the characteristics of a hydrofoil, and offering minimum resistance to the water.

The free tail, from the point at which it leaves the furred base which flares into the body, measures 143 mm to the tip. The proximal 30 mm is circular in cross section and approximately 7 mm in diameter. At the end of this basal portion, there is a constriction to about 6.5 mm diameter and the tail gradually tapers and becomes compressed. In the last 15 mm the tail narrows more rapidly to almost a point in dorsal view and, in lateral aspect, reaches its shallowest dimension (a little less than 5 mm), then expands slightly ventrally and ends in a somewhat rounded tip which gives the appearance of turning a little ventrad. Along the ventral surface of the free tail, particularly from the level of the basal constriction where the cross section of the tail begins to change shape, the hairs arising from the ventral surface of the tail, representing approximately  $\frac{1}{3}$  the tail circumference arc, become abruptly longer (to

about 5 mm) and more dense, forming a kind of broad fringe extending along the undersurface of the tail to the point where it expands ventrally near the tip. The hairs on the rest of the free tail are shorter and relatively sparsely but evenly distributed. Internally the most notable feature of the tail structure is the presence of numerous heavy tendons attaching firmly to the vertebrae, fascia and skin, distal to the basal constriction. The extraction of the tail beyond this point during skinning was difficult. (James H. Brown, personal communication, recalled the same difficulty with the specimens of *R. underwoodi* he prepared from the same locality.) This clearly suggests well developed muscular control of the tail, further evidence of which was obtained by selective pulling of the tendons, while the tail was partially extracted, which caused bending in various directions and at different points in the more distal portions of the tail.

The streamlining provided by reduction and blending of projecting parts of the body and the generally fusiform shape and flared tail base make *Rheomys* a hydrodynamically efficient body. The large hind feet provide the main propulsive force and in recovery strokes tend to give minimum resistance by the combined characters of compressed digits and the foot action mechanism. The tail apparently serves a stabilizing and a supplementary propulsive function, being adapted for both by compression, by effective control through the tendon arrangement, and probably also by the paddle-shaped tip. Dorsal-ventral bending of the tail was noted above, during surface swimming. The slightly ventrally oriented distal portion of the tail (the paddle) probably is significant when the tail is thus curved in such a way that the tip approaches, or is at, the water surface while the rest of the tail is below. The tip then would be more nearly horizontally oriented. This curving might also make the ventral hair fringe stand out more and so contribute to the compressed tail shape. This fringe may serve other functions since the hairs are not particularly stiff. Possibly it protects the ventral surface of the tail from abrasion by streamside rocks and gravel, or it may serve as a drip line for rapid water runoff.

The thoracic vertebrae of the skinned carcass were capable of rather acute kyphotic curvature. The panniculus carnosus is a rather broad, thin sheet posteriorly (lumbosacral region), but gives rise to a number of long, narrow extensions running up over the back to the head and shoulder region. Contraction of this muscle pulls the skin back and forth over the thoracic region. This action separates the hairs of the back when the thoracic region is curved during grooming.

#### DISCUSSION

In attempting to understand aquatic adaptation of *Rheomys underwoodi*, we surveyed certain literature on semi-aquatic mammals. (Anthony, 1921, 1923, 1929; Bauchot and Stephan, 1968; Conaway, 1960; Dickey, 1928; Enders, 1938; Goldman, 1912, 1920; Goodwin, 1959; Guth *et al.*, 1959; Handley and Mondolfi, 1963; Hershkovitz, 1944, 1955; Hooper, 1947, 1968; Howell, 1930; Lönnberg, 1921; Malzy, 1965; Peyre, 1956; Stirton, 1944;

Svihla, 1934; Thomas, 1893, 1897, 1906a, 1906b, 1924a, 1924b; De Winton, 1896). Most of our comparative information was taken from Walker (1968). Although the survey was not exhaustive, we found that relatively little is known about semi-aquatic small mammals, especially the more highly specialized forms. However, limited discussion of the position which *R. underwoodi* occupies in the evolution of specializations in these mammals is possible.

*Rheomys underwoodi* is among the most highly hydrodynamically specialized mammals, particularly when compared with species of comparable size and habits, the smaller semi-aquatic rodents and insectivores, and the marsupial *Chironectes*. On the basis of what we could determine, it is quite likely that most aquatic features of *R. underwoodi* are not unique, but a comparable total combination of specific features is apparently limited to members of only eight other genera: three of rodents (in addition to certain other *Rheomys* species), *Anotomys*, *Ichthyomys* (both closely related to *Rheomys*), and the hydromyine *Crossomys*; five of insectivores, *Limnogale*, and *Micropotamogale* (*M. ruwenzori*) (Tenrecidae), *Desmana* and *Galemys* (Talpidae) and *Nectogale* (Soricidae). As might be expected, the details of specialization are most similar among the rodents. *Limnogale* and *Nectogale* seem to be the most closely comparable of the insectivores.

Davis (1964:323) considered two factors to be "primarily responsible for adaptive modifications in the morphology of mammals: locomotion, and foods and feeding." In the case of forms which are more highly adapted for aquatic living, the locomotor requirements strongly influence the morphological modification related to obtaining food. In those particularly adapted for rapid swimming, morphological feeding specializations not in accord with the hydrodynamic requirements imposed by locomotor specializations are not to be found. Although this applies to semi-aquatic, or amphibious mammals, as well as to the more completely aquatic, the degree of overall modification in the former is limited by the requirements of terrestrial locomotion, and a structural-functional balance is struck according to the relative significances of aquatic and terrestrial locomotion in the lives of these animals. Furthermore, not all aquatic adaptations contribute directly to aquatic locomotion, and the ability to swim does not necessarily involve much in the way of morphological modification (Howell, 1930). *Rheomys underwoodi* must be considered a semi-aquatic rodent with a high degree of morphological specialization reflecting primarily selection for effective, rapid aquatic locomotion as the major influence.

Davis (1964:323) further stated that "In mammals the major forces impinging on locomotion are escape from enemies, pursuit of prey and wandering in search of food or water." These categories can be modified to include as potentially significant functions (forces or factors): 1) simple translocation or unforced movement (wandering for whatever reason); 2) escape from predators; 3) escape in the event of changing environmental conditions; 4) locating and feeding on plants (or mollusks; *i.e.* stationary food); 5) pursuing and capturing other animals (mobile food). All of these can play a part

in determining the degree of adaptation for aquatic locomotion in the evolution of semi-aquatic forms. One other important factor remains which has a basic influence on the selective requirements related to the five functions just listed: namely, the nature of the aquatic environment. Ability to swim in still water requires less in the way of morphological specialization than does the ability to swim in a strong current (function 1 or 4 above), and if forced locomotion (functions 2 and 5) is required, then increased specialization becomes a necessity under both types of aquatic conditions. Escape by swimming from predators that do not swim puts more stress on the ability to get into the water rapidly than it does on swimming. The high degree of hydrodynamic specialization in *Rheomys underwoodi* appears to have evolved as an adaptation of this semi-aquatic rodent for unforced movement, escape from predators and, probably most significantly, for obtaining moving food in the sometimes torrential streams along which it lives. The adaptive features related to these factors doubtless have survival value, as well, when the streams rise rapidly and become swifter and more turbulent during heavy rains (function 3).

The types of food (discussed in more detail by Bauchot and Stephan, 1968) and the type of aquatic environment appear to be the most important factors in the evolution of the semi-aquatic radiation among small mammals. Most semi-aquatic herbivorous mammals occur in level or lowland and coastal regions in which graminoid and low herbaceous vegetation forms a major source of food and where marshes, ponds and river overflows are to be found but rapid streams are unusual. In such situations, water edge species probably took to water, mainly, in order to take advantage of the additional (similar) plant food thus made available and also to survive during periods of flooding. In this category apparently fall most of the semi-aquatic rodents, of which many are little specialized aquatically; others show varying degrees of specialization, but all are still limited by the importance of terrestrial locomotion as a means of dispersal and of relocation during times of change in their aquatic habitats.

Among those showing little or no specific adaptations for aquatic locomotion, but which more or less routinely enter water and swim, can be mentioned species of *Thryonomys* (Thryonomyidae), *Bandicota*, *Dasymys*, *Hybomys* (Muridae), *Microtus*, *Oryzomys* and *Reithrodontomys* (Cricetidae), to name only a few in just these three families (see Walker, 1968; Fislser, 1961, 1965). Species of other genera have evolved definite aquatic locomotor specializations and apparently utilize more of the food occurring in the water: the oryzomine *Nectomys*, the sigmodont *Holochilus*, and the microtine *Arvicola* are obvious examples. Those genera (such as *Hydrochoerus*, *Myocastor*, *Ondatra*, and *Neofiber*), which have become more dependent on semi-aquatic or aquatic plant food, have evolved more aquatic locomotor specializations and are capable of swimming in relatively slow and steady currents present in small streams and rivers. It seems significant that these last mentioned genera are among the larger rodents, suggesting that there is a relationship between

the size of the animal and the ability to enter larger bodies of water and stronger currents where more sustained swimming is required. As must be the case with all aquatic and semi-aquatic mammals, their respective degrees of specialization have evolved in relation to the most severe aquatic conditions (currents, distances to be covered in water) in the bodies of water which they frequent or inhabit. Many of the rodents mentioned may be found in a variety of aquatic situations, but few, if any, characteristically occur in water with rapid currents. None feeds to any extent on active aquatic food although some do utilize inactive aquatic animals at least occasionally. The water opossum, *Chironectes*, seems to be comparable with this group of rodents in terms of degree of aquatic specialization, but it also fits in with the next group of small mammals in that it both feeds on aquatic animals and probably evolved in a forest environment.

Apparently the semi-aquatic insectivores and the more highly specialized semi-aquatic rodents have evolved, for the most part, in hilly or mountainous regions. Here forest is more prevalent than open grassland or other vegetational types which provide much in the way of leafy food, and moving water characterizes the aquatic habitats (streams and small rivers). Some of these conditions, and/or other coincident factors, have apparently been favorable to insectivore radiations, and the presence of good sources of food along the water edge and in the water itself has provided the setting for the evolution of the semi-aquatic members of the order. The more highly specialized insectivores already mentioned are characteristically found associated with streams or small rivers, usually in forested areas. The other known semi-aquatic insectivores show somewhat wider and more variable ecological characteristics but probably have evolved under similar conditions. *Potamogale*, one of the largest insectivores, is unique among semi-aquatic members of the order in having a highly specialized tail as its sole locomotor organ, a feature which probably makes it one of the most efficient swimmers of the group (more nearly comparable to the otters). This African tenrecid is found in all types of water, from lakes to torrential mountain streams. The remaining semi-aquatic members of this order are not highly specialized for aquatic locomotion showing only relatively slight modifications of the terrestrial locomotor apparatus. They do not possess swimming abilities comparable to those of the insectivores already mentioned. The relatively large hind feet, long tail and more streamlined body of the star-nosed mole, *Condylura*, (as compared to typical moles) are of positive value in aquatic locomotion, if not direct specializations for this function, as well may be the less fossorially modified fore limb of this animal. The water shrews belonging to the soricid genera *Neomys* and *Chimarrogale* and species *Sorex palustris* and *S. bendirii* probably can be considered ecological equivalents (roughly) in their respective separate ranges of distribution, having approximately the same morphological adaptations (fringed feet and tail). They appear to be most similar in aquatic adaptations to the less specialized species of the Neotropical rodent genera *Holochilus* and *Nectomys*. Finally, *Micropotamogale lamottei*, characteristically found in

slower waters, seems to be morphologically adapted for aquatic locomotion to about the same extent as the water shrews although it is larger and shows more aquatic specializations.

The insectivores mentioned previously as being adaptively comparable to *Rheomys underwoodi* are more highly specialized for aquatic locomotion and are, in fact, more aquatic than those just discussed, with the exception of *Potamogale*, and they characteristically live in rivers and rapid to torrential streams. Their adaptations have evolved in response to the requirements imposed by more or less active pursuit of food in the currents and turbulence of the aquatic environment.

In comparison with this last group of insectivores, rodents living in regions characterized by forested streams and rivers have less potential food available in and around the water if they depend on plant sources. Those entering the streams have had to assume a diet of moving animal food (most likely before taking to the water), the capturing of which, under the aquatic conditions presented by the active waters, has been a significant factor in the evolution of their locomotor specializations. Two groups of rodents have shown somewhat similar radiations in such situations: the Neotropical ichthyomyine cricetids and the New Guinea-Australian hydromyine murids.

The ten genera of hydromyines (with some 16 species) are diversified and include small mouse and shrew-like forms (*Microhydromys*, *Parahydromys*) and other apparently terrestrial herbivores, as well as three genera which have taken to the water and include animals in their diets. These three, *Xeromys*, *Hydromys* and *Crossomys*, have followed different lines of specialization representing the extremes of the spectrum of aquatic modifications found in other groups of rodents (Lidicker, 1968; Mahoney, 1968; Tate, 1951). *Xeromys*, the only endemic Australian genus of hydromyines, feeds on aquatic vegetation and inactive aquatic mollusks in swampy situations and has little, if any, apparent morphological adaptations for aquatic locomotion. The more widely distributed genus, *Hydromys*, represents a more muskrat-like type of semi-aquatic specialization, with the widespread *H. chrysogaster* being associated with a wide range of aquatic environments and feeding on a variety of animal and plant foods. Finally, the monotypic New Guinean genus *Crossomys*, found along mountain streams and very likely feeding on aquatic animals, appears to be most similar to *Rheomys underwoodi* in ecological characteristics and in both degree and detail of morphological adaptation for aquatic locomotion.

The five genera of ichthyomyines are less diversified than the hydromyines, rather they show differing degrees of specialization for life along mountain streams. Hershkovitz (1962) proposes that the ichthyomyines are derived from pastoral forms, primarily on the basis of dentition; we believe that, in any case, the ancestral forms most likely had to enter the forest to be exposed to the stream habitat, since gallery forest, at least, is almost always associated with permanent streams in the New World Tropics. The monotypic genera *Neusticomys* and *Daptomys* exhibit only slight morphological modifi-

cation for aquatic habits, whereas the various species (16 named forms; eight to 14 species, depending on the authority consulted) of *Rheomys* and *Ichthyomys* carry aquatic locomotor modifications to varying extents of specialization (Cabrera, 1961; Goodwin, 1959; Handley and Mondolfi, 1963; Hooper, 1968). *Anotomys* (monotypic), *Rheomys underwoodi*, probably *R. mexicanus* (according to the informative description provided by Goodwin, 1959) and several other species of *Rheomys* (Hooper, 1968) and of *Ichthyomys* (Anthony, 1929) appear to have attained more or less similar high levels of aquatic locomotor adaptation, along several parallel evolutionary pathways. As already pointed out by Hooper (1968), the other ichthyomyine species found in Costa Rica, *Rheomys hartmanni*, shows less specialization for aquatic locomotion than does *R. underwoodi*. The LACM specimen of *R. hartmanni* (LACM 25418) from north of San Isidro del General, in the Cordillera de Talamanca (Hooper's 5200-ft. station, Río Buena Vista tributaries, Prov. San José: Hooper, 1968) shows the lesser degree of specialization of the fur, ears, hind feet and tail indicated by Hooper (1968) and, furthermore, shows much less (negligible) webbing of the hind feet, and a tail which appears to be round and to lack the ventral hair fringe. This specimen also lacked the specialized tail muscle-tendon complex described above in *R. underwoodi*.

Differences such as those between *Rheomys underwoodi* and *R. hartmanni*, which have been outlined, are not always readily explainable. A more thorough interpretation of the evolution of the adaptations of small mammals to the semi-aquatic habit awaits a detailed knowledge of these adaptations. Most references we have seen have been taxonomic in nature and have discussed mainly diagnostic or comparative features of the mammals described, presenting little useful information on other aspects of their morphology. More ecological data, such as kinds of food consumed and detailed characteristics of habitats where the animals are found, along with information on behavioral adaptations, will provide bases for interpreting the significance of morphological specializations.

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## RESUMEN

Un macho adulto de *Rheomys underwoodi* fué capturado vivo, en Abril, 1966, en la orilla del Río Poasito, a 2000 m en el Volcán Poás, Provincia de Alajuela, Costa Rica. En captividad, éste animal comió sardinas de lata vorazmente, pero reusó varios tipos de plantas de la región de captura que le fueron ofrecidas. En general, sus acciones al moverse en la trampa, como limpiándose y comiendo, fueron rápidas y parecidas a las acciones de musarañas. Basado en observaciones limitadas de éste roedor semi-acuático en el agua de un recipiente restringido, su comportamiento mostró también acciones rápidas al entrar y salir del agua, nadando en la superficie o zambulléndose. La propulsión era efectuada por movimientos alternados de las anchas patas traseras.

Entre las especializaciones morfológicas adaptadas a la locomoción acuática, que éste ratón presenta, las siguientes han sido notadas: un cuerpo hidrodinámico del cual solo las patas traseras y la cola protruden durante la natación, la cola ligeramente compresada longitudinalmente con arreglo complejo de tendones para su control; piés traseros grandes con tela interdigital y crestas de pelos que dan una superficie total de cada pié de aproximadamente 3.9 cm<sup>2</sup>. Además, las patas traseras pueden voltear y doblarse de tal manera que presentan una estructura de "hydrofoil," con una resistencia mínima contra el agua durante el movimiento hacia adelante (de recobro) al nadar.

Finalmente, en una forma general y especulativa, una discusión de la evolución de hábitos semi-acuáticos en pequeños mamíferos es presentada. Dos cursos principales se pueden proponer: 1) en áreas de tierras bajas, donde el habitat acuático consiste principalmente de aguas quietas o lentamente corredizas y la vegetación acuática es abundante, los pequeños mamíferos semi-acuáticos son en su mayoría roedores que comen, principalmente, plantas, y que tienen tendencia a producir especializaciones morfológicas limitadas para locomoción acuática; 2) en áreas de montaña bien forestadas, donde los arroyos y riachuelos tienen aguas rápidas que contienen más animales acuáticos que plantas acuáticas, los hábitos semi-acuáticos se han desarrollado en varios insectívoros y algunos grupos de roedores que han podido adaptarse a una dieta de pequeños animales. *Rheomys underwoodi*, así como otros roedores ichthyomyines Neotropicales y los roedores hydromyines, *Crossomys*, de Nueva Guinea, pertenecen al último grupo y han desarrollado un alto grado de especialización morfológica a la locomoción en aguas rápidas, a veces torrentosas, en que ellos viven.

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# CONTRIBUTIONS IN SCIENCE

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OBSERVATIONS AND RECORDS OF  
*MYOTIS (PIZONYX) VIVESI* MENEGAUX  
(Chiroptera: Vespertilionidae)

By DONALD R. PATTEN AND LLOYD T. FINDLEY



LOS ANGELES COUNTY MUSEUM OF NATURAL HISTORY • EXPOSITION PARK  
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OBSERVATIONS AND RECORDS OF  
*MYOTIS (PIZONYX) VIVESI* MENEGAUX  
(Chiroptera: Vespertilionidae)

By DONALD R. PATTEN<sup>1</sup> AND LLOYD T. FINDLEY<sup>2</sup>

ABSTRACT: A large number of *Myotis (Pizonyx) vivesi* Menegaux were observed at a minimum distance of four nautical miles from land from the research vessel, *Velero IV*, trawling in 800 fathoms of water in the Canal de Salsipuedes, Gulf of California, at a speed of four knots. Bats accompanied the vessel for a minimum of three hours flying into a headwind of 16 knots. Flight patterns in relation to the vessel and apparent feeding behavior are described. Contents of the intestinal tracts of three specimens included finely masticated muscle tissue, fish scales, at least one piece of a caridean shrimp and a structure thought to be the abdomen of an unidentified polychaete larva. New records for *Myotis vivesi* are Isla de Alcatraz, Sonora, and Bahía Rosario, Baja California Sur, the latter being the southernmost distributional record.

Detection of localized surface disturbances of the water are discussed as a possible means of food detection. The correspondence between the distribution of *M. vivesi* and areas of large scale upwellings and subsequent phytoplankton blooms in the Gulf of California and adjacent Pacific Ocean is noted.

Three roundworms, genus *Trichuris*, the mites *Spinturnix mexicanus* Rudnick and *Steatonyssus leptus* Radovsky and ticks of the genus *Ornithodoros* were found as parasites on *M. vivesi*. All known ectoparasite records from *M. vivesi* are presented.

Similarity in morphological and behavioral characteristics (including piscivorous habits) between *M. (Pizonyx) vivesi* and other species of *Myotis* is noted. The taxonomy of *Pizonyx* Miller is discussed, and the taxon is considered a subgenus of *Myotis* Kaup.

In the course of a midwater trawl in the Gulf of California on the evening of November 30, 1967 the research vessel, *Velero IV*, was nearly engulfed by a large aggregation of bats. The circumstances and observations of this incident merit reporting.

*Observations and distributional records:* At 11:30 PM three non-gravid, non-lactating females were caught in large dip nets as they flew past the fantail and were subsequently prepared and identified as *Myotis (Pizonyx) vivesi* Menegaux (LACM 28273-28275).

When the bats were caught, the vessel was trawling in a northwesterly

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direction in 800 fathoms of water in the Canal de Salsipuedes (sometimes written Sal si Puedes) at a speed of four knots. The exact location was 4.2 nautical mi. W ( $263^\circ$  Radar Target) of Isla Salsipuedes,  $28^\circ 43' 58''$  N,  $113^\circ 04' 00''$  W. Barometric pressure was 29.97 in. Hg, sea temperature was  $21.1^\circ$  C ( $70^\circ$  F), and the wet and dry bulb air temperatures were  $16.1^\circ$  C ( $61^\circ$  F) and  $19.7^\circ$  C ( $67.5^\circ$  F), respectively.

At approximately 11 PM a single bat was noticed when it flew up the port passageway outside the gallery. This was the first time that any of the scientists were cognizant of the situation. Personnel on the bridge, however, reported that the bats first appeared at 10 PM and were continuously present until about 2 AM of December 1 when they all left abruptly. A minimum of 17 nautical miles was traversed during this four hour time interval. At 10 PM the vessel was a minimum of four nautical miles from the closest land mass, Isla las Ánimas, while at 2 AM Isla Partida was 4.7 nautical miles to the east, and Punta de las Ánimas (mainland Baja California Norte) was 2.5 nautical miles to the west. The vessel was never closer than four nautical miles to any land during the first three hours.

Due to its specialized habitat, it is unlikely that *M. vivesi* is ubiquitously distributed throughout the islands of the Gulf of California and adjacent land areas. Maya (1968) found *Pizonyx* present in January, spring and summer on the following four islands in the vicinity of the Canal de Salsipuedes: Partida (= Isla Cordonosa, the type locality), Raza, Salsipuedes and San Lorenzo. For a summary of distributional records see Maya (1968), Reeder and Norris (1954), and Banks (1964). In addition to the Canal de Salsipuedes record, there are specimens in the Los Angeles County Museum of Natural History (LACM) mammal collection from two unpublished localities as follows: Isla de Alcatraz, Bahía Kino, Sonora, Mexico (33 specimens, LACM 13109-13140, collected by A. L. Gardner, June 25 through July 9, 1960) and Bahía Rosario, Baja California Sur, Mexico (9 specimens, LACM 28276-28286, collected by K. E. Stager, March 23, 1963). The latter specimens were taken from under rocks on a small island at the south end of Bahía Rosario ( $24^\circ 15'$  N,  $110^\circ 09'$  W), ca. 7 mi. SE Punta Coyote, and constitute the southernmost record for this species.

Reeder and Norris (1954) reported a probable sight record of this species at sea two miles off Punta Malarrimo, Bahía de Sebastian Vizcaino, Pacific side of Baja California. Our specimens from Salsipuedes appear to be the first conclusive evidence of *M. vivesi* occurring at considerable distances from land.

According to the ship's log the wind was from the southeast at 6 knots at 9 PM, "calm" at 10 PM, and thereafter from the northwest at an average velocity of 16 knots. Several observers noted that the bats first appeared during the period of calm and for the remaining four hours flew alongside the vessel into a 16 knot headwind.

Despite the absence of moonlight, observation was made possible by the vessel's running lights, a portable spotlight, and special lights on the fantail and A-frame which supported the trawl. Extent of visibility is estimated to have been 13.7 m (45 ft.) from the vessel. No phosphorescence or bioluminescence was observed in the water.

Approximately two hundred individuals were estimated to be visible around the fantail at any one moment. The total number is conservatively estimated to have been at least twice that number. It is not known if the same individual bats were present during the entire four hours or even if those visible at any one moment were just part of a much larger, and unobservable number.

Bats were observed flying all around the vessel except directly in front of and under the bow, but they appeared to be concentrated around the stern, presumably because of the lights and wake of the vessel. Most individuals remained more than 2.4 m (8 ft.) from the vessel, but some bats flew diagonally across the stern of the vessel and maneuvered to avoid the superstructure of the vessel and the attempts of observers to catch them in dip nets. Those alongside the vessel appeared to fly repeatedly in an oval pattern, the long axis parallel to the ship. From the vicinity of the bow individuals would fly adjacent to the sides of the ship until reaching the stern where they would disperse over the wake of the ship, reorient into the wind, drop down to the water surface, and fly forward toward the bow. In the forward flight bats were observed just above the sea surface until reaching the vicinity of the bow where they abruptly rose in altitude. Flight speed in the sweep toward the stern was discernibly faster than that toward the bow. The bats appeared to be definitely interested in the area of crests produced by the wake of the vessel as well as the choppy sea surfaces lateral to the vessel.

Bats at the stern were estimated to be flying 2 in. to 1 ft. above the surface and were definitely observed to dip downward touching the water. Several observers reported that they actually saw the bats touching the water surface but could not distinguish which body part made contact. Robert J. Lavenberg states, that while operating the spotlight, he observed individual bats swoop down until just above the water surface and then alternately lower and raise their feet, making contact with the water.

Lavenberg's observation is pertinent in light of the controversy over the manner in which food is procured. Miller and Allen (1928) and Burt (1932) reasoned that the elongated, laterally compressed and recurved feet functioned to capture small fish or crustacea. On the basis of several observations, Reeder and Norris (1954) stressed that the tail, uropatagium and calcar cartilages appeared to be the primary mechanism. Walker (1950) observed a V-shaped ripple mark remaining after a low swoop by a bat and believed that this was made by the animal's chin. To our knowledge no one has recorded observing *M. vivesi* actually obtaining prey from the sea, although Maya

(1968, p. 65) observed several individuals “. . . with fish in their claws.” In addition to the feet, the tail and uropatagium were considered by Maya (1968) to be used in capturing prey because these were often wet and frequently bore fish scales.

*Food:* After examination of both guano and stomach contents, Burt (1932, p. 364) found definite evidence of “. . . fish remains, chiefly scales with an occasional small fish bone.” Burt further reported (p. 363) that one of the bat stomachs was found to contain fish “. . . belonging to the sardine tribe.” On the basis of circumstantial evidence, Walker (1950) believed the diet to consist of small shrimp. He further theorized that upon approaching the water surface the white venter (atypical for the genus *Myotis*) served to agitate and frighten schools of crustaceans, thus facilitating their capture. Reeder and Norris (1954) recorded in stomach contents small crustaceans and, in one specimen, many insect fragments. Norris (Reeder and Norris 1954, p. 85) observed one bat in flight “. . . holding a shining little fish in its hind feet.” Of an undisclosed number of fecal pellets obtained from roosting sites, Carpenter (1968, p. 956) found “. . . 62.5 per cent contained remains of only crustacea, 26.3 per cent contained only fish remains and 11 per cent contained remains of both.” Maya (1968) found the presence of crustaceans, fish, insects, and algae in the stomachs of 22 specimens. In droppings he found some indication of seasonal variations in the relative frequencies of the above food items, but concluded that crustaceans were the major food source. Examination of the digestive tracts of our three specimens disclosed finely masticated pieces of muscle tissue, fish scales, at least one piece of a shrimp (Decapoda: Caridea) and a structure thought to be the abdomen of an unidentified polychaete larva. Analysis of the fish scales revealed that the majority were from the family Myctophidae (lantern fishes), comparing well in size, shape and other scale characters to those of the genera *Hygophum*, *Diaphus* and *Triphoturus*. Thirteen of the 65 scales showed a definite, raised center portion which appeared to be the lens remnant of a myctophid photophore scale whereas 50 additional scales were non-photophore myctophid scales. Two scales were small and ctenoid and were not myctophid in origin, those of the latter being larger and cycloid. Many myctophids are vertical migrators from great depths at night when they would occur at the surface.

From roosts of *M. vivesi* Maya (1968) found the dry and partially chewed remains of the following fishes: *Lile stolifera*, *Ophisthonema liboleta* [sic, *Opisthonema libertate*], bothids, and perhaps flying fish, with bothid remains being the most common. Adult flatfishes of the family Bothidae are benthic whereas the larvae and prejuveniles live in plankton. Scale development is probably slight, if at all, during the planktonic stages. The degree of scale development of the bothid remains mentioned by Maya (1968, fig. 15) would indicate that they were probably recently developed juveniles which

inhabit shallow waters near shore. *Lile stolifera* and *Opisthonema libertate* are herrings (Clupeidae) and are surface schooling fishes.

When removed from the dip net, one of the three bats was discovered to have a small unidentified shrimp adhering to the surface of the uropatagium. During the frantic efforts to capture the bats as they flew close to the sides of the vessel and across the fantail, one of the specimens was caught in a dip net which subsequently touched the water before being raised to the deck. It is not known whether or not the specimen bearing the crustacean was the one involved nor is it known if the shrimp was present when the bat was initially caught or if it was originally adhering to the dip net and subsequently transferred to the bat.

*Food detection:* The bats emitted audible sounds described as short, high pitched squeals, which were readily discernible. The overall intensity of sound varied in direct proportion to the height of flight, being loudest when the bats were closest to the water. No noticeable change in pitch was reported by the observers whereas Maya (1968, p. 66) states that "As they approach the surface, their vocal chatter, a series of short bursts, becomes high pitched, more rapid, and finally inaudible."

Suthers (1965) found that in captivity *Noctilio leporinus* Linnaeus, a neotropical bat known to be piscivorous, could readily detect small wires projecting vertically above the water as well as localized minor disturbances in the water surface. *M. vivesi* probably detects prey in the same manner as *N. leporinus* although in a subsequent study Suthers (1967) reported a difference in the orientation sounds produced by these two species. He was unable to induce captive *M. vivesi* to take pieces of shrimp from the surface of an experimental pool.

The behavior and apparent feeding forays by *M. vivesi* in the areas adjacent to the stern and sides of the vessel may have resulted from disturbances of the water by the wind and the passage of the vessel. The choppy sea produced by the wind was similar to the wake of the vessel. Once agitated, any small fish or crustacean could well have produced small surface disturbances, thus facilitating their capture by the bats.

Maya (1968, p. 67) mentions that *M. vivesi* cannot select only small fish, pointing out that ". . . many [of the fish] caught are frequently too large for effective feeding." On another occasion he witnessed a bat ". . . hovering above and actively pursuing an object" (1968, p. 66). Maya recovered the object which was an unidentified shrimp (1968, pp. 61 and 66, fig. 16). Judging from the scale in the figure the shrimp appears about 6 cm. long and too large for effective feeding by *M. vivesi*. This would seem to be a logical consequence if *M. vivesi* was reacting to a localized surface disturbance rather than discriminating as to the kind and size of organism producing the disturbance.

The known distribution of *M. vivesi* conforms in general with areas of the Gulf of California and adjacent areas of the Pacific Ocean subject to large

scale upwellings and subsequent phytoplankton blooms, e.g. the Canal de Salsipuedes (Parker, 1964, p. 35). Perhaps *M. vivesi* actively seeks out those areas where their prey species, higher trophic level consumers, would be relatively more abundant.

*Parasites:* Three female roundworms of the genus *Trichuris* (Dorylaimida: Trichinellidae) were found as intestinal parasites in one of our three specimens. In addition, three types of ectoparasites were found: one mite, *Spinturnix mexicanus* Rudnick (Acarina: Spinturnicidae); two protonymphs of the mite, *Steatonyssus leptus* Radovsky (Acarina: Macronyssidae); and four specimens of a tick of the genus *Ornithodoros* (Acarina: Argasidae), which apparently are not *O. dyeri* Cooley and Kohls (Glen M. Kohls, personal communication).

The following ectoparasites have been recorded from *M. (Pizonyx) vivesi*: *Ornithodoros dyeri* Cooley and Kohls (1940) (Acarina: Argasidae); *Whartonia sonorensis* Hoffmann (1960) (Acarina: Trombiculidae); *Trombicula thompsoni* Brennan (1966) (Acarina: Trombiculidae); *Speleocola cortezi* Loomis and Webb (1969) (Acarina: Trombiculidae); and the batfly, *Basilina pizonychus* Scott (1939) (Diptera: Nycteribiidae). The latter has also been reported by Reeder and Norris (1954) and Maya (1968). Rupert L. Wenzel (personal communication) reports that there are no Streblidae known from *M. vivesi*. *Whartonia sonorensis*, *Speleocola cortezi* and *Basilina pizonychus* are known only from *M. vivesi*. Apart from the one record on *M. vivesi*, *Trombicula thompsoni* is known only from marine birds in the Caribbean. At one time, *Ornithodoros dyeri* was known only from guano and rock crevices of bat caves, mines, and tunnels from several localities in the western United States and Mexico, but it is now known from both *M. vivesi* and the sac-winged bat, *Balantiopteryx plicata* (Kohls, Sonenshine, and Clifford, 1965). Because it is incomplete, current parasitological information can furnish little evidence concerning the taxonomic relationships between *M. vivesi* and the other species of *Myotis*.

*Taxonomy:* We have followed the suggestions of Ellerman and Morrison-Scott (1951, p. 138) and subsequent investigators that *Pizonyx* Miller and *Myotis* Kaup be regarded as congeneric. These two have been shown to be essentially similar in hair structure (Benedict, 1957), baculum (Hamilton, 1949), and karyotype (Baker and Patton, 1967). Characteristics used to distinguish *Pizonyx* from *Myotis* have been summarized by Baker and Patton (1967) and are primarily associated with a piscivorous habit (Miller, 1906 and 1907).

To support the generic retention of *Pizonyx*, Maya (1968) stressed piscivorous behavioral adaptations and specializations in water metabolism. However, other species of *Myotis* are now known, or strongly suspected, to be piscivorous and exhibit many of the same specialized morphological and behavioral characteristics formerly regarded as unique to *Pizonyx*. These species

are as follows: *M. (Leuconoe) megalopus* (Dobson), Africa, (Aellen and Brosset, 1968); *M. (Rickettia) ricketti* Thomas in Asia [discussed as *Vespertilio pilosus* Peters by Allen, 1936]; *M. (Leuconoe) macrotarsus* Waterhouse, Asia, and *M. (Leuconoe) daubentoni* Kuhl, Europe (Brosset and Deboutteville, 1966).

The subgeneric designations follow Tate (1941) and are distinguished by enlarged feet, *Leuconoe*, versus enormous feet, *Rickettia*, in addition to other characteristics similar to those of *Pizonyx*. The big-footed condition according to Tate (1941), at least in *Leuconoe*, is due to phalangeal elongation (as in *Pizonyx*) and not to metatarsal elongation as stated by Maya (1968). In addition to the aforesaid species, *Myotis dasyncneme* Boie (Europe and Asia), *Myotis macrodactylus* Temminck (Japan), and *Myotis stalkerii* Thomas (Kei Islands) also have large feet.

Although a white venter is not common in the genus *Myotis*, it cannot be considered unique to *Pizonyx*. Specimens in the American Museum of Natural History of *M. ricketti*, *M. daubentoni* and *M. dasyncneme* all possess a conspicuous and extensive white frosting to the venter.

Braun (1965) and Carpenter (1968) have shown that kidney structure and water metabolism, respectively, of *M. vivesi* are highly specialized, but without equivalent information for the other species of *Myotis*, it is difficult to interpret the taxonomic significance, if any, of this information. Surely the desert species of *Myotis*, if not the others, are also specialized in renal physiology, morphology and water metabolism. Dalquest (1948) reports that both *Myotis californicus* (Audubon and Backman) and *Myotis yumanensis* (H. Allen) apparently drink saltwater.

Whether or not the characteristics common to both *M. vivesi* and the several old world species indicate convergence or a common phylogenetic origin is a question yet to be resolved. Certainly the present taxonomic arrangement appears illogical and inconsistent, and pending a revision of all the taxa concerned, we have considered *Pizonyx* a subgenus of *Myotis*.

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*CONOCARDIUM LANGENHEIMI* SP. N.  
(MOLLUSCA: BIVALVIA) IN THE LOWER PERMIAN SERIES  
OF THE McCLOUD LIMESTONE, NORTHERN CALIFORNIA

By EDWARD C. WILSON



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*CONOCARDIUM LANGENHEIMI* SP. N.  
(MOLLUSCA: BIVALVIA) IN THE LOWER PERMIAN SERIES  
OF THE McCLOUD LIMESTONE, NORTHERN CALIFORNIA

By EDWARD C. WILSON<sup>1</sup>

ABSTRACT: *Conocardium langenheimi* sp. n. (Mollusca: Bivalvia) occurs in the Wolfcampian Stage, Lower Permian Series of the McCloud Limestone in Shasta County, California. It is a large shell with a non-carinate posterior end, three pairs of perforate "shelves" within the gaping anterior end, a tube enclosed dorsally in the shell layers of each valve, unique internal hinge structures, and microstructure unlike most other bivalves. The functions of these and other characters is unknown. The entire Order Conocardidoida needs investigation to determine the significance of such characters, especially for placing the group in higher categories of classification.

INTRODUCTION

At the suggestion of R. L. Langenheim, Jr., Professor of Geology at the University of Illinois, I began a study of the paleontology of the McCloud Limestone in Shasta County, California, in the spring of 1963. Two previous papers (Wilson, 1967a, 1967b) resulted from this study and this paper is another contribution.

ACKNOWLEDGMENTS

I am grateful for opinions on the morphology and systematic position of the Conocardidoida from J. Wyatt Durham of the University of California at Berkeley, John Pojeta, Jr. of the U.S. National Museum, and Norman D. Newell of the American Museum of Natural History. Professor Durham kindly visited the type localities with me. Most of the photographs are by Lawrence S. Reynolds of the Los Angeles County Museum of Natural History.

Field work in 1963 and 1964 was financed in part by the University of California Museum of Paleontology (UCMP) and the University of California Committee on Research, both at Berkeley. The Los Angeles County Museum of Natural History (LACM) provided funds for further field work in 1968.

<sup>1</sup>Curator of Invertebrate Paleontology, Los Angeles County Museum of Natural History.

## SYSTEMATIC DESCRIPTION

Phylum MOLLUSCA

Class BIVALVIA Linnaeus, 1758

Order CONOCARDIDOIDA Neumayr, 1891

Family CONOCARDIIDAE Miller, 1889

Genus *Conocardium* Bronn, 1834

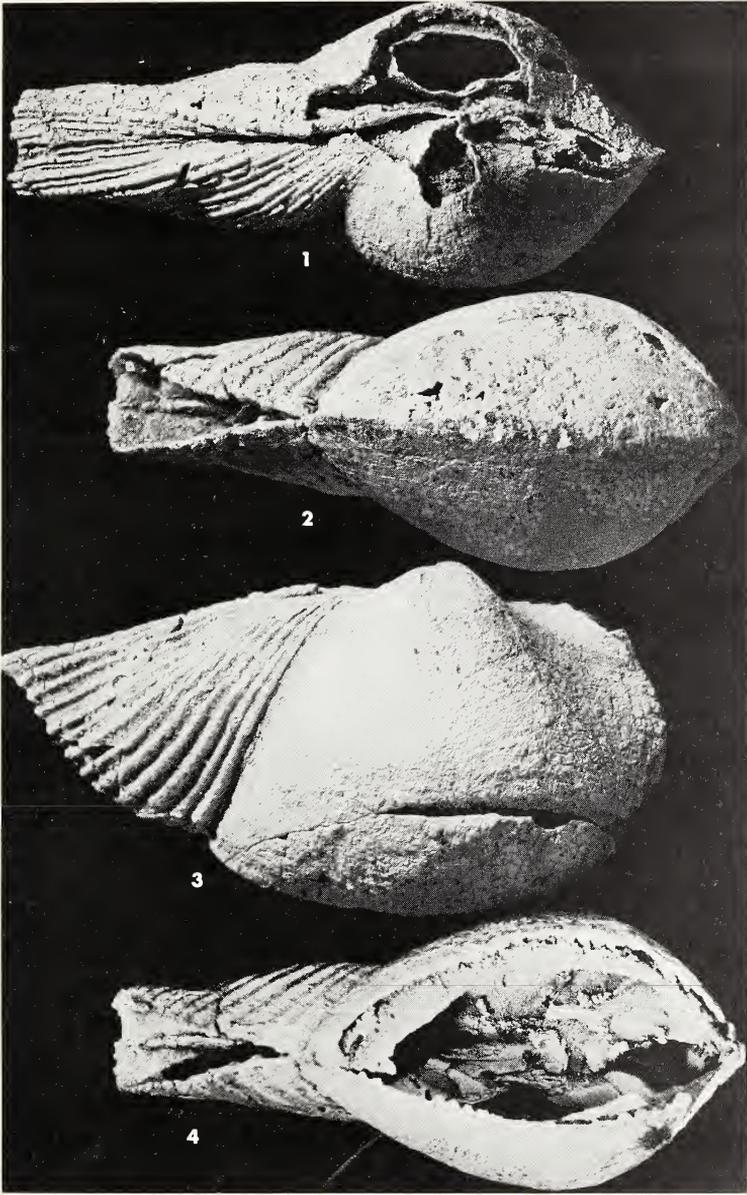
*Remarks:* Terminology has not been standardized for the unique characters of the Conocardidoidea. I have used where possible the terminology for other bivalve mollusks, although this is partially unsatisfactory. The structures called "auricles" are probably not homologous with the auricles of other bivalves. The "shelves" in the gaping anterior "auricle" are without parallel in the rest of the Bivalvia. The openings in the "shelves" and the tubes enclosed in the shells have no formal names. The kind of "teeth" on the ventral and posterior edges should probably be named. It is not even possible to use uniformitarianism to orient the shell with certainty. It may seem reasonable that dorsal and ventral are accurately delineated, but there is no such certainty about anterior and posterior. The figures and legends indicate usage of morphological terms in this paper.

*Conocardium langenheimi*, sp. n.

Fig. 1

*Description (external):* Valves equivalve, inequilateral, opisthogyrate, alate (?), not ankylosed; main body of valves inflated, rounded (not carinate posteriorly); posterior "auricle" small, sloping smoothly into main body of valves, not gaping; anterior "auricle" separated by constriction from main body of valves, large, rostrate, gaping anteriorly and ventrally, with large trigonal aperture having scalloped margins; hinge line straight, except anterior part of anterior "auricle" may dip to 25° (preservation?), occupied by groove, shallow in anterior part of anterior "auricle," deep in posterior part of anterior "auricle" and main body of shell; commissure straight on exterior of ventral parts of shells; holotype shell length 6.5 cm, height 4.3 cm, width 2.9 cm (largest specimen, LACM paratype 2443, is 4 mm. higher, but incomplete

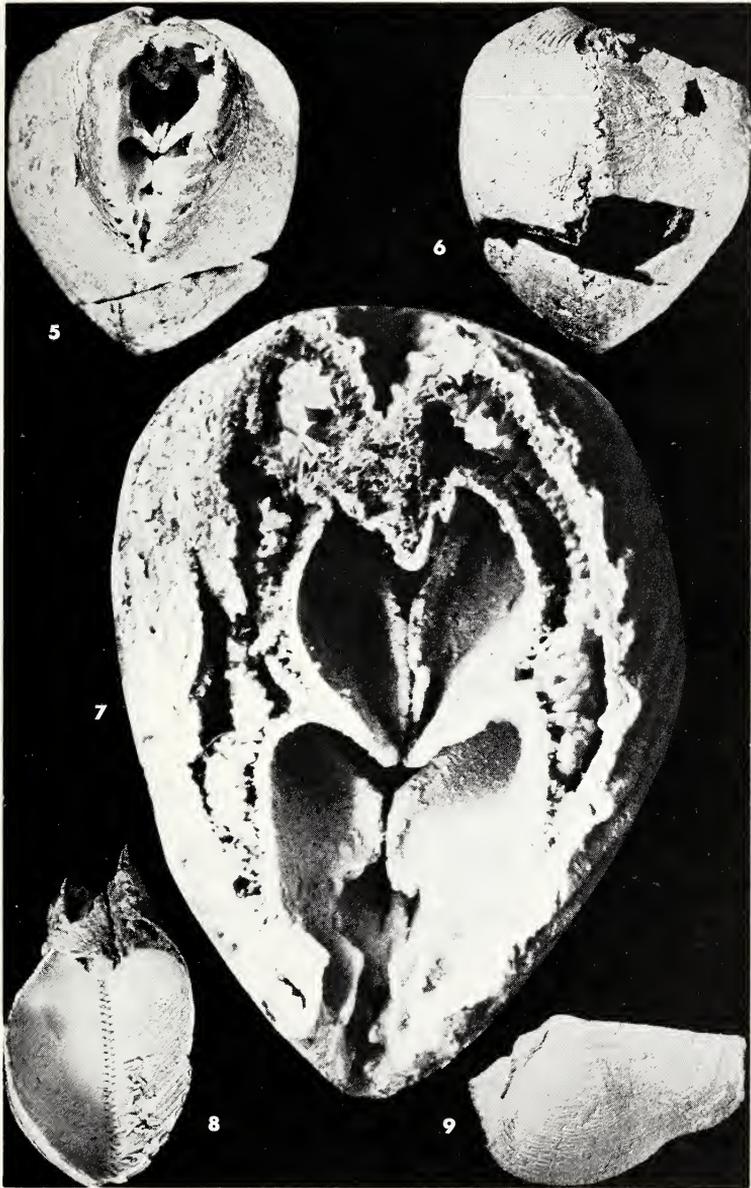
Figures 1-4. *Conocardium langenheimi* sp. n. UCMP holotype 10589, UCMP locality D-831, all figures X 1.3; (1) dorsal view, anterior "auricle" at left, posterior "auricle" at right, main body of shell inflated, openings in umbos caused by post-burial weathering, double wall caused by dissolution in HCl of calcareous layer between silicified layers, note absence of posterior carina; (2) ventral view, showing straight exterior commissure of main body, gape of anterior auricle, internal ridge at hinge line; (3) lateral view of left valve, sculpture on main body possibly dissolved in part during etching; (4) ventral view, with piece of shell removed to show dorsal interior, dorsal ridge along hinge line of main body broken with fragments lying in right valve, note trigonal cross sections of ridges remaining in shell wall after etching.



in other dimensions); sculpture concentric or cancellate (?) on main body of valves, with about 4 evenly spaced concentric riblets in one mm., with possible traces of radial riblets; sculpture radial on "auricles" (UCMP paratype 10590, juvenile, shows some concentric), about 17 ribs on anterior "auricle" of each holotype valve, fewer on posterior "auricle" (UCMP paratype 10590, juvenile, has 9 ribs on each posterior "auricle"); ribs straight to very gently sigmoid, sloping down from hinge line at angles varying from 65° on posterior part of anterior "auricle" to 25° on anterior part, flat topped with straight to rounded sides sloping down and out at less than 45°; rib interspaces about equal to rib widths, lirate, with about 20 dorsally convex lirae in 1 mm, rarely occupied by single riblet.

*Description (internal)*: Main body of valves smooth; pallial line, muscle scars not observed; ventral and posterior commissure zig-zag, formed by series of trigonal "teeth" and intervening sockets in each valve, 3 occurring every 5 mm each side of both valves (holotype), sockets showing plainly only in section ("teeth" are surficial extensions of radial rods, trigonal in cross section, apex pointing inward, that dorsally form part of the internal shell layer); hinge line a complex ridge, low in anterior end, becoming higher posteriorly, developing horizontal distal bar (inverted T-shaped in cross section) within main body cavity of valves, where narrow trough borders each side (marking lateral limits of apparent separate hinge plate in this area), becoming lower and broader posteriorly, troughs continuing alongside into posterior "auricle," where termination not observed because of preservation; 3 pairs of complex "shelves" lining lateral interior of anterior "auricle," sloping in and up same angles as exterior ribs, each pair meeting in midline, dividing "auricle" roughly horizontally into 4 unequal areas; dorsal pair of shelves beginning about 15 mm back of "auricle" anterior edge, about 8 mm below top of "auricle," forming large heart shaped opening in cross section above "shelves," turned up along midline by lip-like ridge, sloping upward, separating along midline below

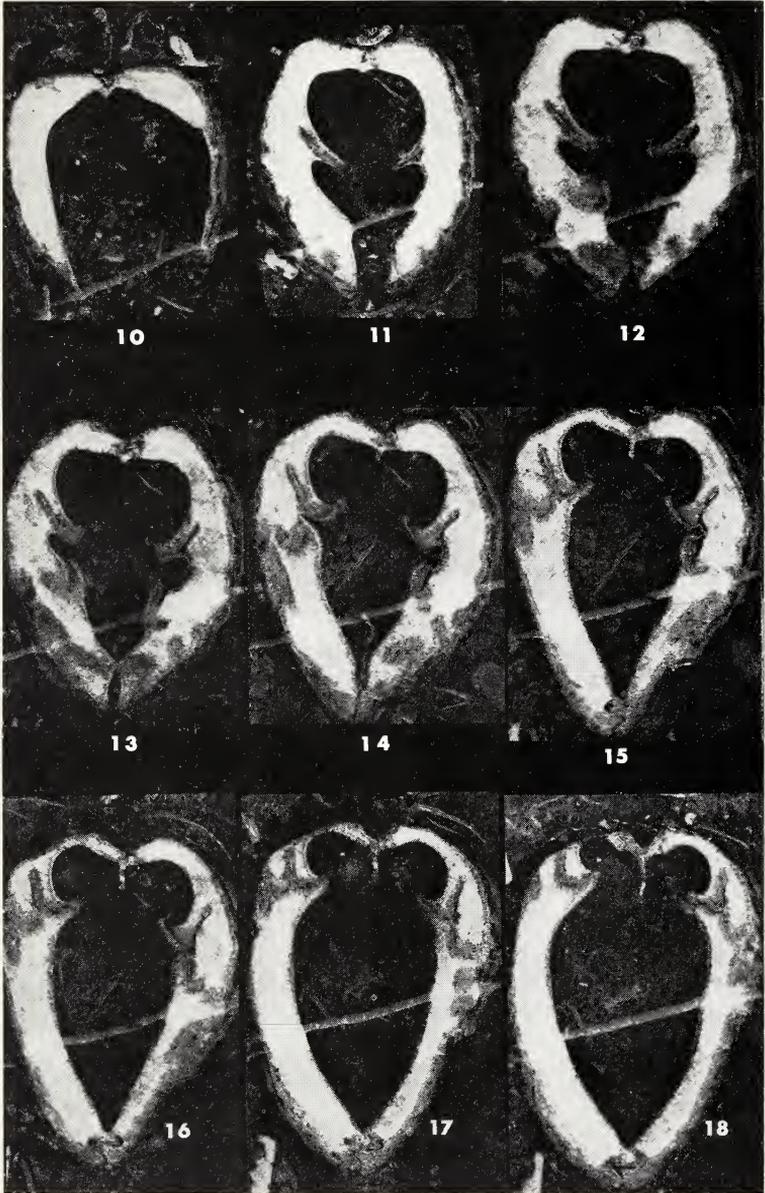
Figures 5-9. *Conocardium langenheimi* sp. n. (5) holotype, anterior view into gaping "auricle" showing 3 pairs of "shelves," X 1.3; (6) same specimen, posterior view, umbos partially weathered away, note zig-zag commissure of "auricle," straight commissure of main body, X 1.3; (7) same specimen, same view as figure 5 with part of auricle removed, missing parts of wall dissolved during etching, note exterior groove and interior ridge of hinge line with grooves bordering latter, dorsal "shelves" meeting along midline with opening into main body visible just above, middle shelves similar but extending anteriorly to form keyhole shaped opening, partly obscured small ventral "shelves" shaped like middle "shelves," X 3.6; (8) LACMNH paratype 2443, LACMNH locality 1133, fragment showing zig-zag interior ventral commissure formed of series of teeth and sockets, note left valve showing original smooth interior, right valve showing etched layer of shell wall with internal trigonal ridges which terminate ventrally as teeth, X 0.6; (9) UCMP paratype 10590, UCMP locality D-831, lateral view of right valve of juvenile specimen, note concentric sculpture on main body and anterior auricle, offset posterior "auricle," outline of anterior "auricle" varying from figure 3, X 1.4.



hinge line, leaving opening here into main part of shell, shelves continuing dorsally and posteriorly with lips incurving to form tubes passing into shell layers before leaving "auricle," tubes continuing posteriorly in shell above main body of shell, lateral to hinge line, becoming closer posteriorly and apparently dropping into external groove above hinge line, with posterior course unknown due to preservation (no apparent natural external opening observed in posterior "auricle" or hinge line); middle "shelves" also large, paralleling dorsal ones, similar in shape and slope, but extending to anterior edge of "auricle," forming key-hole shaped opening in anterior ends as well as heart-shaped opening posteriorly into main body of shell, with anterior lips as in dorsal "shelves," extending into grooves in "auricle" walls under dorsal "shelves" posteriorly, ending at posterior termination of dorsal "shelves," without continuing internal tube; ventral "shelves" small, shaped like middle "shelves."

*Description (microstructure)*: Preservation very imperfect, shell partially silicified, some layers separated by silica, some missing (erosion?) in places; shell calcium carbonate, 1.5 to 3.5 mm thick, with 3 layers throughout plus 3 highly restricted layers; exterior layer 0.33 to 1.0 mm thick, prismatic, distal crystal tips reflected ventrally, elsewhere normal to shell surface; middle layer 0.2 to 0.3 mm thick (generally replaced by silica and difficult to measure), lamellar, showing ventrally convex concentric growth lines crossed by finer radial lines, separated in places from prismatic layer by dark line (concholin?); inner layer 2 to 3 mm thick, much wider than other layers, formed of large calcium carbonate crystals (apparently recrystallized), showing residual (?) growth lines in some areas, etching in dilute hydrochloric acid in main body of shell into trigonal ridges (see above), evidence of which not observed in polished or thin sections; myostracum (?) in 3 bands in each valve, extending from opposed axial edges of "shelves" to umbos, straight to V-shaped in

Figures 10-18. *Conocardium langenheimi* sp. n. UCMP paratype 10591, UCMP locality D-831, specimen ground down from anterior to posterior to show successive cross sections, all figures X 2.2; (10) section near anterior of anterior "auricle," note great shell thickening (left) from thin anterior edge (right); (11) dorsal "shelves" begin to form, note rod like myostracum (?) protruding from "shelves," internal scalloped outline of outer shell layers; (12) three pairs of "shelves" forming, note deepening grooves between dorsal and middle "shelves"; (13) three pairs of "shelves" formed here, each with associated myostracum (?); (14) upper "shelves" move dorsally, curl inwards, middle "shelves" pass into two grooves, lower "shelves" have disappeared, internal dorsal ridge along hinge line begins to lengthen; (15) dorsal "shelves" move dorsally, other "shelves" disappear (groove extending from middle "shelf" on right still present), rods of myostracum (?) move dorsally in shell wall, teeth and sockets appear ventrally marking ventral beginning of main body of valves; (16) dorsal ridge lengthens, pre-burial erosion noticeable on dorsal edge of valve at left; (17) dorsal ridge lengthens; (18) dorsal ridge lengthens, dorsal edge of eroded valve thins, dorsal "shelves" move higher, accompanied by their myostracum (?) rods and those from two lower "shelves."



cross section (varies), about 0.2 mm thick, apparently exposed at "shelf" edges (indicates muscles joining opposing "shelves"?), showing concentric and radial lines as in middle layer.

*Name:* This species is named for R. L. Langenheim, Jr. in recognition of his contributions to our knowledge of the paleontology and stratigraphy of North America and for his inspiration and training of many students in this work.

*Type specimens:* Holotype UCMP 10589, paratypes UCMP 10590-10591, paratype LACM 2443, all UCMP locality D-831 (=LACM locality 1133); paratype UCMP 10592, UCMP locality D-819.

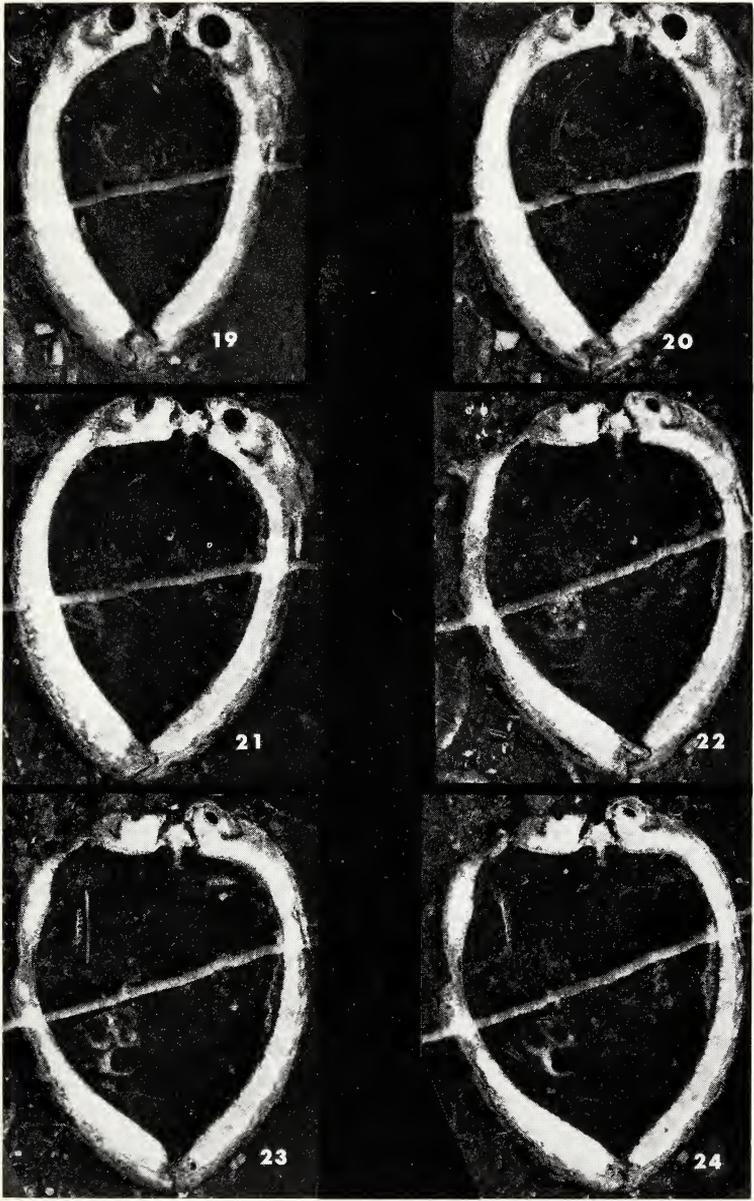
*Localities:* UCMP locality D-819. 1140 feet stratigraphically above the lowest exposure of the McCloud Limestone on the first spur south of the eastern end of the McCloud River bridge as shown in the northwest  $\frac{1}{4}$  of the southwest  $\frac{1}{4}$  of section 32, township 35 north, range 3 west of the United States Geological Survey topographic quadrangle (15 minutes, 1957) of Bol-libokka Mountain, Shasta County, California. Series of one foot high ledges of limestone, fine to medium grained, black to medium gray, weathering medium to light gray; little chert; many silicified fossils, including large caninoid corals, *Conocardium*, *Omphalotrochus*, fusulinids.

UCMP locality D-831 (= LACM locality 1133). Estimated 200 yards south of locality D-819 along strike and about 15 feet higher in the section. Narrow bench of thin-bedded, black, silty limestone below a sheer massive cliff. Abundant syringoporidae corals, very large solitary rugose corals, fusulinids, bryozoans, *Conocardium*.

*Age:* The fusulinids have the most refined stratigraphic ranges of the fossils found with *Conocardium langenheimi*. Two species were identified: *Pseudofusulina soluta* Skinner and Wilde, 1965 and *Triticites mulleri* Skinner and Wilde, 1965, both having type localities in the McCloud Limestone nearby the *Conocardium* localities. Skinner and Wilde (1965, pl. 4) considered the former fusulinid to indicate definite Permian age (the genus is a Wolfcampian index fossil) and the latter to be of either Pennsylvanian (Virgilian) or Per-

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Figures 19-24. *Conocardium langenheimi* sp. n. Continuation of sections of same specimen as figures 10-18, same magnification; (19) dorsal "shelves" have incurved and passed into tubes in shell wall, marking dorsal beginning of main body of valves, myostracum (?) rods now wholly within shell wall, dorsal ridge greatly lengthened and now having horizontal distal end (not clear in this photograph but see fig. 34), possibly developing into separate plate along hinge line, with lateral grooves internally, midline groove externally, tube at left opened by erosion; (20) dorsal tubes narrow, note ventral teeth showing how ventral commissure can be exteriorly straight yet interior zig-zag, also shows shell not ankylosed; (21) dorsal tubes narrow, dorsal ridge shortens; (22) dorsal tubes narrow and move toward midline, dorsal ridge shortens; (23) dorsal tubes narrow, valve at left badly eroded; (24) dorsal tubes smaller, dorsal ridge shorter, dorsal part of valves move ventrally, deepening external groove.



mian (Wolfcampian) age. It seems clear, therefore, that the interval of the McCloud Limestone from which *C. langenheimi* was collected is definitely occupied by Lower Permian Series, Wolfcampian Stage rocks.

*Diagnosis:* *C. langenheimi* can be separated readily from most other species because it lacks a carina on the posterior part of the main body of the shell. It is also larger than most species and the anterior "auricle" is proportionately longer in relation to the rest of the shell than in many other species.

*Discussion:* *C. langenheimi* resembles closely only *C. uralicum* (Verneuil, in Murchison, Verneuil, and Keyserling, 1845, p. 301, pl. 20, figs. 11a, 11b) from Upper Carboniferous rocks of the Ural Mountains. Both species lack posterior carinae and have elongate anterior "auricles." However, *C. uralicum* is smaller (length 36 mm) and has an anterior "auricle" that is much more elongate in proportion to its height than that of *C. langenheimi*. Internal structures and shell microstructure of *C. uralicum* are unknown as yet.

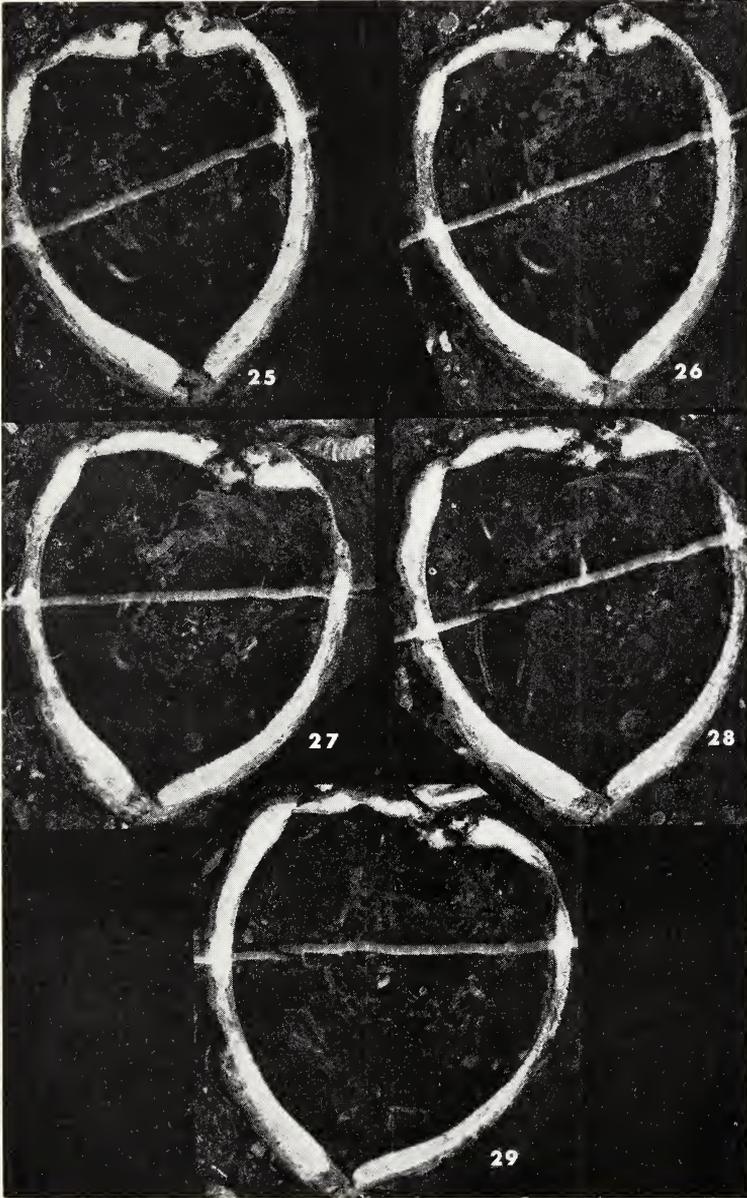
The microstructure of *C. langenheimi* apparently lacks "roofed-over pits" like those figured by Pannella and MacClintock (1968, pl. 8, fig. 5) in *C. sp.* from Upper Pennsylvanian rocks of Oklahoma. The "outer complex-prismatic shell layer" shown by Pannella, MacClintock, and Thompson (1968, fig. 1A) of *C. herculeum* Konick from Lower Carboniferous rocks of Belgium resembles a similarly positioned layer in *C. langenheimi*, but lacks the reflected tips that are present in the latter species.

The presence of complex internal structures in *Conocardium* was early reported by Hind (1900, p. 451, pl. 51, fig. 11a) in some detail, although he apparently worked from specimens somewhat worn internally. Curiously, no further refined work on them seems to have been published, although Dechaux (1952, p. 319, fig. 162a) and Branson, LaRoque, and Newell (1969, p. 859, fig. G1) cursorily discussed and figured some internal characters. Future workers should examine the internal structure of specimens of *Conocardium* with great care.

I have tried to find clues that would help determine the habitat and functional morphology of *C. langenheimi*. The associated fossils show that the salinity of the water must have been whatever was normal for the open oceans in Permian time. Permian near-shore faunas with restricted access to the sea in western North America generally lacked corals and fusulinids, both of which

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Figures 25-29. *Conocardium langenheimi* sp. n. Continuation of sections of same specimen as figures 10-24, same magnification; (25) dorsal ridge shorter but horizontal expansions of distal end still present, dorsal tube openings smaller (not seen in valve at left), some of dorsal part of valve at right shows erosion; (26) dorsal tube moves inward and downward, dorsal ridge shortens, distal expansions disappear, erosion of both valves and distortion of valve at left apparent; (27) continuation of movements seen in figure 26; (28) continuation, myostracum (?) rod (dark chevron) shows beside eroded tube in valve at right; (29) dorsal tubes move ventrally, hinge line plate broadens.

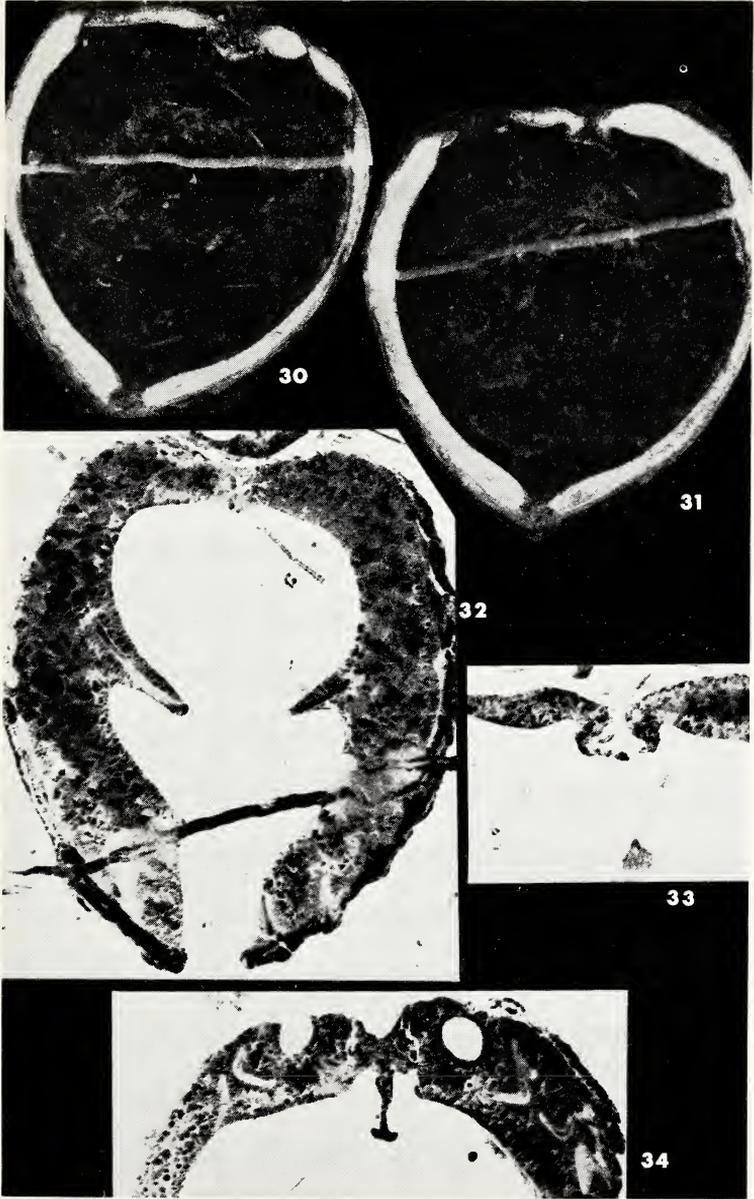


are abundant at the *C. langenheimi* localities. The shell itself is sturdy, especially the thick walled anterior "auricle," which suggests exposure to some strong current or wave action. Seemingly eroded parts of some of the specimens indicates that they may have been moved by currents from their original habitats. However, some fine silty layers in the limestone indicate that sedimentation was generally not rapid. None of the specimens shows evidence of having been buried in a burrow, which seems to me the most likely habitat by analogy with Recent bivalves of the most similar external form, size, and sturdiness (Pholadidae). Branson (1969, p. 860, figs. 3a, 3b, in Branson, LaRoque, and Newell) figured, but did not discuss, a restoration of a *Conocardium* apparently occupying a burrow, but having the anterior "auricle" innermost, which is unlike the Pholadidae. Nicol (1970, p. 70) also compared *Conocardium* with Recent bivalves, but reached the different conclusion that it "was attached by a short, stout byssus . . ." All the specimens of *C. langenheimi* appeared to be lying randomly on surfaces parallel to the bedding planes. They are all tightly closed pairs, which is unlike other Bivalvia, if one assumes because of the eroded areas that they were buried after death.

Reconstruction of the soft part morphology of *C. langenheimi* will not be simple. I have been unable to create a satisfactory model for incurrent and excurrent siphons. The complex form of the "shelves" indicates that some extremely specialized soft part morphology was present. The apparent absence of muscle scars in the anterior end may be explained by the existence of muscles between the edges of opposing "shelves," as suggested by the myostracum (?) exposed there. One would expect posterior muscles also, which seemingly are not represented by muscle scars or a posterior myostracum. Perhaps the function of the unique hinge line structures and the ventral and posterior "teeth" rendered posterior muscles unnecessary. The internal ridge along the hinge line looks greatly like a support, but one wonders for what, since the other bivalves seem to function well without such a rigid support for the ctenidia, alimentary canal, or other systems. It is tempting to postulate a

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Figures 30-34. *Conocardium langenheimi* sp. n. (30) continuation of sections of same specimen as figures 10-29, same magnification, dorsal tubes drop into exterior grooves bordering hinge line, dorsal ridge disappears; (31) same specimen, same magnification, dorsal tubes not present (preservation?), external grooves coalesce, with narrowed opening above, hole in shell at left caused by erosion, shell not preserved posterior to this section and nature of structures there unknown; (32) thin section made from polished section shown in fig. 11, note especially exposed end of myostracum (?) at edge of "shelf" at left and indeterminate nature of hinge articulation, X 3.2; (33) thin section made from polished section shown in fig. 31, showing nature of hinge and apparent absence of dorsal tubes seen in figs. 19-30, X 3.2; (34) thin section made from polished section shown in fig. 21, showing dorsal tubes, myostracum (?) layers, elongate internal hinge line ridge with horizontal distal bar, exterior ligament (?) groove, and apparent separate nature of plate along hinge line, X 3.2.



function such as brood chambers to the tubes in the dorsal parts of the valves, but, again, close analogies in living bivalves seem absent. Some of the grooves in the shell suggest ciliated tracts, but there is no certainty about this.

#### CONCLUSIONS

*C. langenheimi* is a member of the Conocardidoida, which is externally like the Bivalvia, has a world wide distribution, and ranges from Ordovician through Permian (Triassic?) rocks. The degree of complexity shown by the shell microstructure definitely appears to be molluscan. The paired valves suggest that the Order belongs in the Class Bivalvia, however the internal morphology and shell microstructure is unlike others in that class. If typical of the order, these suggest need for a reconsideration of the systematic position at the class or higher level.

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# CONTRIBUTIONS IN SCIENCE

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APRIL 17, 1970

FIVE NEW EPITONIID GASTROPODS FROM THE  
WEST COAST OF THE AMERICAS

By HELEN DUSHANE



LOS ANGELES COUNTY MUSEUM OF NATURAL HISTORY • EXPOSITION PARK  
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# FIVE NEW EPITONIID GASTROPODS FROM THE WEST COAST OF THE AMERICAS

By HELEN DUSHANE<sup>1</sup>

ABSTRACT: Five epitoniids (Mollusca: Gastropoda) are described as new, including (*Asperiscala longinosanum* from the west coast of Baja California, Mexico; *Epitonium (Asperiscala) macleani* from Ventana Bay, Baja California, Mexico; *Epitonium (Acirsa) cerralvoensis* from Cerralvo Island, Baja California, Mexico; *Epitonium (Acirsa) murrha* from Panama; and *Amaea contexta* from Guerrero, Mexico.

The epitoniid collections of the Los Angeles County Museum of Natural History (LACM), including those now on loan from the Allan Hancock Foundation, contain five new species described here. Two of the new species were dredged by the R/V *Velero III* in the 1930's and are from the Hancock Foundation Collection. Two are from a 1966 Museum expedition to the Cape San Lucas area of Baja California, sponsored by Mr. Richard Dwyer of Corona del Mar, on the R/V *Sea Quest*. One other new species was collected by Fred E. Lewis and remained unidentified until now.

## ACKNOWLEDGMENTS

I am grateful to the Los Angeles County Museum of Natural History for the opportunity to study their collections and for the help rendered by Dr. James H. McLean and Mr. Gale Sphon of the Invertebrate Zoology section. I also thank the photography department of the Museum for the illustrations.

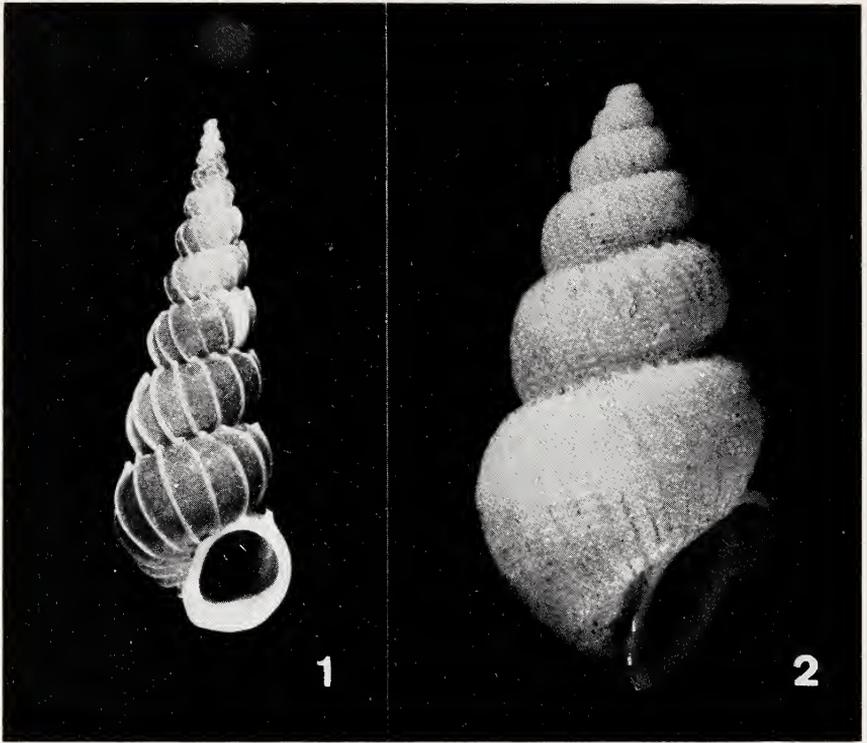
*Epitonium (Asperiscala) longinosanum*, sp. nov.

Fig. 1

*Diagnosis*: An elongate species with 11 low varices differing from all other epitoniids from the Panamic molluscan province in having a brown shell with white ribs and unevenly spaced minute spiral striae.

*Description*: Shell large, tall and slender, thin but strong, medium brown in color, shining, with 11 gradually enlarging, rounded whorls, nuclear whorls missing; suture distinct, varices white, 11, low and slightly reflected with a small, sharp spine on shoulder of whorl, varices continuous from whorl to whorl, an occasional costa thicker than others; spiral striations uneven, visible only under 10 X magnification; columellar lip curved, peritreme continuous, reflected over the ends of the varices, outer lip thickened by last varix; um-

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Figures 1-2. 1, *Epitonium (Asperiscala) longinosanum* sp. nov., holotype, LACM 1196. X 3; 2, *Epitonium (Asperiscala) macleani* sp. nov., holotype, LACM 1197. X 9.

bilicus lacking, operculum missing in holotype. Dimensions (in mm): length 16.5, width 5.5.

*Type Locality:* Rancho Inocentes, Baja California del Sur, Mexico, 23° 45' N, 110° 40' W. Collected by Captain Fred E. Lewis prior to 1945, one specimen.

*Type Material:* Holotype, LACM 1196.

*Discussion:* The coloring and 11 varices with sharp, shoulder spines distinguish *E. longinosanum* from all other west American epitoniids. It differs from *E. appressicostatum* Dall, 1917 (p. 482), which it most resembles, in having fewer costae, a less glassy surface, and fine spiral striations between the costae.

*Epitonium longinosanum* is named for José Longinos Martínez who established a museum of natural history in Mexico City in 1791 and the following year collected shells from La Paz to San Francisco (Longinos Martínez, 1938).

*Epitonium (Asperiscala) macleani*, sp. nov.

Fig. 2

*Diagnosis:* A small species differing from all others in having rounded whorls, numerous low axial costae of differing strengths and numerous fine spiral ribs.

*Description:* Shell small, white, fragile, with approximately 32 fine costae of varying size, nuclear whorls two, smooth, rounded, light brown, first postnuclear whorl with axial striations; remaining whorls six; suture distinct, deeply impressed; umbilicus small and nearly covered by peritreme; surface between whorls with raised spiral threads, approximately 28 on the body whorl; whorls rapidly expanding, rounded, basal disk or cord lacking; aperture oval (lip broken in holotype); operculum unknown. Dimensions (in mm): length 7.0; width 3.5 (holotype).

*Type Locality:* Off Punta Ventana, Baja California del Sur, Mexico (opposite Cerralvo Island), 24° 4' N, 109° 49' W, 15-25 fms, sand bottom, LACM Invertebrate Zoology locality 66-23, James H. McLean, Peter M. Oringer, and Louis Marincovich, R/V *Sea Quest*, 8 April 1966, ten specimens.

*Type Material:* Holotype, LACM 1197; 8 paratypes, LACM 1198; 1 paratype, DuShane Collection.

*Discussion:* This species differs from all others known from the Panamic province. Less globose than the brownish *Epitonium (Asperiscala) huffmani* DuShane and McLean, 1968 (fig. 1), it is white and has somewhat similar sculpture.

*Epitonium (Asperiscala) macleani* is named for Dr. James H. McLean, Curator of Invertebrate Zoology, Los Angeles County Museum of Natural History.

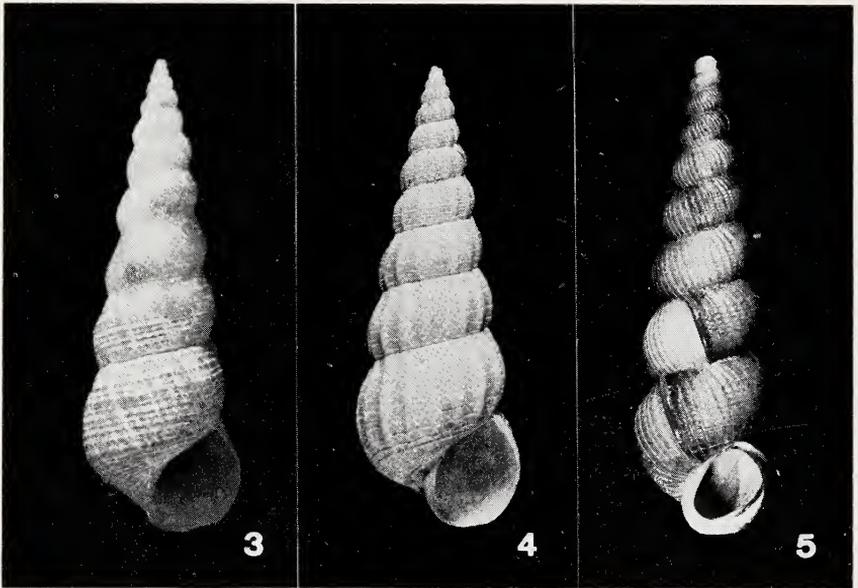
*Epitonium (Acirsa) cerralvoensis*, sp. nov.

Fig. 3

*Diagnosis:* A slender, pale brown species differing from other epitoniids from the Panamic molluscan province in having reduced axial costae and unevenly spaced spiral striae.

*Description:* Shell of medium size, tall and slender, thin but strong, light brown in color, with 10-12 gradually enlarging, rounded whorls, two opaque nuclear whorls; suture moderately impressed; axial ridges pale brown, 16 on the fourth whorl, gradually becoming obsolete on succeeding whorls, spiral ridges wider than the interspaces, 19 on last whorl; peritreme incomplete, lip thin, columella arched; no basal ridge; operculum horn colored, paucispiral. Dimensions (in mm): length 11.8, width 3.7 (holotype).

*Type Locality:* West side, Cerralvo Island, Baja California del Sur, Mexico, 24° 11' N, 109° 55' W, 7 fms, sand bottom, LACM Invertebrate Zoology locality 66-24, James H. McLean, Peter M. Oringer, and Louis Marincovich, R/V *Sea Quest*, 9 April 1966, two specimens.



Figures 3-5. 3, *Epitonium (Acirsa) cerralvoensis* sp. nov., holotype, LACM 1200. X 5; 4, *Epitonium (Acirsa) murrha* sp. nov., holotype, LACM 1232. X 3; 5, *Amaea (s.l.) contexta* sp. nov., holotype, LACM 1199. X 4.

*Type Material:* Holotype, LACM 1200; 1 paratype, LACM 1201. Although larger (15.3 mm in length), the paratype is worn and has several holes in the shell.

*Referred Material:* LACM 66-17, 10-20 fms off Cape San Lucas, Baja California, 1 specimen; LACM 66-17, 10-20 fms off Rancho Palmilla, Baja California, 1 specimen; LACM 66-20, 4 fms, Pulmo Bay, Baja California, 1 specimen; AHF 1051-40, 21 fms off Puerto Refugio, Angel de la Guardia Island, Baja California, 1 specimen.

*Discussion:* No other epitoniid from the west coasts of the Americas has sculpture like this species.

*Epitonium (Acirsa) cerralvoensis* is named for Cerralvo Island, its type locality.

*Epitonium (Acirsa) murrha*, sp. nov.

Fig. 4

*Diagnosis:* A large species with 19 low axial ribs over which the spiral sculpture crosses; differing from other *Acirsa* from the west coasts of the Americas in having more pronounced axial sculpture on the body whorl.

*Description:* Shell of medium size, white, texture of opaque china;

nuclear whorls two, opaque (first nuclear whorl missing in holotype), first postnuclear whorl with faint indication of axial sculpture; second postnuclear whorl with incised spiral lines; remaining convex whorls 10, gradually enlarging; 19 retractive axial ridges on body whorl giving a sinuous appearance; penultimate whorl with 15 spiral cords, uneven in width, separated by narrow, incised lines riding over the axial ridges; suture moderately impressed; basal ridge with 10-11 flat cords separated by incised lines; aperture oval, peritreme incomplete, umbilicus lacking, operculum unknown. Dimensions (in mm): length 19.1, width 6.9 (holotype).

*Type Locality*: Ten miles southwest of Secas Islands, Panama, 7° 51' 10" N, 82° 12' 05" W, 30 fms, gray sand, R/V *Velero* III station 944-39, 27 March 1939, one specimen.

*Type Material*: Holotype, LACM-AHF 1232.

*Discussion*: No other epitoniid from the west American coast has the color or sculpture of this species. The north Atlantic species, *Acirsa costulata* Mighels and Adams, 1842, figured by Clench and Turner (1950, p. 230) is similar in proportions but has weaker axial and spiral sculpture.

The name *murrha*, a Latin noun, meaning porcelain clay, refers to the chinalike surface of the shell. It is intended as a noun in apposition.

*Amaea (s.l.) contexta*, sp. nov.

Fig. 5

*Diagnosis*: An epitoniid differing from all other species in having many whorls, a dark brown color, numerous low axial ribs, and coarse spiral ribs.

*Description*: Shell of medium size, slender, dark brown, with four smooth, white, glassy nuclear whorls (missing in holotype), first postnuclear whorl axially ribbed; the following 10 whorls dark brown, convex; suture deeply impressed; axial sculpture of thin, strong ribs, about 24 on the body whorl, with occasionally a very heavy rib; these ribs continue to the columellar wall; spiral sculpture of about 18 ridges per whorl, beaded on the anterior face of the ribs; basal ridge present; outer lip formed by the extension of the last varix, aperture oval, umbilicus lacking; operculum lacking in holotype. Dimensions (in mm): length 15.4, width 4.5 (holotype).

*Type Locality*: Petatlan Bay, Guerrero, Mexico, 17° 31' 45" N, 101° 27' 34" W, 5-10 fms, hard sand and shell bottom, R/V *Velero* III station 265-34, 3 February 1934, one specimen.

*Type Material*: Holotype, LACM 1199.

*Referred Material*: Two smaller, damaged specimens with intact nuclear whorls were dredged by Laura and Carl Shy off Manzanillo, Colima, Mexico, in 5-10 fms, November 1967. These two specimens are uniformly dark brown, suggesting that the color of the holotype has faded.

*Discussion*: No other epitoniid from the west American coast is related

to this species. Sculpture is unique, making the generic allocation uncertain. Since the general features suggest *Amaea* H. and A. Adams, 1853, it is placed here provisionally.

The Latin name is derived from *contextus*, meaning interwoven, and refers to the woven texture of the axial and spiral sculpture.

#### RESUMEN

Cinco epítónidos (Mollusca: Gastropoda) se describen como nuevas especies, incluyendo (*Asperiscalia*) *longinosanum* de la costa oeste de la Baja California, México; *Epitonium* (*Asperiscalia*) *macleani* de la Bahía de Ventana, Baja California; México; *Epitonium* (*Acirsa*) *cerralvoensis* de la Isla Cerralvo, Baja California, México; *Epitonium* (*Acirsa*) *murrha* procedente de Panamá; y *Amaea contexta* de Guerrero, México.

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# CONTRIBUTIONS IN SCIENCE

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A GENERIC REVISION AND CATALOG OF THE WESTERN  
HEMISPHERE GLENURINI WITH THE DESCRIPTION OF A  
NEW GENUS AND SPECIES FROM BRAZIL  
(NEUROPTERA:MYRMELEONTIDAE)

*By* L. A. STANGE



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A GENERIC REVISION AND CATALOG OF THE WESTERN  
HEMISPHERE GLENURINI WITH THE DESCRIPTION OF A  
NEW GENUS AND SPECIES FROM BRAZIL  
(NEUROPTERA:MYRMELEONTIDAE)

By L. A. STANGE<sup>1</sup>

ABSTRACT: Studies of the type species of described glenurine genera have led to considerable new synonymy as follows: *Elachyleon* Esben-Petersen 1927 (= *Sericoleon* Esben-Petersen 1932); *Eremoleon* Banks 1901 (= *Incamoleon* Banks 1913, = *Sosa* Navás 1914, = *Cortesius* Navás 1914, = *Dobla* Navás 1926, = *Joergenia* Esben-Petersen 1932, = *Antilloleon* Banks 1943); *Psammoleon* Banks 1899 (= *Diazus* Navás 1914). *Pachyleon alvarengai*, new genus and new species, is described from Mato Grosso, Brazil. Eight genera are now recognized and a key is given for their identification. Each genus is characterized and briefly discussed, including new synonyms. A complete bibliography and catalog is provided for the Western Hemisphere Glenurini. New information contained in this catalog includes the following new species synonyms: *Psammoleon cautus* (Walker) 1853 (= *Feinerus nebulosus* Navás 1922); *Psammoleon serrei* (Navás) 1920 (= *Formicaleo chaperi* Navás 1922); *Glenurus peculiaris* (Walker) 1859 (= *Glenurus brasiliensis* Navás 1920); *Eremoleon macer* (Hagen) 1861 (= *Hesperoleon atomarius* Navás 1933). Also a number of new combinations are indicated. The tribe Dimarellini Markl 1954 is now considered a synonym of the Glenurini Banks 1928. The tribe Glenurini is now referred to the subfamily Myrmeleontinae.

INTRODUCTION

The tribe Glenurini is one of the largest tribes of antlions in the world in numbers of described genera. Markl (1954:246) lists 30 genera of Glenurini from all major zoogeographical regions of which sixteen are restricted in distribution to the Western Hemisphere. However, no modern comprehensive generic study has ever been made of the Glenurini. Furthermore the definition of the tribe is probably deficient judging from the paucity of taxonomic characters given by Markl (1954, p. 245) and earlier authors. The present account deals only with the glenurine genera of the Western Hemisphere. An attempt is made to signal taxonomic characters of importance and to point out the variation that exists in others that have been used in the classification of the tribe. Terminology is adopted from Stange (1970).

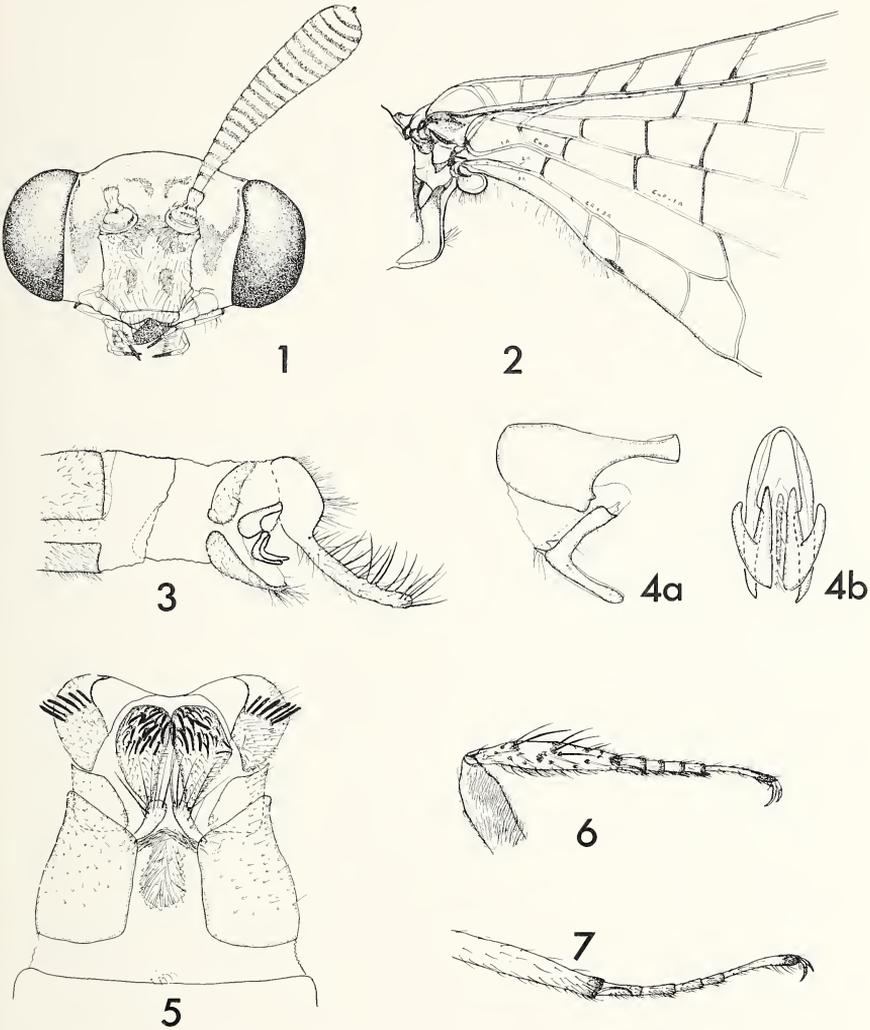
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## ACKNOWLEDGMENTS

Study of nearly all of the types of the type species of glenurine genera by me was made possible only by the cooperation of numerous individuals and organizations. I am especially indebted to the Society of Sigma Xi for a Grant-in-Aid of research which enabled me to study type material in Europe during the summer of 1964. I would also like to thank Dr. S. L. Tuxen, Copenhagen University, and Dr. Max Beier, Vienna Museum, for the loan of type material. The following list of collections mentioned in the present study also includes the names of persons who facilitated my studies: AMNH, American Museum of Natural History, Dr. Jerome Rosen; Barcelona, Museo de Zoología, Barcelona, Dr. Francisco Español Coll.; Berlin, Institut für spezielle Zoologie und zoologisches Museum, East Berlin, Dr. E. Königsmann; BM(NH), British Museum (Natural History), London, Mr. D. E. Kimmins; CAS, California Academy of Sciences, Dr. Edward Ross; Copenhagen, Universitets Zoologiske Museum, Copenhagen, Dr. S. L. Tuxen; Greifswald, Zoologisches Institut und Museum, Ernst-Moritz-Arndt-Universität, Greifswald. Dr. Iselotte Groth. Halle, Zoologisches Institut, Martin-Luther-Universität, Halle-Saale, Dr. J. O. Hüsing; Havana, Instituto de Biología, La Habana; LACM, Los Angeles County Museum of Natural History, Dr. Charles Hogue; La Plata, Museo de La Plata, Facultad de Ciencias Naturales, La Plata, Prof. Luis De Santis; MACN, Museo Argentino de Ciencias Naturales, Buenos Aires, Dr. Manuel Viana; MCZ, Museum of Comparative Zoology, Harvard University, Dr. Howard Evans; Paris, Muséum National d'Histoire Naturelle, Paris, Miss S. Kelner-Pillault; Hamburg, Zoologisches Staatsinstitut und Zoologisches Museum, Hamburg; Turin, Instituto e Museo di Zoologia, Università di Torino, Turin; USNM, United States National Museum, Dr. Oliver Flint; Vienna, Naturhistorisches Museum, Vienna, Dr. Max Beier; Zaragoza, Colegio del Salvador, Zaragoza.

## SYSTEMATIC POSITION OF THE GLENURINI

Banks (1943, p. 166) classified genera of the Glenurini in the subfamily Macronemurinae. Markl (1954) published a comprehensive world classification of the Myrmeleontidae but eliminated subfamilies and only dealt with tribes. Stange (1968) placed the Glenurini in the subfamily Dendroleontinae. My attempts to provide a satisfactory definition of the Dendroleontinae from the Myrmeleontinae have now convinced me that this separation can not be maintained. Therefore I consider the subfamilies Dendroleontinae and Macronemurinae to be synonyms of the Myrmeleontinae. Essentially only two venational characters have been employed in the past for separating these subfamilies. One is the condition of vein 2A of the forewing. In some groups (*Dendroleon* and *Brachynemurus*) vein 2A is evenly curved from its base to its termination whereas it is strongly angled in *Myrmeleon* L, *Macronemurus* (an old world genus), and in nearly all of the Glenurini. However the close struc-



Figures 1-7: *Pachyleon alvarengai*. 1. Head of holotype. 2. Base of forewing. 3. Male terminalia (right ectoproct removed). 4. Male genitalia (a) side view; (b) posterior view. 5. Female terminalia, ventral view. 6. Foreleg of holotype, apex of femur, tibia and tarsus. 7. Hindleg of holotype, apex of tibia and tarsus.

tural resemblance between *Dendroleon* and some genera of the Glenurini (i.e. *Glenurus*) argues against such an extreme separation. Furthermore vein 2A shows some variation in the Glenurini. In a new genus to be described later in this paper, vein 2A is closely associated with 3A and not with 1A as is typical in the tribe. Also in an undescribed species (*Mystroleon praedator* Sensu Banks) vein 2A is intermediate in condition between typical Glenurini and Dendroleontini. For these reasons I consider this character insufficient for separating subfamilies. The second venational character that has figured prominently in subfamily classifications is the number of hindwing presectoral cross veins. In the Myrmeleontinae there are four or more such crossveins whereas the typical number in the Dendroleontinae is one. However, within the tribe Brachynemurini, which I consider closely related to the Glenurini, there are sometimes several crossveins depending upon the point of origin of the radial sector. This indicates that the number of presectoral crossveins is of limited value as a subfamily character.

Markl (1954) recognizes numerous tribes that are referable to the Myrmeleontinae. Probably many of these are invalid. Markl defines the Glenurini almost entirely on wing venational characters some of which I have found to be variable. Markl emphasizes the forking of forewing veins 2A and 3A. In the Glenurini, Nyutini (restricted to Africa) and Dimarellini (restricted to the Neotropical Area), vein 2A is forked and 3A is simple. Other related tribes, all restricted to the Eastern Hemisphere, have vein 2A simple and 3A forked. This condition is given for the Formicaleontini, Creoleontini, Obini, Nemoleontini and Protoplectrini. However this character is variable, even at the specific level in some instances. In the glenurine genus *Eremoleon*, most species fit the concept of Markl (vein 2A forked, 3A simple in *insipidus*, *longior*, etc.) but other species show the opposite condition (as in some *nigribasis*). Therefore this character is of limited taxonomic importance. Another venational character that Markl uses in differentiating the Glenurini (from the Dimarellini and Nyutini) is the presence of the anterior banksian line. This prominent longitudinal line is found in either wing and is formed by the bending of the branches of the radial sector. It is highly variable in its development in the genus *Brachynemurus*, a member of the related tribe Brachynemurini. In the tribe Glenurini, nearly all of the Western Hemisphere species that I have examined show no development of the banksian lines. It is apparent that Markl was in error employing this character in the diagnosis of the Glenurini (at least the Western Hemisphere component).

Markl (1954, p. 247) defined the tribe Dimarellini on venational characters which Stange (1963, p. 810) criticized. Stange offered the character of the pretarsal claws as a possible means of separating the Dimarellini from the Glenurini. With this new criterion the genera *Elachyleon* and *Navasoleon* were removed from the Glenurini and placed with *Dimarella* in the Dimarellini. In these three genera the pretarsal claws are capable of closing against the distal

tarsomere whereas the claws are ordinary in other genera. However it is now apparent that this specialized condition of the pretarsal claws have evolved several times in unrelated groups of Myrmeleontidae as evidenced by the occurrence of this character in the Dendroleontini (*Tricholeon* Esben-Petersen from Africa; *Froggattisca* Esben-Petersen from Australia) and in the Glenurini (*Megistopus* Rambur from Europe). The genus *Elachyleon*, possessor of the specialized pretarsal claws, agrees with the glenurine genus *Eremoleon* in all generic level taxonomic characters except the condition of the pretarsal claws. Thus, I now consider the pretarsal claw character to be a generic character. In search of a possible new means of maintaining the tribe Dimarellini I have reconsidered all the specialized features of the genus *Dimarella*. The members of this genus differ from other Glenurini in the following characters: (1) wing venation (CuP + 1A run parallel with the posterior fork of forewing CuA); (2) antennal fossa widely separated from eye; (3) male ectoproct with elongate postventral lobe; (4) form of the male gonarcus (large lateral expansions) and shape of the parameres (not in the form of flat plates). A new genus to be described later in this paper also shares these characters (but has ordinary pretarsal claws). However recent study of the poorly known species *Psammoleon-cautus* has revealed that this species is intermediate between the genus *Dimarella* and the glenurine genus *Psammoleon*. This species appears to be a rather ordinary *Psammoleon* in regards to the wing venation, head structure and legs but possesses the elongate postventral lobe of the male ectoproct as in *Dimarella* as well as comparable development of the male gonarcus and parameres.

From the foregoing discussion it is apparent that we are confronted with a weak tribal classification of the Myrmeleontinae. More study is needed of the Old World genera of the Glenurini as well as of the related Old World tribes Formicaleontini, Creoleontini, Obini, Nemoleontini, Protoplectrini and Nyutini before a satisfactory world-based classification can be given. The new world tribe Dimarellini can not be maintained and I now consider *Dimarella* as a rather specialized genus of the Glenurini.

In the Western Hemisphere there is less diversity in the Myrmeleontinae, at least from the point of view of described tribes. The following key will distinguish the Glenurini from other Western Hemisphere groups of antlions.

1. Sensory pit of the distal labial palpomere slitlike; hindleg with femoral sense hair or femoral sense hair absent.....*Palparinae* and *Acanthaclisinae*  
Sensory pit of the distal labial palpomere oval-shaped; femoral sense hair present on foreleg and midleg (except few species of *Brachynemurus*) but not on hindleg.....(*Myrmeleontinae*) 2
2. Forewing vein 2A evenly curved from base to hind margin, widely separated from 3A at least at basal one-half.....*Dendroleontini* and *Brachynemurini*  
Forewing vein 2A runs close to vein CuP + 1A for a short distance, then

- abruptly angles toward hind margin or veins 2A and 3A closely associated.... 3
3. Radial sector of hindwing arises beyond cubital fork, four or more presectoral crossveins present; pilula axillaris present.....*Myrmeleontini* and  
.....*Porrerini*  
Radial sector of hindwing arises well before cubital fork, one (rarely two or three) presectoral crossveins present; pilula axillaris absent.....*Glenurini*

#### WESTERN HEMISPHERE GENERA OF THE GLENURINI

All of the glenurine genera known from the Western Hemisphere are restricted to that area. It is possible that this reflects the regionalism of former workers on this group since no modern world study has been made. Even the Nearctic and Neotropical faunas of the Glenurini have not been treated together. Banks provided keys to the Nearctic genera (1928) and the Neotropical genera (1943). The Nearctic fauna is relatively small. The three genera represented in this region are also found in both the North American and South American Neotropical areas. All of the new world glenurine genera are found in South America and three of these are restricted to that continent. Twenty-four generic names have been proposed for the Western Hemisphere Glenurini. Some of these have been placed in synonymy. My study of nearly all of the type species of Western Hemisphere genera of the Glenurini has led to the discovery of further generic synonymy. In the following account of the glenurine genera this synonymy will be discussed.

#### **Araucoleon Banks**

*Araucoleon* Banks, 1938. Proc. Ent. Soc. Wash. 40:127.

Type-species: *Araucoleon inca* Banks, by original designation.

*Description:* Antennal fossa separated from ocular rim by less than greatest diameter of pedicel; antenna long and slender; pronotum longer than wide; mesoscutellum smaller than metanotum; all legs about equal in length; tibial spurs longer than forecoxal length; pretarsal claws not capable of closing against distal tarsomere; forewing with anterior margin abruptly angled and swollen near coalescing of subcostal and radial veins, costal area at this point nearly twice as high as at middle of wing; forewing radial sector originates well basad to forking of CuA; posterior fork of forewing vein CuA at an oblique angle to hind margin; forewing vein 2A widely separated from normal 3A before strong angle; hindwing vein CuA ends well before midpoint to forking of MP<sub>2</sub>; male ectoproct simple, without postventral lobe; male paramere in form of rigid plate; male gonarcus not greatly expanded laterally.

*Discussion:* This genus is rare in collections. I have seen only two males of the type-species. In addition, *Glenurus withycombei* Esben-Petersen, described from Trinidad, belongs to *Araucoleon*. This species is known only from the holotype female. This genus appears to be allied with *Eremoleon* Banks

but differs from that genus and other known glenurine genera by the swelling of the forewing costal margin near the point of coalescing of the subcostal and radial veins and by the termination of vein CuA of the hindwing well before the midpoint between the wing base and forking of  $MP_2$ .

### **Dimarella** Banks

*Dimarella* Banks, 1913. Trans. Amer. Ent. Soc. 39:229.

Type-species: *Eremoleon angustus* Banks, by original designation.

*Description*: Antennal fossa separated from ocular rim by more than greatest diameter of pedicel; antenna variable in length; pronotum wider than long; mesoscutellum as long as metanotum; legs different in lengths, often midleg shortest; tibial spurs much shorter than forecoxal length; pretarsal claws capable of closing against distal tarsomere; forewing with anterior margin evenly curved toward apex, costal area at point of coalescing of subcostal and radial veins usually lower than at middle of wing; forewing radial sector originates well beyond forking of CuA; forewing vein CuP + 1A runs parallel with posterior branch of CuA for a long distance; forewing vein 2A usually widely separated from normal 3A before strong angle toward posterior margin; hindwing vein CuA ends near forking of  $MP_2$ ; male ectoproct with elongate post-ventral lobe; male paramere with hook; male gonarcus expanded laterally as a round plate; female ectoproct with strong digging setae ventrally, shorter than on lateral gonapophyses.

*Discussion*: *Dimarella* is limited to the Neotropical Region. Synonymical notes on the genus were given by Stange (1963;1968). The Mexican species were revised by Stange (1963). This genus stands apart from other described genera by the prominent postventral lobe of the male ectoproct, the parallel course of veins CuP + 1A and CuA of the forewing and the wide space between the ocular rim and antennal fossa. All of these features are shared with a new genus to be described later in this paper. The specialized pretarsal claws is a morphological trait shared only with *Navasoleon* and *Elachyleon*.

### **Elachyleon** Esben-Petersen

*Elachyleon* Esben-Petersen, 1927. Ann. Mag. nat. Hist. (Ser. 9) 20:348. Type-species: *Elachyleon punctipennis* Esben-Petersen, by original designation.

*Sericoleon* Esben-Petersen, 1932. Vidensk. Medd. Dansk. naturh. Foren 94:114. Type-species: *Sericoleon paessleri* Esben-Petersen, by original designation. *New Synonymy*.

*Description*: Antennal fossa separated from ocular rim by less than greatest diameter of pedicel; antenna long and slender; mesoscutellum shorter than metanotum; all legs about equal in length; tibial spurs shorter than forecoxal length; pretarsal claws capable of closing against distal tarsomere; forewing with anterior margin evenly curved toward apex, costal area at point

of coalescing of subcostal and radial veins either somewhat lower or higher than at middle of wing; forewing radial sector originates only somewhat before forking of CuA or well beyond; posterior fork of forewing vein CuA at an oblique angle to hind margin; forewing vein 2A widely separated from normal 3A before strong angle toward posterior margin; hindwing vein CuA extends nearly to forking of MP<sub>2</sub>; male ectoproct simple, without postventral lobe; male paramere in form of rigid plate; male gonarcus not greatly expanded laterally; female ectoproct usually with weak digging setae; posterior gonapophysis longer than wide, digitiform.

*Discussion:* I have studied one of the paratypes of the type-species of *Sericoleon*, *S. paessleri* Esben-Petersen, described from Chile. This species possesses all of the generic characters of *Elachyleon* and therefore I am placing *Sericoleon* in synonymy with *Elachyleon*. *Elachyleon* can be distinguished from all other Western Hemisphere Myrmeleontidae by the specialized pretarsal claws, except for *Navasoleon* (which lacks tibial spurs) and *Dimarella* (which has forewing veins CuP + 1A and CuA parallel). This genus agrees closely with *Eremoleon* in both morphological and biological characters. I have reared an undescribed species from Mexico and from Argentina. Both species are found in the silt floors of caves. This is the same habitat for various species of *Eremoleon*. *Elachyleon* is now constituted of four described species. The most widespread species, *E. punctipennis* (ranges from Mexico to Argentina) has been illustrated in part by Stange (1963). Additional generic synonymy is given by Stange (1968).

#### **Eremoleon** Banks

- Eremoleon* Banks, 1901. Trans. Amer. Ent. Soc. 27:366. Type-species: *Myrmeleon macer* Hagen, by original designation.
- Incamoleon* Banks, 1913. Trans. Amer. Ent. Soc. 39:229. Type-species: *Psammoleon punctipennis* Banks, by original designation. *New Synonymy*.
- Sosa* Navás, 1914. Broteria 12:218. Type-species: *Sosa conspicuus* Navás, by original designation. *New Synonymy*.
- Cortesi* Navás, 1924. Broteria 21:107. Type-species: *Cortesi* *genini* Navás, by original designation. *New Synonymy*.
- Dobla* Navás, 1926. Deutsch. ent. Zeitschr. :428. Type-species: *Dobla arcuata* Navás, by original designation. *New Synonymy*.
- Joergenia* Esben-Petersen, 1932. Vidensk. Medd. Dansk. naturh. Foren 94:118. Type-species: *Joergenia pulchra* Esben-Petersen, by original designation. *New Synonymy*.
- Antilloleon* Banks, 1943. Bol. ent. venezolana 2:168. Type-species: *Glenurus cerverai* Navás, by original designation. *New Synonymy*.

*Description:* Antennal fossa separated from ocular rim by less than great-

est diameter of pedicel; antenna long and slender; pronotum variable, usually longer than wide; mesoscutellum shorter than metanotum; legs about equal in length except usually hindlegs longer; tibial spurs variable in length, usually shorter than forecoxal length; pretarsal claws not capable of closing against distal tarsomere; forewing with anterior margin evenly curved toward apex, costal area at point of coalescing of subcostal and radial veins usually lower than at middle of wing; forewing radial sector originates somewhat before forking of CuA or well beyond; posterior fork of forewing vein CuA at an oblique angle to hind margin; forewing vein 2A widely separated from normal 3A before strong angle toward posterior margin; hindwing vein CuA extends nearly to forking of MP<sub>2</sub> or somewhat beyond; male ectoproct simple without postventral lobe; male paramere in form of rigid plate; male gonarcus not greatly expanded laterally; female ectoproct usually with weak digging setae; posterior gonapophysis longer than wide, digitiform.

*Discussion:* There is considerable new generic synonymy in addition to that reported by Navás (1916) Banks (1928) & Adams (1957, 1958). These new synonyms will be discussed in chronological order.

*Incamoleon* Banks 1913—The type-species of this genus, *punctipennis* Banks, was originally described in the genus *Psammoleon*. Banks separated this species in its own genus apparently based on the longer, more slender legs of *punctipennis*. Also the wing shape is more slender than in *Psammoleon*. All of these features are found in the genus *Eremoleon*. Banks (1943:166) distinguishes *Incamoleon* from *Eremoleon* (= *Glenopsis* Banks) by the relative length of the tarsomeres. In *Incamoleon* the distal tarsomere is about equal to the other tarsomeres together whereas in *Eremoleon* the distal tarsomere is shorter. However my studies on *Incamoleon punctipennis* have revealed that this tarsomere proportion character is not constant and although useful for identification it is not important enough for generic distinction. Further studies have revealed two characters found in *Incamoleon* that are unknown in other *Eremoleon*. First, there is marked sexual dimorphism. The female wings usually have conspicuous dark spots, whereas the wings are not spotted (or only weakly so) in the males. Also the female genitalia appear somewhat distinct in that the posterior gonapophysis is more inflated than in other members of the genus *Eremoleon*. However I am of the opinion that these two characters are not sufficient to maintain *Incamoleon* as a distinct genus so that I am now referring *punctipennis* to the genus *Eremoleon*.

*Sosa* Navás 1914—I studied the holotype female of the type-species, *Sosa conspicuus*, in 1962 from the collections of the Vienna Museum. Navás gave few notes in his original description as to the basis of this new genus but did point out that it was related to *Formicaleon* (an old world genus) but with longer and more slender legs and that the genus might belong to the Dendroleontini. However my studies of the holotype revealed no important differences from the current generic concept of *Eremoleon* Banks. *Sosa conspicuus* re-

sembles *Eremoleon macer* (Hagen) except that the wings are more slender. This species is now placed in *Eremoleon*.

*Cortesi* Navás 1924—I studied the two syntypes of the type-species, *Cortesi* *genini* Navás, in the Paris Museum in 1964. Navás (1924:107) did not give much information in his original description as to the relationships of this genus except to point to a similarity with the genus *Glenurus* Hagen. My studies revealed that *Cortesi* *genini* agrees with all generic characters of *Eremoleon*. The only unusual feature of this species is that the forewing costal area is biareolate to triareolate. Interconnected crossveins in the costal area are found otherwise only in the genus *Psammoleon* among the *Glenurini*.

*Dobla* Navás 1926—The holotype female of the type-species, *Dobla arcuata* Navás, is located in the Paris Museum. My studies of the holotype indicate that it is a synonym of *Cortesi* *genini* Navás. Therefore the genus *Dobla* is a synonym of *Eremoleon* Banks.

*Joergenia* Esben-Petersen 1932—I have just recently received for study the holotype female of the type-species, *Joergenia pulchra* Esben-Petersen, on loan from the Copenhagen Museum. Although this species is quite distinctive by virtue of the unusual narrowing of the wings, especially of the costal area, I have not found characters that would warrant generic separation from *Eremoleon*. There is considerable range in the relative broadening of the costal area in *Eremoleon* and I am of the opinion that *J. pulchra* represents one extreme. The other extreme, broadening of the costal area, is exemplified by *E. genini* (Navás) and *E. anomalus* (Rabur), whereas intermediate conditions are found in *E. conspicuus* (Navás), *E. gracile* Adams and many others. I have also seen an undescribed species of *Eremoleon* from Venezuela which has the costal area nearly as narrow as in *J. pulchra*.

*Antilloleon* Banks 1943—I have studied the type material of the type-species, *Glenurus cerverai* Navás, in the collections of the Museum of Comparative Zoology, Harvard University. Banks (1943:167) pointed out the unusual venational feature present in the Caribbean species. The radial sector originates only a little beyond the level of forking of CuA in the forewing. In most other species of the *Glenurini* the radial sector originates well beyond the forking of CuA. However in the genus *Araucoleon* Banks, the radial sector originates well before the forking of CuA, a peculiarity in the *Glenurini*. In other respects *A. cerverai* Navás agrees well with species of the genus *Eremoleon*. Considerable variation is present in the genus *Eremoleon* in the relative position of the origin of the radial sector and forking of CuA. I am, therefore, of the opinion that *Glenurus cerverai* belongs to the genus *Eremoleon*, *Antilloleon* thus falling as a synonym of *Eremoleon*.

Revisionary studies are needed of the genus *Eremoleon* which appears to be a complex taxon. Adams (1957) presented a key to most of the Nearctic species. There is no one key character of the genus which permits easy recognition, although the genus differs considerably from other glenurine genera

except *Elachyleon* Esben-Petersen, which has specialized pretarsal claws. I have reared four species of *Eremoleon* (from Arizona, Mexico and Argentina) and all exhibit similar biological characteristics. The larvae live in the silt of caves or rock crevices and seem to be good climbers.

### **Glenurus** Hagen

*Glenurus* Hagen 1866. Stettin. ent. Ztg. 27:372.

Type-species: *Formicaleo grata* Say.

*Description*: Antenna fossa separated from ocular rim by less than greatest diameter of pedicel; antenna long and slender; mesoscutellum shorter than metanotum; all legs about equal in length except hindlegs usually somewhat longer; tibial spurs longer than forecoxal length; pretarsal claws not capable of closing against distal tarsomere; forewing with anterior margin evenly curved toward apex, costal area at point of coalescing of subcostal and radial veins somewhat lower or higher than at middle of wing; forewing radial sector originates well beyond forking of CuA; posterior fork of forewing vein CuA at an oblique angle to hind margin; forewing vein 2A widely separated from normal 3A before strong angle toward posterior margin; hindwing vein CuA extends nearly to or somewhat beyond forking of  $MP_2$ ; male ectoproct simple without postventral lobe; male paramere in form of rigid plate; male gonarcus not greatly expanded laterally; female ectoproct with prominent digging setae; posterior gonapophysis weakly produced as a swelling.

*Discussion*: This is a very homogeneous genus easily recognized by the considerable brown suffusion of the wing apices. *G. heteropteryx* is the only known species that lacks this prominent suffusion in the forewing, although the hindwing conforms with the rest of the genus. Structurally *Glenurus* seems close to *Eremoleon* but differs from that genus as well as all other glenurine genera in having the posterior gonapophysis poorly developed. Banks (1922) has provided a key to the South American species and (1928) to the Nearctic species.

### **Navasoleon** Banks

*Navasoleon* Banks 1943. Bol. ent. Venez. 2:168. Type-species: *Gymnocnemis boliviana* Banks, by original designation.

*Description*: Antenna fossa separated from ocular rim by less than greatest diameter of pedicel; antenna long and slender; mesoscutellum shorter than metanotum; foreleg (at least females) much longer than midlegs and hindlegs; tibial spurs absent; pretarsal claws capable of closing against distal tarsomere; forewing with anterior margin evenly curved toward apex, costal area at point of coalescing of subcostal and radial veins lower than at middle of wings; forewing radial sector originates well beyond forking of CuA; posterior fork of forewing vein CuA at an oblique angle to hind margin; forewing vein 2A widely separated from normal 3A before strong angle toward posterior margin;

hindwing vein CuA extends somewhat beyond forking of  $MP_2$ ; female ectoproct with small digging setae; posterior gonapophysis swollen thumb-like.

*Discussion:* *Navasoleon* is a poorly known genus and male specimens are unavailable for study. The genus appears very distinct. The lack of tibial spurs is diagnostic and the specialized pretarsal claws is found only in *Elachyleon* and *Dimarella*. In the type-species of the genus and also in an undescribed species the foreleg is unusually long. The species known from Argentina has shorter front legs but the specimen is damaged to such an extent that the sex is undeterminable.

### **Pachyleon** Stange, new genus

*Diagnosis:* This genus is distinguished from other glenurine genera in the Western Hemisphere except *Dimarella* by the following characters: (1) forewing vein 2A is closely associated with vein 3A for its entire course (see Fig. 2); (2) radial and subcostal veins in both wings crowded together; (3) antennal fossa separated by more than greatest diameter of scape from ocular rim; (4) forewing veins CuP + 1A and posterior branch of CuA run parallel for a long distance. *Pachyleon* is closely allied to *Dimarella* but differs from that genus in two important characters: (1) pretarsal claws simple in *Pachyleon*, specialized in *Dimarella* (capable of closing against tarsomere); (2) hindwing broadly triangular in *Pachyleon* (greatest breadth about equal to forewing) whereas it is more slender in *Dimarella* (greatest breadth of hindwing much less than that of forewing). The structural gap between *Pachyleon* and *Dimarella* would be even greater if it were not for a recently discovered (apparently undescribed) species of *Dimarella* which has the condition of forewing vein 2A (closely associated with 3A) very similar to that in *Pachyleon*. *Pachyleon* and *Dimarella* share so many characters that are not found in almost all other Glenurini that they form a group apart. However *Psammoleon cautus* (Walker) represents an intermediate type between *Psammoleon* and these two genera. The unusual shape of the hindwing of *Pachyleon* provides a key character for the genus. It remains to be seen whether or not the broad hindwing is of generic or specific importance since considerable variation exists in the relative broadening of the hindwing in the allied genus *Dimarella*.

*Description:* Antennal fossa separated from ocular rim by more than greatest width of antennal scape; antenna short and thick; pronotum much broader than long; thorax depressed, mesoscutellum as long as metanotum; foreleg moderately short and thickened, midleg greatly swollen and short, hindleg relatively long, about twice as long as foreleg; tarsomeres of foreleg and midleg about equal, those of hindleg much longer; tibial spurs present, much shorter than forecoxal length; pretarsal claws not capable of closing against distal tarsomere; femoral sense hair of foreleg short, much less than one-half length of femur; banksian lines absent; subcostal and radial veins crowded together, nearly touching well before their apical fusion; forewing



Figure 8. Photo of holotype (male terminalia removed).

vein CuP + 1A runs parallel with posterior branch of CuA for a long distance; forewing vein 2A widely separated from 1A, closely associated and almost fused with vein 3A, not greatly angled; male ectoproct with elongate postventral lobe; male genitalia not rigid, paramere with hook; gonarcus expanded laterally as a large round plate; female ectoproct simple with strong digging setae ventrally; lateral gonapophyses separated, with longer digging setae than on ectoproct; posterior gonapophysis digitiform, longer than wide.

The generic name is from the Greek words *Pachys* meaning wide and *leon* meaning lion, in reference to the broad wings, pronotum and head. The following new species is the type-species of the genus.

#### ***Pachyleon alvarengai* Stange, new species**

*Diagnosis:* As the only species in the genus, the generic characters serve to distinguish this species. The unusually short and broadened wings, especially the rather triangular hindwing (see Fig. 8) is distinctive among all known species of ant-lions in the Western Hemisphere. This unusual hindwing shape is also unknown to me in Old World species but I do not have a perfect knowledge of the Old World fauna. The most similar species is a *Dimarella* (probably undescribed) in which the wings are similar in shape although not as extreme as in *P. alvarengai* and in which vein 2A is closely associated with vein 3A.

*Description* (Holotype male): Length of body about 19 mm, forewing 15 mm, hindwing 11 mm, greatest wing width (about equal in forewing and hindwing) 4.75 mm.

*Color*: Face (Fig. 1) pale yellowish with  $\Delta$ -shaped dark brown mark at middle below antennae and crescent-shaped dark brown mark above each antenna, sublateral spot on each side of clypeus, larger dark brown area laterad of antenna toward eye, extending ventrally and dorsally nearly to first row of vertex scars; vertex with grayish bloom, scar pattern about as in Fig. 8; antenna with scape and pedicel pale yellow with dark brown behind, flagellomeres dark brown basally and much paler distally; maxilla and labius nearly all pale yellow except distal palpomere and cardo with dark brown; postgena mostly dark brown; pronotum mostly dark brown with grayish bloom interrupted by irregular paler areas; notum II and III dark brown with grayish bloom, darker velvety areas as follows: submedial triangular area on each side of prescutum II; dark brown oval spot each side of middle and touching, surrounded by golden colored microtrichia on prescutum III; large curved dark brown mark sublaterally near anterior margin of scutum; postscutellum II and III nearly all black; cervical sclerites pale yellow; pleuron and sternum mostly dark brown with grayish bloom, paler brown areas mostly in front of midcoxa and hindcoxa, mesopleural wing process yellowish; forecoxa mostly pale brown, other coxae darker brown; forefemur pale brown with numerous dark brown spots, spots becoming confluent on most of exterior face and on distal one-third of closing face; foretibia pale brown with dark brown spots and small dark brown stripes at basal one-third of exterior face, larger dark brown areas at middle, mostly complete but smaller apical rings, dark brown areas interconnected along closing face; midtibia and midfemur with large, mostly separated dark brown spots on exterior face, somewhat denser and forming short transverse dark brown bands on closing face of tibia, subapical interrupted dark brown ring on femur, solid dark brown one on tibia; hindfemur pale brown with dark brown spots at setal bases, infuscated between spots especially on exterior face, large subapical dark brown band; hindtibia pale brown with large, mostly separated dark brown spots at setal bases on closing face, small dark brown stripe near base, spots becoming more stripelike distally, exterior face nearly all pale brown except dark brown apical ring and smaller dark brown area toward base; tarsi of all legs similarly patterned, pale brown with apical dark brown ring on tarsomeres; wings nearly without suffusion, pale white stigmal area preceded by small darkish brown area in forewing; wing veins mostly pale brown, especially hindwing, with dark brown streaks along longitudinal veins principally at crossvein junctions, many crossveins dark brown especially apically in forewing; abdomen with tergites mostly pale brown with complicated pattern formed by dark brown areas (see Fig. 8), sternites mostly dark brown with a prominent although narrow median longitudinal pale brown line.

*Chaetotaxy*: Head with few prominent setae except on most of clypeus, white ones on dark brown areas of frons, longer ones on labrum and many long white setae on mentum and stipes; vertex with few inconspicuous appressed dark setae; pale with very sparse, short dark brown setae; pronotum with some short setae on disc, longer dark brown ones at lateral and posterior margin; row of five long white setae on each side of middle along anterior margin of scutum II, several smaller dark brown setae on prescutum II, elsewhere nearly absent or very short; pleuron and coxa with rather conspicuous long white hairlike setae; forefemur with dense, mostly appressed white setae on exterior surface, some black and some white erect setae distally, closing surface with fewer setae and with more black ones; foretibia with subbasal row of three black bristles, followed by another similar row, then one of two bristles and finally a subapical black bristle on exterior face, interspersed with shorter, mostly dark setae, closing surface with many stout setae, predominately white; midfemur with row of white bristles on exterior surface, many other setae elsewhere but more hairlike and white; midtibia with mostly black setae of various sizes, larger black ones toward apex of lateral face, larger white ones near base of median face; hindfemur with many short, mostly appressed white setae; hindtibia with many setae along closing surface, white ones mostly concentrated in middle, exterior surface nearly without setae, only a few scattered minute ones; femoral sense hair of foreleg and midleg shorter than width of femur at that point; tarsi with rather dense, dark brown setae on closing surface flanked (typically) on the four basal tarsomeres by one white seta near apex, exterior surface with fewer setae, especially hindtarsus; abdomen with only microsetae on tergites I-V; starting with tergite VI, dark brown setae mostly laterally increasing in abundance toward terminalia; sternites with numerous, mostly white hairlike setae; postventral lobe with rather prominent black bristles toward apex (Fig. 3).

*Structure*: Head with vertex not much raised above eyes; greatest ocular width about one-third interocular distance (measured just below antennal fossae); antenna short and rather flattened with 19 flagellomeres, flagellomere I longer than wide, II about 1.5 times wider than long (in flat view) with increasing width toward apex; distal palpomere of labius rather slender, not much swollen, sensory pit oval and close to base; pronotum about twice as wide as long; femur of all legs broadened beyond base, tibia much more slender except midtibia, which is subequal to midfemur; midleg much shorter than either foreleg or hindleg; wing venation and shape as in Fig. 8; abdomen shorter than forewing, segments larger basally, decreasing in diameter beginning with segment IV; tergites I-V and sternite II with numerous scalelike spicules; terminalia as in Fig. 3, genitalia as in Figs. 3 and 4.

*Types*: Male holotype and 1 female paratype from Jacaré (N. Xingu), Mato Grosso, Brazil, XI 1961, M. Alvarenga collector 52° 24' W; 12° 00' S.

Holotype deposited in the collections of the Los Angeles County Museum of Natural History. Paratype female retained in the author's collection.

*Variation:* The female paratype agrees well in color, chaetotaxy and structure with the male except that the scalelike spicules on the abdomen are lacking. Female terminalia as in Fig. 5.

*Discussion:* This species is dedicated to Moacir Alvarenga, Brazilian coleopterist, for his efforts in securing critical ant-lion material from Brazil. The holotype male upon arrival at the depository was found damaged in transit. Most of the broken parts (pieces of wings, legs and antenna) are associated with the specimen and no difficulty in identification is foreseen although this was an unfortunate mishap. The photo (Fig. 8) shows the holotype before shipment.

### **Psammoleon Banks**

*Psammoleon* Banks 1899. *Canad. Ent.* 31:69. Type-species: *Myrmeleon ingeniosus* Walker, by original designation.

*Diazus* Navás 1914. *Broteria* 12:220. Type-species: *Diazus clavatus* Navás, by original designation.

*Description:* Antennal fossa separated from ocular rim by much less than greatest diameter of scape; antenna variable; pronotum wider than long; mesoscutellum smaller than metanotum; legs about equal in length, hindleg sometimes longer than foreleg; tibial spurs variable, usually shorter than fore-coxal length; pretarsal claws not capable of closing against distal tarsomere; forewing with anterior margin evenly curved toward apex, costal area at point of coalescing of subcostal and radial veins lower than at middle of wing; forewing radial sector originates well beyond forking of CuA; posterior fork of forewing vein CuA at an oblique angle to hind margin; forewing vein 2A widely separated from normal 3A before strong angle toward posterior margin; hindwing vein CuA extends nearly to forking of MP<sub>2</sub> or somewhat beyond; male ectoproct simple without postventral lobe, except in *P. cautus* (Walker); male paramere in form of rigid plate (except *cautus*); male gonarcus not greatly expanded laterally (except *cautus*); female ectoproct without digging setae (sometimes long bristles present), often produced ventrally as a lobe; posterior gonapophysis well developed, often somewhat inflated.

*Discussion:* I studied the holotype male of the type-species of *Diazus* (*D. clavatus* Navás) in 1962 on loan from the Vienna Museum. The specimen is in good condition except that the hindlegs and abdominal terminalia are missing. My studies of this type indicate that *D. clavatus* is a typical *Psammoleon*, rather similar to *Psammoleon minor* Banks. Navás (1914:220) gave few remarks concerning the diagnostic features of *Diazus* except to point to a relationship with *Incamoleon* and *Glenopsis*. Probably the swollen femora of *D. clavatus* prompted him to consider this species generically distinct. However it is clear that *Diazus* is a synonym of *Psammoleon*.

The genus *Psammoleon* is the largest genus in the Western Hemisphere Glenurini, with twenty-seven described species. Also I have seen a number of undescribed species, mainly from Mexico. Most species are found in North America. The genus is unknown south of Mato Grosso, Brazil. The long fore-femoral sense hair (over one-half length of femur) is diagnostic. Also the rather swollen forefemur is characteristic except for *Pachyleon* and *Dimarella*. *P. cautus* (Walker) is intermediate between *Psammoleon* and *Dimarella* and perhaps should be placed in a distinct genus. However this situation suggests a relationship between these genera. The modified female ectoproct in many species of *Psammoleon* is also without known counterpart among Western Hemisphere Glenurini. Considerable variation is present between species in the development of the tarsus, forewing costal area and in chaetotaxy.

#### KEY TO GENERA OF WESTERN HEMISPHERE GLENURINI

1. Pretarsal claws capable of closing against distal tarsomere..... 2  
 Pretarsal claws not capable of closing against distal tarsomere..... 4
2. Posterior fork of forewing vein CuA and vein CuP + 1A parallel with each other and hind margin for a long distance; antennal fossa separated by more than greatest width of antennal pedicel from ocular rim; male ectoproct with elongate postventral lobe.....*Dimarella*  
 Posterior fork of forewing vein CuA at an oblique angle to hind margin; antennal fossa separated by less than greatest width of antennal pedicel from ocular rim; male ectoproct without elongate postventral lobe..... 3
3. Tibial spurs present; foreleg about equal or shorter than hindleg..*Elachyleon*  
 Tibial spurs absent; foreleg (at least in female) usually longer than hindleg ..... *Navasoleon*
4. Antennal fossa separated by more than greatest width of antennal pedicel from ocular rim; hindwing about twice as long as wide, much shorter than forewing (Fig. 8); forewing vein 2A closely associated with 3A, not much angled (Fig. 2); subcostal and radial veins of both wings nearly touching, especially before their apical fusion; male ectoproct with elongate post-ventral lobe.....*Pachyleon*  
 Antennal fossa separated by less than greatest width of antennal pedicel from ocular rim; hindwing over three times longer than wide, about equal in length to forewing; forewing vein 2A widely separated from normal 3A before strong angle toward hind margin; subcostal and radial veins widely separated until their apical fusion; male ectoproct without postventral lobe (except *P. cautus*)..... 5
5. Forewing with anterior margin abruptly angled and swollen near coalescing of subcostal and radial veins, costal area at this point nearly twice as wide as at middle of wing; hindwing vein CuA ends well before midpoint to forking of MP<sub>2</sub>; forewing radial sector originates well basad to forking of CuA .....*Araucoleon*

- Forewing with anterior margin evenly curved toward apex, costal area at point of coalescing of subcostal and radial veins usually somewhat narrower than at middle of wing; hindwing vein CuA extends nearly to forking of MP<sub>2</sub> or beyond; forewing radial sector originates near or well beyond forking of CuA..... 6
6. Forefemur swollen, at widest point much wider than interantennal distance, with abundant pubescence, especially on closing surface; femoral sense hair or foreleg elongate, over one-half length of femur; female ectoproct often with ventral projection.....*Psammoleon*  
Forefemur slender and elongate, at widest point about equal at most to interantennal distance, with sparser pubescence; femoral sense hair of foreleg less than one-third length of femur; female ectoproct not produced ventrally ..... 7
7. Apical one-fifth of hindwing and usually forewing with predominant dark brown suffusion in marked contrast to basal one-fifth; posterior gonapophysis of female weakly produced as a swelling.....*Glenurus*  
Apical one-fifth of wings predominantly transparent, sometimes many scattered dark brown spots present; posterior gonapophysis of female well developed, digitiform.....*Eremoleon*

SYNOPTIC CATALOG OF THE WESTERN HEMISPHERE GLENURINI  
WITH TYPE INFORMATION

Genus **Araucoleon** Banks

- Araucoleon* Banks 1938b:127. Type-species: *Araucoleon inca* Banks, orig. design.  
*inca* Banks 1938b:128. Hol. ♂, Huachi, Bolivia, IX.1925 (USNM).  
*withycombei* (Esben-Petersen) 1927:347 (as *Glenurus*). Hol. ♀, St. Augustine, Trinidad, VI. 1924 (BM). *New Comb.*

Genus **Dimarella** Banks

- Dimarella* Banks 1913a:229. Type-species: *Eremoleon angustus* Banks, orig. design.  
= *Nobra* Navás 1915b:6. Type-species: *Nobra martinsi* Navás, orig. design.  
= *Furgus* Navás 1921:51. Type-species: *Nobra riparius* Navás, orig. design.  
= *Mystroleon* Banks 1924:436. Type-species: *Myrmeleon praedator* Walker.  
Taxonomy: Banks (1943:166); Stange (1963:810-812; 1968:59).  
*angusta* (Banks) 1908:31 (as *Eremoleon*). Hol. ♀, Santa Elena, Ecuador (MCZ).  
= *Nobra nevermanni* Navás 1936:167. Syntypes, Costa Rica, Farm Hamburg am Reventazon, V.2.1934 (Zaragoza).  
Taxonomy: Banks (1913a:230; 1943:168); Stange (1963:812).

- Distribution: Neotropical (Costa Rica, Colombia, Ecuador, Venezuela, Brazil, Peru).
- campestris* (Navás) 1930:107 (as *Furgus*). Hol. ♂, Guayaquil, Ecuador 1930 (Barcelona). *New Comb.*
- garciai* (Navás) 1932:12 (as *Nobra*). Hol. ♀, Vinces, Ecuador (Turin). *New Comb.*
- martinsi* (Navás) 1915b:6 (as *Nobra*). Hol. ♀, Río Purús, Brasil 1904 (Paris). Taxonomy: Stange (1963:812).
- menkei* Stange 1963:814. Hol. ♂, Río Cuchujachi, 10 miles S.E. Alamos, Sonora, Mexico, V.22.1962 (CAS).
- praedator* (Walker) 1853:391 (as *Myrmeleon*). Hol. ♀, Santarem, Brazil (BM).  
Taxonomy: Hagen (1860:364); Stange (1963:812).
- psammophila* Stange 1963:814. Hol. ♀, Veracruz, Mexico, IV.29.1962 (CAS).
- riparius* (Navás) 1918b:16 (as *Nobra*). Lect. ♂, Santa Fe, Argentina, I.9.1917 (Barcelona).  
= *Dimarella pallida* Navás 1933a:89. Hol. ♀, S. Miguel, Argentina, XI.25.1932 (Barcelona).  
Taxonomy: Stange (1968:59).  
Distribution: Neotropical (Uruguay, Argentina).
- silvaicus* (Navás) 1918b:6 (as *Nobra*). Hol. ♀, Mato Grosso, Brasil (La Plata). *N. Comb.*
- tarsalis* (Guilting) 1829:47 (as *Formicaleo*). Type (?s), ?Demerara (not located).  
= *Myrmeleon efferus* Walker 1853:388. Hol. ♀, Para, Brazil (BM).  
Taxonomy: Hagen (1860:364); Banks (1913a:229; 1913b:86; 1943:168); Stange (1963:812).

#### Genus **Elachyleon** Esben-Petersen

- Elachyleon* Esben-Petersen 1927:348. Type-species: *Elachyleon punctipennis* Esben-Petersen, orig. design.  
= *Oroleon* Navás 1927:49. Type-species: *Oroleon serranus* Navás, orig. design.  
= *Sericoleon* Esben-Petersen 1932:114. Type-species: *Sericoleon paessleri* Esben-Petersen, orig. design. *New Synonymy.*  
Taxonomy: Banks (1943:166); Stange (1963:810; 1968:56).
- gentilis* (Banks) 1943:171 (as *Sosa*). Hol. ♂, Kartabo, British Guiana, XI.4 (MCZ). *New Comb.*
- paessleri* (Esben-Petersen) 1932:115. (as *Sericoleon*). Hol. ♀, Taltal (Antofagasta), Chile, I.30.1906 (Copenhagen). *New Comb.*
- punctipennis* Esben-Petersen 1927:348. Hol. (sex undet.), St. Augustine, Trinidad, V.20.1925 (BM).

=*Elachyleon punctipennis pulchellus* Esben-Petersen 1932:113. Syntypes: ♀, Las Mercedes, Costa Rica, IV.27.1922 (Hamburg, destroyed); sex undet., Brazil (Berlin?).

Taxonomy: Banks (1943:168); Stange (1963:815; 1968:56).

Distribution: Neotropical (Mexico to Argentina).

*serranus* (Navás) 1927:50 (as *Oroleon*). Hol. ♀, Alta Gracia, La Granja, Sierras de Córdoba, Argentina, I.8.1928 (Buenos Aires).

Taxonomy: Stange (1968:57).

#### Genus **Eremoleon** Banks

*Eremoleon* Banks 1901:366. Type-species: *Myrmeleon macer* Hagen, orig. design.

=*Incamoleon* Banks 1913a:229. Type-species: *Psammoleon punctipennis* Banks, orig. design. *New Synonymy*.

=*Glenopsis* Banks 1913a:229. Type-species: *Myrmeleon anomalus* Rambur, orig. design.

=*Sosa* Navás 1914a:218. Type-species: *Sosa conspicuus* Navás, orig. design. *New Synonymy*.

=*Segura* Navás 1914c:18. Type-species: *Segura vitreus* Navás, orig. design.

=*Belen* Navás 1921:119. Type-species: *Belen cerverinus* Navás, orig. design.

=*Cortesius* Navás 1924:107. Type-species: *Cortesius genini* Navás, orig. design. *New Synonymy*.

=*Novulga* Navás 1925:189. Type-species: *Novulga mexicana* Navás, orig. design.

=*Dobla* Navás 1926:428. Type-species: *Dobla arcuata* Navás, orig. design. *New Synonymy*.

=*Joergenia* Esben-Petersen 1932:118. Type-species: *Joergenia pulchra* Esben-Petersen, orig. design. *New Synonymy*.

=*Antilloleon* Banks 1943:168. Type-species: *Glenurus cerverai* Navás, orig. design. *New Synonymy*.

Taxonomy: Navás (1916:232; 1917:275); Banks (1928:69-71; 1942:144); Adams (1957:85; 1958:6); Alayo (1968:62, 70); Stange (1968:57).

*anomalus* (Rambur) 1842:388 (as *Myrmeleon*). Type (?s), Colombia (not located).

=*Glenurus mollis* Gerstaecker 1888:101. Hol. (sex undet.) Colombia (Greifswald).

Taxonomy: Banks (1913a:229; 1943:171); Navás (1916:232); Stange (1968:57).

Distribution: Neotropical (Colombia, Venezuela, Brazil, Argentina).

- capitatus* (Navás) 1913:52 (as *Formicaleo*) Hol. (sex undet.), Rio de Janeiro, Brasil, VI.1911 (not located). *New Comb.*
- ceverai* (Navás) 1921:118 (as *Glenurus*). Hol. ♀, Santiago (de las) Vegas, Habana, Cuba, VIII.23.1907 (MCZ). *New Comb.*  
Taxonomy: Banks (1943:68); Alayo (1968:68).
- ceverinus* (Navás) 1921:120 (as *Belen*). Hol. ♀, Río Almendares, Habana, Cuba, VIII.1.1915 (MCZ).  
Taxonomy: Adams (1957:6); Alayo (1968:70).
- conspicuus* (Navás) 1914a:219 (as *Sosa*). Hol. ♂, Brasil (Vienna). *New Comb.*
- femoralis* (Banks) 1942:146 (as *Psammoleon*). Hol. (sex undet.), 20 miles N.W. La Paz, Lower California VII.16.1938 (CAS). *New Comb.*
- genini* (Navás) 1924:108 (as *Cortesius*). Syntypes (sex undet.), Veracruz, Mexico, 1921 (Paris). *New Comb.*  
= *Dobla arcuata* Navás 1926:428. Hol. ♀, San José, Costa Rica (Paris).  
*New Synonymy.*
- gracile* Adams 1957:90. Hol. ♀, Riverside, California, VIII.31.1939 (CAS).
- impluviatus* (Gerstaecker) 1893:30 (as *Glenurus*). Hol. ♀, Locotal, Bolivia (Greifswald), *New Comb.*
- insipidus* Adams 1957:88. Hol. ♂, 5 miles S. San Miguel, Lower California, VII.20.1938 (MCZ).  
Distribution: Nearctic (Mohave-Colorado Desert; Vizcaino Desert).
- longior* Banks 1938a:225. Syntypes ♀♀, Yucatan, Mexico (MCZ).  
Taxonomy: Adams (1957:92).
- macer* (Hagen) 1861:236 (as *Myrmeleon*). Hol. (sex undet.), Mexico (not located).  
= *Segura vitreus* Navás 1914c:18. Hol. ♂, Cuernavaca, Mexique, 1871 (Paris).  
= *Novulga mexicana* Navás 1925:189. Hol. ♂, Veracruz, Mexique, 1921 (Paris).  
= *Hesperoleon atomarius* Navás 1933b:105. Hol. (sex undet.), Cuernavaca, Mexico, 1929-30 (Hamburg, destroyed). *New Synonymy.*  
Taxonomy: Banks (1928:70); Adams (1957:86).  
Distribution: Nearctic (Arizona); Neotropical (Mexico).
- nigribasis* Banks 1920:329. Syntypes ♂, ♀, St. George, Utah, VI.5,6 (MCZ)  
= *Eremeleon affine* Banks 1942:144. Hol. ♂, Miraflores, Lower California, VII.8.1938 (CAS).  
Taxonomy: Banks (1928:71); Adams (1957:91).  
Distribution: Nearctic (deserts).
- ornatipennis* (Alayo) 1968:69 (as *Antilloleon*). Hol. ♂, Soroa, Pinar del Río, Cuba, IV.1963 (Havana). *New Comb.*
- pallens* Banks 1941c:101. Syntypes, Picacho Peak, Arizona, VII.23 (MCZ).  
Taxonomy: Adams (1957:92).

- peterseni* (Banks) 1922:59 (as *Glenopsis*). Lect. ♀, Chanchamayo, Peru, XI (MCZ). *New Comb.*  
 Taxonomy: Stange (1961:674).
- psilocerus* (Gerstaecker) 1893:32 (as *Glenurus*). Hol. (sex undet.), Merida, Venezuela (Greifswald). *New Comb.*  
 Taxonomy: Banks (1922:59; 1943:172).
- pulchra* (Esben-Petersen) 1932:118 (as *Joergenia*). Hol. ♀, Paraguay, II, 1932 (Copenhagen). *New Comb.*
- punctipennis* (Banks) 1910:147 (as *Psammoleon*). Hol. ♀, San Antonio, Colombia (MCZ). *New Comb.*  
 =*Formicaleo tetrastictus* Navás 1913:51. Types(?), Venezuela (not located).  
 =*Formicaleo stictopterus* Navás 1916:232. New name for *punctipennis* Banks 1910. (nomen nudum).  
 Taxonomy: Banks (1913a:299; 1943:169); Stange (1968:58).  
 Distribution: Neotropical (Colombia to Argentina).
- sectoralis* Adams 1958:7. Hol. ♀, 5 miles S. San Miguel, Lower California, VII.20.1938 (CAS).
- triguttatus* (Navás) 1914c:19 (as *Formicaleo*). Hol. ♀, San Pedro de Sula, Honduras (Vienna). *New Comb.*

#### Genus **Glenurus** Hagen

- Glenurus* Hagen 1866:372. Type-species: *Formicaleo grata* Say, design. by Banks (1928:67).  
 =*Ledoscius* Navás 1918:493. Type-species: *Ledoscius penningtoni* Navás, orig. design.  
 SYNONYMY: Navás (1924:107).
- gratus* (Say) 1839:45 (as *Formicaleo*).  
 =*Myrmecoleon roseipennis* Burmeister 1839:995. Hol. (sex undet.), Nordamerika (Halle).  
 Taxonomy: Walker (1853:392); Hagen (1861:225; 1866:405); Banks (1892:360; 1928:67).  
 Distribution: Nearctic (East 100° Meridian).
- heteropteryx* Gerstaecker 1885:17. Hol. ♀, Chiriqui (Greifswald).  
 =*Glenurus discors* Navás 1920:202. Hol. ♀, La Trinité, 1916 (Paris).  
 Taxonomy: Banks (1922:58); Navás (1922b:187; 1935:362).  
 Distribution: Neotropical (Panama, Venezuela, Trinidad, Ecuador).
- incalis* Banks 1922:58. Syntypes, Chanchamayo, Peru (MCZ).
- luniger* Gerstaecker 1893:125. Hol. ♀, Chiriqui (Greifswald).  
 Taxonomy: Banks (1938:420).  
 Distribution: Nearctic (Arizona); Neotropical (Mexico to Panama).
- peculiaris* (Walker) 1859:194 (as *Myrmeleon*). Hol. ♀, Brazil (BM).

- =*Glenurus brasiliensis* Navás 1920:416. Lect. ♀, São Sebastião, Brasil (not located). *New Synonymy*.  
Taxonomy: Hagen (1866:405); Banks (1922:58); Navás (1923:771).  
*penningtoni* (Navás) 1918:493 (as *Ledoscius*). Hol. ♂, La Rioja, Argentina (not located).  
=*Glenurus croesus* Banks 1922:59. Syntypes, Sara, Bolivia, 450 m. (MCZ).  
Taxonomy: Navás (1922b:187; 1924:107).  
Distribution: Neotropical (Bolivia, Argentina).  
*proi* Navás 1929:17. Hol. ♀, Colima, Mexico (Paris).  
*snowii* Banks 1907:100. Hol. ♀, Baboquivari Mts., Arizona (MCZ).  
Taxonomy: Banks (1928:67, 69).

#### Genus **Navasoleon** Banks

- Navasoleon* Banks 1943:168. Type-species: *Gymnocnemia boliviana* Banks, orig. design.  
Taxonomy: Stange (1963:810).  
*boliviana* (Banks) 1929:330 (as *Gymnocnemia*) Hol. ♀, Río Longo, Bolivia (MCZ).  
Taxonomy: Banks (1943:168).  
*bosqui* (Navás) 1922:258 (as *Gymnocnemia*). Hol. ♀, Santiago del Estero, Argentina (not located).  
Taxonomy: Stange (1968:58).  
*leptocera* (Navás) 1915:125 (as *Gymnocnemia*). Hol. (sex undet.) Catamarca, Argentina, I.21.1910 (Buenos Aires).  
Taxonomy: Stange (1968:58).

#### Genus **Pachyleon** Stange

- Pachyleon* Stange 1970: Type-species: *Pachyleon alvarengai* Stange, orig. design.  
*alvarengai* Stange. Hol. ♂, Jacaré, Mato Grosso, Brazil, XI.1961 (LACM).

#### Genus **Psammoleon** Banks

- Psammoleon* Banks 1899:69. Type-species: *Myrmeleon ingeniosus* Walker, orig. design.  
=*Diazus* Navás 1914:220. Type-species: *Diazus clavatus* Navás, orig. design.  
Taxonomy: Banks (1913:226; 1928:60-67; 1942:166; 1943:169); Alayo (1968:65).  
*albovaria* (Banks) 1942:146 (as *Puren*). Hol. (sex undet.), Venancio, Lower California, VII.17.1938 (CAS). *New Comb*.  
*arizonensis* Banks 1935:53. Syntypes: 1 ♀, Tucson, Arizona (MCZ); 2 ♀ ♀, Phoenix, Arizona (MCZ).

- Distribution: Nearctic (Arizona-Sonora Desert; Mohave-Colorado Desert).  
*banksi* Esben-Petersen 1932:115. Hol. ♂, Amapala, Honduras, XI.12.1907 (Hamburg, destroyed).
- bipunctatus* (Navás) 1915:465 (as *Formicaleo*). Hol. ♀, Guyana Francesa (Paris).
- Taxonomy: Banks (1943:170).
- bistictus* (Hagen) 1861:235 (as *Myrmeleon*). Hol. (sex undet.), Cuba (Berlin?).
- Taxonomy: Navás (1921:117); Banks (1928:61; 1941:177); Alayo (1968:65).
- Distribution: Neotropical (so. Florida, West Indies, Yucatan, Mex.).  
*cautus* (Walker) 1853:349 (as *Myrmeleon*). Hol. ♂, Brazil (BM).  
 =*Feinerus nebulosus* Navás 1922:21. Hol. ♀, Perú 1920 (Paris). *New Synonymy*.
- Taxonomy: Banks (1943:170).
- clavatus* (Navás) 1914:221 (as *Diazus*). Hol. ♂, Amazones 1860 (Vienna).  
*New Comb.*
- connexus* (Banks) 1920:329 (as *Puren*). Hol. ♂, San Jacinto Mts., California VI.25 (MCZ).
- Taxonomy: Banks (1928:61, 64).
- cubensis* Alayo 1968:67. Hol. (sex undet.), Tortuguilla, Guantánamo, Oriente, Cuba, VI.1964 (Havana).
- debilis* (Gerstaecker) 1893:44 (as *Formicaleo*). Hol. ♀, Chiriqui (Greifswald).
- Taxonomy: Banks (1943:170).
- Distribution: Neotropical (Panama; Colombia).
- decepiens* Banks 1935:54. Syntypes: 1 ♂, Georgia (MCZ); sex undet., Shreveport, Louisiana (MCZ).
- guttipes* Banks 1906:99. Hol. ♂, Tryon, North Carolina (MCZ).
- Taxonomy: Banks (1928:61, 63).
- inbellis* (Banks) 1941:102 (as *Puren*). Hol. ♀, Port au Prince, Haiti, XI.20 (MCZ). *New Comb.*
- ingeniosus* (Walker) 1853:337 (as *Myrmeleon*). Syntypes, Brazil & no data (BM).
- Taxonomy: Hagen (1861:236; 1866:404); Banks (1899:69; 1906:99; 1943:169).
- Distribution: Neotropical (Colombia, Brazil).
- iniquus* (Navás) 1914:208 (as *Formicaleo*) new name for *Formicaleo inaequalis* Navás 1913:51 (Preoccupied by *F. inaequalis* Navás 1912): Hol. (sex undet.), Amapala, Honduras, XI (not located). *New Comb.*
- inscriptus* (Hagen) 1861:230 (as *Myrmeleon*). Hol. ♂, Pecos River, Western Texas (MCZ).
- Taxonomy: Hagen (1866:424); Banks (1904:106; 1928:66).

- Distribution: Nearctic (Arizona-Sonora Desert).  
*leachii* (Guilding) 1829:49 (as *Formicaleo*). Types (?), Jamaica (not located).  
*minor* Banks 1928:62. Lect. ♀, Dry Tortugas, Loggerhead Key, Florida, VI.1917 (MCZ).  
 Taxonomy: Banks (1941:176, 177); Stange (1961:674); Alayo (1968:66).  
 Distribution: Neotropical (So. Florida; West Indies).  
*normalis* Banks 1942:145. Hol. ♀, Venancio, Lower California, VII.17.1938 (CAS).  
*nubipennis* (Navás) 1917:275 (as *Formicaleo*). Hol. (sex undet.), Coachí, Colombia, VI.1915 (not located). *New Comb.*  
*parallela* Banks 1935:54. Syntypes, Honduras (MCZ).  
*parvulus* Banks 1920:331. Hol. ♂, Chapada, Brazil (MCZ).  
 Taxonomy: Banks (1943:170).  
*posticatus* Banks 1941:3. Hol. (sex undet.), Colombia (AMNH).  
 Taxonomy: Banks (1943:169).  
*reductus* Banks 1941:177. Hol. ♂, Stakes Bay, Cayman Brac, Cayman Islands (MCZ).  
*serrei* (Navás) 1920:201 (as *Formicaleo*). Hol. ♂, La Trinité, 1914 (Paris). *New Comb.*  
 =*Formicaleo chaperi* Navás 1922:256. Hol. ♂, Venezuela, 1885 (Paris). *New Synonymy.*  
 Taxonomy: Banks (1943:170).  
*sinuatus* Currie 1903:275. Hol. ♂, Santa Rita Mts., Arizona, V.31 (USNM).  
 =*Psammoleon serpentinus* Navás 1922:185. Hol. (sex undet.), Jemez Springs, New Mexico, VII.1916 (Zaragoza).  
 Taxonomy: Banks (1928:5, 64).  
*zayasi* Alayo 1968:67. Hol. ♀, Península de Guanahacabibes, Pinar del Río, Cuba, 1956 (Private coll. Zayas, Habana).

## RESUMEN

Revisión Genérica y Catálogo de la Tribu Glenurini del Hemisferio Occidental con la Descripción de un Nuevo Género y Especies de Brasil.

Estudios sistemáticos de la Glenurini del hemisferio occidental han llevado a grandes cambios en su clasificación. Ocho nombres genéricos han sido reducidos a sinónimos y un género y especie nueva, *Pachyleon alvarengai* es descrito de Brasil. Estos sinónimos son: *Elachyleon* Esben-Petersen 1927 (= *Sericoleon* Esben-Petersen 1932); *Eremoleon* Banks 1901 (= *Incamoleon* Banks 1913, = *Sosa* Navás 1914, = *Cortesius* Navás 1924, = *Dobla* Navás 1926, = *Joergenia* Esben-Petersen 1932, = *Antilloleon* Banks 1943); *Psammoleon* Banks 1899 (= *Diazus* Navás 1914). Se dan ahora ocho géneros válidos. Se incluyen descripciones y observaciones sobre cada género además

de una clave para su identificación. Se discute la posición sistemática de la tribu Glenurini que se pasa a la subfamilia Myrmeleontinae, con la inclusión de los géneros de la tribu Dimarellini. Se agrega un catálogo sinóptico de las especies y géneros de la tribu con datos sobre los tipos y se indican muchas combinaciones nuevas además de cuatro sinónimos específicos nuevos. Estos son: *Psammoleon cautus* (Walker) 1853 (= *Feinerus nebulosus* Navás 1922); *Psammoleon serrei* (Navás) 1920 (= *Formicaleo chaperi* Navás 1922); *Glenurus peculiaris* (Walker) 1859 (= *Glenurus brasiliensis* Navás 1920); *Eremoleon macer* (Hagen) 1861 (= *Hesperoleon atomarius* Navás 1933).

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FURTHER STUDIES ON AUDIBLE VOCALIZATIONS  
OF THE AMAZON FRESHWATER  
DOLPHIN, *INIA GEOFFRENSIS*

By MELBA C. CALDWELL AND DAVID K. CALDWELL

LOS ANGELES COUNTY MUSEUM OF NATURAL HISTORY • EXPOSITION PARK  
LOS ANGELES, CALIFORNIA 90007



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*Editor*

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DOLPHIN, *INIA GEOFFRENSIS*

By MELBA C. CALDWELL<sup>1</sup> AND DAVID K. CALDWELL<sup>2</sup>

**ABSTRACT:** Evidence is presented indicating the absence of a *quasi*-pure tone or whistle type of sound production by the Amazon freshwater dolphin. A discussion and sonagrams are given of the audible squeal or screech often attributed to *Inia geoffrensis*.

Phonations of the toothed whales and dolphins fall roughly into three categories. These include two types which generically are related (Norris, 1969) and probably are produced by the same mechanism, as they both consist of discrete clicks. One type demonstrates a slower click repetition rate and is usually associated with environmental investigation (echolocation), whereas the other is made up of bursts of clicks of higher repetition rates of 150 per second or more (Caldwell, Caldwell and Evans, 1966b). The latter create tonal sounds variously labeled by such names as barks, squawks, screeches or squeaks. These are associated with behavioral situations wherein we find a positive correlation between the time of their emission and the usefulness of a signal that could cue conspecifics to approach or withdraw (Caldwell and Caldwell, 1967). The third type of sound, most frequently termed a whistle, is a *quasi*-pure tone sound that cannot be resolved into individual clicks. These are the harmonic emissions of Tavolga (1965: 9) and Evans (1967). All odontocetes probably emit click sounds (Norris, 1968), but some do not emit the so called pure tone.

No whistles have been reported in sound work on the primitive Amazon freshwater dolphin, *Inia geoffrensis* (see Schevill and Watkins, 1962; Schevill, 1964; Caldwell, Caldwell and Evans, 1966a, 1966b; Caldwell and Caldwell, 1967; Evans, 1967; Poulter, 1968; Caldwell and Caldwell, 1969b).

All of these earlier works contain two deficiencies. First, on only one brief occasion was work done with more than one or two animals in a tank (Caldwell and Caldwell, 1967). This lack of community tank sound studies constitutes a potentially serious deficit, as vocalizations of odontocete cetaceans of the marine species with which we have worked tend to diminish in relative number in captivity if other animals are not present. Second, several

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people handling *Inia* have reported a loud squeal or screech emitted by the animal which, from the observers' descriptions, might have been interpreted as a whistle (Allen and Neill, 1957; Layne and Caldwell, 1964; Caldwell, Caldwell and Evans, 1966b; Caldwell and Caldwell, 1969a, 1969b). This sound also has been described to us in personal conversation with Earl S. Herald of the Steinhart Aquarium, San Francisco; Lawrence Curtis, formerly of the Fort Worth Zoo, Texas; Leo Baumer of Iquitos, Peru; and W. J. LeBlanc and William C. Raulerson, Marineland of Florida. Until recently we had heard the sound out of water on one occasion, but did not record it. Further studies on this sound were thus considered necessary to determine whether these sounds are broad-band pulsed sounds and not a narrow-band whistle. Correction of these two deficiencies seemed mandatory, not only to help solidify our basic knowledge of cetacean phonations, but also because we have come to regard the absence or presence of the pure tone whistle as one of the significant characters in the precariously understood familial relationships between members of the order Cetacea. Evidence to date suggests that the species of cetaceans considered to be more primitive also either lack the *quasi*-pure tone whistle or that when present it is less clear-cut than in those species considered to be more advanced.

We recorded *Inia* phonations from a community tank over a period of two years for a total of some 25 hours. The dolphins were held in a large display tank at Marineland of Florida and at various times the community contained from four to eleven animals of mixed sizes and sexes. Sound recordings were made with the animals at rest or swimming slowly, feeding, fighting, copulating, sick, dying, and semi-stranded. The community tank contained eleven animals during one seven hour recording session of a semi-stranding. The animals were recent captives which, in our experience, along with stranding increases the possibility of eliciting at least a few cetacean phonations. Additionally we have air recorded isolated individuals as they were being handled and medicated, as well as during venipuncture and force feeding.

Within the range of our equipment (40 to 20,000 Hz), we have not detected *quasi*-pure tone sounds, nor did Evans (*in Herald, et al.*, 1969; personal conversation, August, 1969) indicate the production of such sounds in his studies of *Inia* phonations with equipment sensitive to frequencies up to 100,000 Hz. The loud squeals that we recorded are pulsed as shown when they are subjected to detailed analysis, and the *quasi*-pure tone or whistle is still unknown in the vocal repertoire of *Inia* and we believe now that it is not to be expected.

An adult female emitted squeals both singly and in series 22 and 19 times on two successive days when she was removed from her tank for medication. On another occasion this same female, although not being handled, intermittently emitted loud squeals for about an hour when the water level in her tank was so low that she was partly stranded; but no recordings were

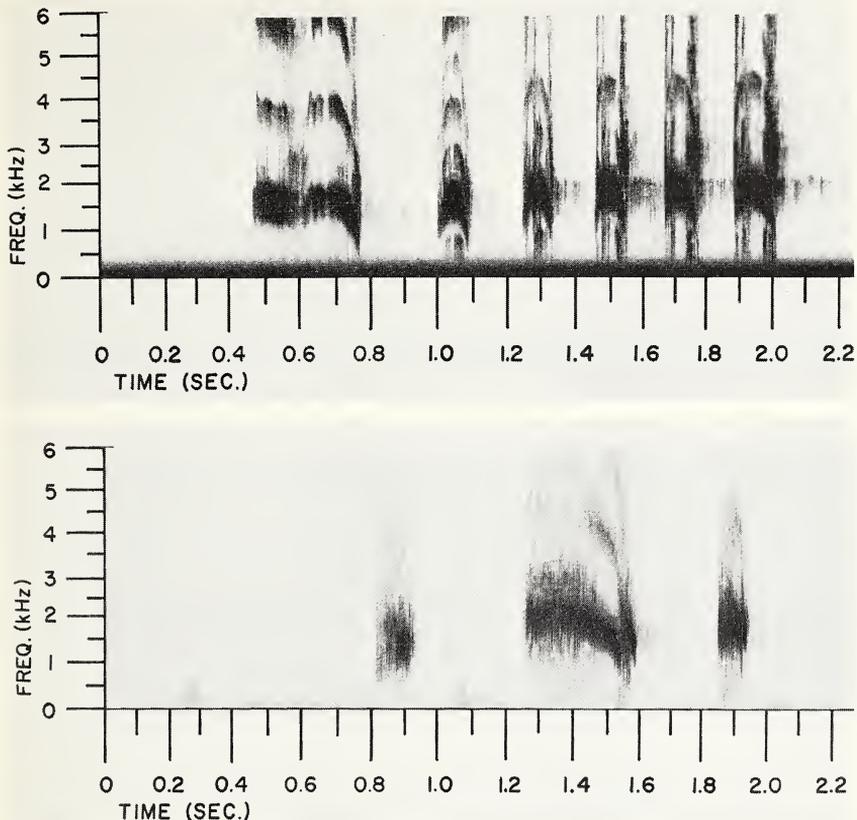


Figure 1. Phonations of *Inia geoffrensis*. Squeals emitted in air in daylight by isolated animals during application of medication. *Upper*: Adult female (MLF 165), January 27, 1969. *Lower*: Juvenile male (MLF 202), March 10, 1969. Effective filter bandwidths 300 Hz. (Photographs courtesy Marineland of Florida).

made. A juvenile male emitted seven squeals on one occasion when removed for medication and venipuncture. The four occasions are the only times of perhaps 30 to 40 in-air recording or listening sessions that the squeal was emitted by any individual of this species although all were subjected to the same amount of handling.

Sound spectrograms (sonograms) of the squeals of both animals (Fig. 1) show them to be the burst-pulse type with a high click repetition rate (Watkins, 1967). Although these are broad band clicks with some energy extending above 12 kHz (Fig. 2), a strong fundamental frequency at one to two kHz is demonstrated on the sonograms of the sounds of both animals (Fig. 1). These sonograms show several characteristics in common with the type 2

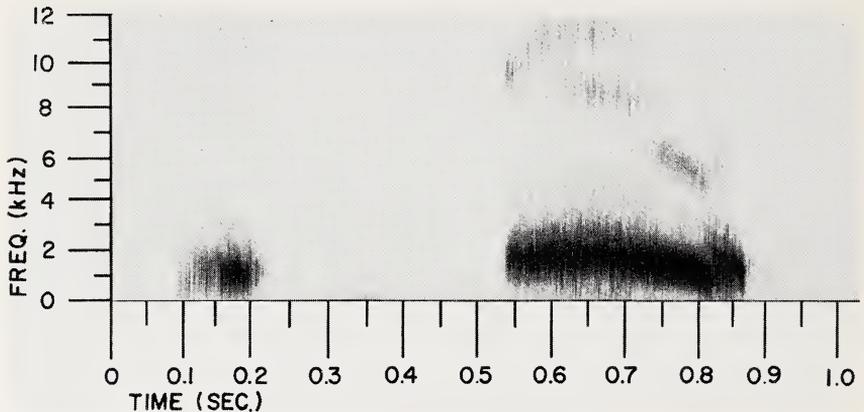


Figure 2. Phonations of *Inia geoffrensis*. First two of the same three squeals illustrated in Fig. 1 (lower), but played at half recorded speed. Effective filter bandwidth 600 Hz. (Photograph courtesy Marineland of Florida).

or complaint type of signal of the pilot whale, *Globicephala melaena*, (Busnel and Dziedzic, 1966: 615, fig. 11), the tin horn sound emitted when excited by a strong stimulus by the Pacific whitesided dolphin, *Lagenorhynchus obliquidens*, (Caldwell and Caldwell, 1967: 889, figs. 5-7), and the squawk component of the whistle-squawk emitted in air by an excited Atlantic bottle-nosed dolphin, *Tursiops truncatus*, (Caldwell and Caldwell, 1967: 897, fig. 22). Fundamental frequencies, depicted harmonics, and durations are similar in the four species. However, to the human ear the sounds are not alike.

#### SOUND EQUIPMENT

The recordings discussed in this paper were made with a Uher 4000 Report-L recorder operating at a tape speed giving it a frequency response of 40 to 20,000 Hz with a compatible Uher microphone. Sound spectrograms were prepared on a Kay Sona-Graph model 662A Sound Spectrograph Analyzer calibrated in two sections from 85 to 12,000 Hz. When the recorded tape speed is reduced by half, and then fed into the analyzer, the response of the latter is doubled to 24,000 Hz. The effective filter bandwidths used for the illustrated analyses are indicated in the figure captions.

#### ACKNOWLEDGMENTS

Financial support for certain phases of this work came from the National Science Foundation (GB-1189), the National Institute of Mental Health (MH-07509-01), the Office of Naval Research (N00014-67-C-0358, and modifications P001 and P002), and Marineland, Inc. The photographs are by William A. Huck. One of our associates, Nicholas R. Hall, made the air recordings that included the squeals.

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## FOUR NEW TEREBRID GASTROPODS FROM EASTERN PACIFIC ISLANDS

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# FOUR NEW TEREBRID GASTROPODS FROM EASTERN PACIFIC ISLANDS

By TWILA BRATCHER<sup>1</sup> AND R. D. BURCH<sup>2</sup>

ABSTRACT: Four new terebrids are described from Eastern Pacific islands: *Terebra hertleini*, *T. jacquelineae*, and *T. purdyae* from the Galápagos Islands, Ecuador, and *T. stohleri* from Socorro Island, Mexico.

While examining the terebrid collections dredged by the R/V *Valero III* during the Allan Hancock Foundation Pacific Expeditions and by the expeditions of California Academy of Sciences to the Eastern Pacific islands, we discovered three new species of *Terebra*; the fourth was brought to our attention by Mrs. Jacqueline DeRoy, who dredged specimens at Academy Bay in the Galápagos Islands.

The following abbreviations are used in the text: AHF, Allan Hancock Foundation (material on loan to LACM); AMNH, American Museum of Natural History; ANSP, Academy of Natural Sciences of Philadelphia; B&B, Bratcher and Burch collection; BM(NH), British Museum (Natural History); CAS, California Academy of Sciences; LACM, Los Angeles County Museum of Natural History; MCZ, Museum of Comparative Zoology, Harvard University; SB, Santa Barbara Museum of Natural History; SD, San Diego Museum of Natural History; SU, Stanford University; USNM, United States National Museum; WAM, Western Australia Museum.

## ACKNOWLEDGMENTS

We wish to express our appreciation to Drs. James H. McLean of the Los Angeles County Museum of Natural History, Leo G. Hertlein of the California Academy of Sciences, and Harald Rehder and Joseph Rosewater of the U.S. National Museum for their cooperation and loan of materials. We thank Ben and Ruth Purdy of San Diego, California, and Laura Shy of Westminster, California, in whose collections additional specimens of some of the new species were found, for making their collections available to us. We are indebted to Mrs. Jacqueline DeRoy for sending material from the Galápagos Islands for study. We also wish to thank Maurice Giles of the California Academy for preparing several of the photographs and Mrs. Margaret Hanna for retouching them.

***Terebra hertleini***, sp. nov.

Figures 1-2

*Diagnosis*: A small species distinguished from other small terebrids by turreted whorls and large subsutural nodes.

<sup>1</sup>Research Assistant in Invertebrate Zoology, Los Angeles County Museum of Natural History, 8121 Mulholland Terrace, Los Angeles, California 90046.

<sup>2</sup>Formerly Research Assistant in Invertebrate Zoology, Los Angeles County Museum of Natural History. (Deceased, February 22, 1970.)

*Description of holotype:* Size small; color white, whorls flat, turreted, ten in number plus two glassy, convex nuclear whorls; first postnuclear whorl constricted; sculpture of three spiral cords per whorl and obsolete axial ribs beginning in large nodes anterior to suture (nine on penultimate whorl); sculpture on body whorl of three spiral cords crossing obsolete ribs that end in faint nodes at periphery, these nodes being less prominent than those at suture; anterior to periphery spiral cords cross minute axial striations; aperture semi-quadrate; outer lip thin, white within; columella straight with one weak plication; siphonal fasciole well developed with sharp keel; anterior canal of medium length, recurved. Length, 11.8 mm; diameter, 5.0 mm.

*Type locality:* Academy Bay, Santa Cruz (Indefatigable) Island, Galápagos Islands, Ecuador, 08° 46' 16" S, 90° 19' 38" W, CAS loc. 27536, 3.5-5.5 fms, dredged, 45 specimens. Most of the specimens are very small and appear not to have been live taken as they have a chalky appearance.

*Type material:* Holotype, CAS 13222. Paratypes: AMNH 157281; ANSP 316670; B&B 741; BM(NH); CAS 13223-13227; LACM-AHF 1288; SB 27147; SD 51962; SU 9996; USNM 680212. The LACM paratype is from AHF station 168-34, 15-25 fms, and was live collected, Academy Bay.

*Discussion:* This species shows variation in the spiral cords being well developed in some specimens and almost obsolete in others. The nodes at the periphery of the body whorl are inconspicuous in some individuals. *Terebra hertleini* has a superficial resemblance to *T. jacquelinae* sp. nov., but is a much smaller species. The holotype of the former with ten whorls measures 11.8 mm in length while that of the latter with 13 whorls measures 33.2 mm. *Terebra jacquelinae* has a row of large nodes posterior to the suture which are absent in *T. hertleini*.

*Terebra hertleini* is named for Dr. Leo G. Hertlein of the California Academy of Sciences in appreciation of his encouragement and assistance in our work on the eastern Pacific Terebridae.

### ***Terebra jacquelinae*, sp. nov.**

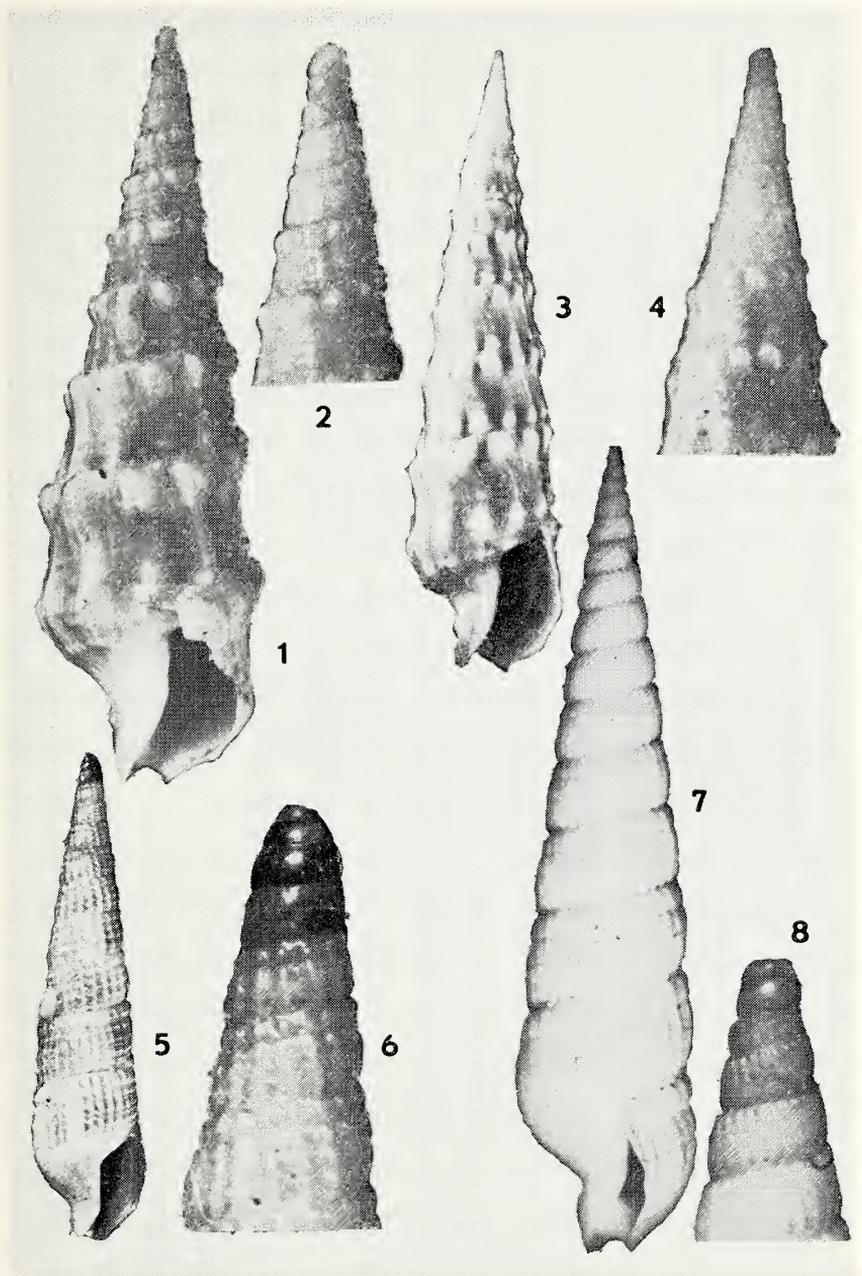
Figures 3-4

*Diagnosis:* A species differing from other west American terebrids in having extremely concave whorls and axial ribs that fade at the center of the whorl and become large nodes at each end.

*Description of holotype:* Size medium; color shiny cream; first four postnuclear whorls flat, remainder of whorls very concave, 13 in number plus 1.5 shiny, opaque, somewhat bulbous nuclear whorls; sculpture on first five

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Figures 1-8. 1. *Terebra hertleini* sp. nov. Holotype, CAS 13222. X 9. 2. *T. hertleini*, early whorls of holotype. 3. *T. jacquelinae* sp. nov. Holotype, CAS 13215. X 2.5. 4. *T. jacquelinae*, early whorls of holotype. 5. *T. purdayae* sp. nov. Holotype, LACM-AHF 1182. X 5. 6. *T. purdayae*, early whorls of holotype. 7. *T. stohleri* sp. nov. Holotype, LACM-AHF 1180. X 5.5. 8. *T. stohleri*, early whorls of holotype. Photos 1-5 by Maurice Giles; 6-8 by Twila Bratcher.



postnuclear whorls of weak axial ribs ending in small nodes at suture and of obsolete spiral grooves that cross the ribs; apical angle increases after sixth postnuclear whorl and ribs begin to fade at center of whorl while nodes at rib endings become more prominent, those anterior to suture being slightly more prominent than posterior ones; interspaces on later whorls contain minute striae, body whorl of medium length with 12 obsolete ribs ending in nodes at periphery; anterior to periphery weakly incised spiral grooves cross equally weak axial grooves; aperture elongate, white within; columella white, straight, with one rounded plication that continues to become keel of well developed siphonal fasciole; anterior canal short, recurved. Length, 33.2 mm; diameter, 8.4 mm.

*Type locality:* Academy Bay, Santa Cruz (Indefatigable) Island, Galápagos Islands, Ecuador, 0° 46' 16" S, 90° 19' 38" W, CAS loc. 39585, about 10 fathoms, on hard packed coralline sand bottom, collected by Allyn G. Smith and André and Jacqueline DeRoy, February, 1964, holotype and four paratypes.

*Type material:* Holotype, CAS 13215; 4 paratypes, CAS 13216-13219. Additional paratypes are all from Academy Bay. CAS Templeton Crocker Expedition, May, 1932, loc. 27536, 3.5-5.5 fms., 11 specimens, distributed as follows: 8 paratypes, CAS 13220; 1 paratype, BM(NH); 1 paratype, SU 9997; 1 paratype, USNM 680213. Hancock Expeditions, AHF sta. 807-38, 10-25 fms., January, 1938, 28 specimens, distributed as follows: 26 paratypes, LACM-AHF 1179; 1 paratype, MCZ 271946; 1 paratype, SD 51963. Thirteen additional paratypes were dredged by the DeRoys, 5-6 fms., 6 remain in the DeRoy collection, others distributed as follows: 1 paratype, AMNH 157282; 1 paratype, ANSP 316671; 1 paratype, SB 27148; 1 paratype, WAM; 3 paratypes, B&B.

*Referred material:* Numerous specimens of this species were among material taken by the Hancock and California Academy of Sciences expeditions and by the DeRoys at collecting stations in the vicinity of Santa Cruz (Indefatigable), San Salvador (James), and Baltra (Seymour) Islands in the Galápagos Islands at depths of 2-20 fathoms.

*Discussion:* Although there is little variation among mature individuals of this species except that some are more slender than others, occasional immature specimens have the peripheral nodes forming a sharp keel that differs in appearance from that of adults. Most of the specimens examined are of a light cream color, but a number of specimens, most of which were collected at San Salvador Island, range in color from beige to light brown with cream colored nodes. The largest specimen examined measures 36.3 mm in length and 10.8 mm in width and is in the DeRoy collection. This species should not be confused with *Terebra frigata* Hinds, 1844, which has less concave whorls, pronounced spiral sculpture, a more slender profile, and ribs that are continuous from suture to suture. The Gulf of Mexico species, *T. concava* (Say, 1827), is a smaller and much more slender species with definite spiral sculp-

ture, having small sharp nodes at the subsutural band and periphery of the body whorl.

*Terebra jacquelinae* is named for Mrs. Jacqueline DeRoy of Isla Santa Cruz, Galápagos Islands, who first brought this species to our attention.

### ***Terebra purdyae*, sp. nov.**

Figures 5-6

*Diagnosis:* A small slender species that differs from other west American species in having finely cancellate sculpture and a straight columella.

*Description of holotype:* Size small, slender; color shiny pale cream with weak fulvous blotches; whorls almost flat, 11 in number plus four purple-beige convex nuclear whorls; suture fairly well defined; barely evident subsutural band of beading, slightly more prominent than beading on remainder of whorl; sculpture finely cancellate, remarkably consistent from second postnuclear whorl through body whorl, consisting of axial ribs (29 on penultimate whorl) crossed by cords (four on penultimate whorl) giving a beaded effect; axial ribs about equal to interspaces; body whorl of medium length with sculpture continuing anterior to periphery but less well defined; aperture elongate and slender; columella straight with no plication; faint siphonal fasciole with posterior keel; anterior canal short, recurved. Length, 13.9 mm; diameter, 3.3 mm.

*Type locality:* North of Santa Maria (Charles) Island, Galápagos Islands, Ecuador, 0° 59' S, 90° 25' W, 70-80 fms., sand and rock bottom, AHF station 195-34, January 29, 1934, 2 specimens.

*Type material:* Holotype, LACM-AHF 1182; 1 paratype LACM-AHF 1183. An additional paratype, CAS 13221, is from Post Office Bay, of the same island, 8-10 fms., sand and rock and algae bottom.

*Referred material:* LACM, Hill coll. 1363, Costa Rica, 2 specimens; AHF 201-34, Panama, 4 specimens; USNM 192963, Panama, 4 specimens.

*Discussion:* The sculpture of this species resembles that of *Terebra shyana* Bratcher and Burch, 1970, but *T. purdyae* is a smaller species having a nucleus of four whorls and a straight columella with no plication. *Terebra shyana* has a nucleus of three whorls and a slightly curved columella with a faint plication. *Terebra panamensis* Dall, 1908, also has cancellate sculpture, but it is a heavier, broader shell with coarse sculpture.

*Terebra purdyae* is named for Ruth Purdy of San Diego, California, in recognition of her generosity in sharing specimens, not only with us in our work on Terebridae, but with those studying other families of mollusks.

### ***Terebra stohleri*, sp. nov.**

Figures 7-8

*Diagnosis:* A sturdy, medium-small, ivory colored species with little resemblance to other species of *Terebra*.

*Description of holotype:* Size medium-small; color shiny ivory with slightly darker blotches; whorls convex, 14 in number plus remaining 2.5 (part missing) glassy convex nuclear whorls; suture deeply channeled, constricted; subsutural band inconspicuous; whorls slightly shouldered anterior to suture; sculpture of slightly curved axial ribs (28 on penultimate whorl), about equal to interspaces and of evenly spaced spiral grooves (three including subsutural groove), the two whorls posterior to body whorl having an additional groove immediately posterior to suture; body whorl of medium length; sculpture posterior to periphery remains constant; anterior to periphery axial ribs continue and spiral grooves become more numerous and close set (seven between periphery and siphonal fasciole); aperture elongate; outer lip thin with sculpture pattern showing through; columella straight with no plication; siphonal fasciole striate; anterior canal short, recurved. Length, 21.4 mm; diameter, 5.1 mm.

*Type locality:* Braithwaite Bay, Socorro Island, Mexico, 18° 42' 20" N, 110° 56' 15" W, sand and red mud bottom, March 17, 1939, AHF station 922-39, 1 specimen.

*Type material:* Holotype, LACM-AHF 1180; 1 paratype, LACM-AHF 1181. The paratype is from Cape Rule, Socorro Island, AHF station 291-34, 4-10 fms.

*Referred material:* LACM A. 5498, Galápagos Islands, 1 specimen; LACM, Hill coll. 1365, Chamela Bay, Mexico, 2 specimens; LACM A. 375, Tres Marias Islands, Mexico, 1 specimen; Shy collection, Manzanillo, Mexico, 1 specimen.

*Discussion:* There is no other species with which this beautifully sculptured, shiny species can be easily confused.

This species is named in honor of Dr. Rudolph Stohler who has given so much of his time, his personal finances, and himself to the publishing of *The Veliger*, for the advancement of conchology and malacology.

#### RESUMEN

Se describen cuatro nuevos terébridos procedentes de las Islas del Pacífico Este: *Terebra hertleini*, *T. jacquelineae* y *T. purdyae* procedentes de las Islas Galápagos, Ecuador, y *T. stohleri* de la Isla Socorro, México.

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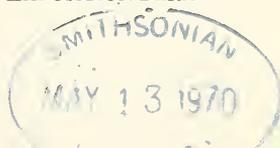
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REINSTATEMENT OF THE TURRID GENUS *BELLASPIRA*  
CONRAD, 1868 (MOLLUSCA: GASTROPODA)  
WITH A REVIEW OF THE KNOWN SPECIES

By JAMES H. MCLEAN AND LEROY H. POORMAN

LOS ANGELES COUNTY MUSEUM OF NATURAL HISTORY • EXPOSITION PARK  
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REINSTATEMENT OF THE TURRID GENUS *BELLASPIRA*  
CONRAD, 1868 (MOLLUSCA: GASTROPODA)  
WITH A REVIEW OF THE KNOWN SPECIES

By JAMES H. MCLEAN<sup>1</sup> AND LEROY H. POORMAN<sup>2</sup>

**ABSTRACT:** The clavinid turrid genus *Bellaspira* Conrad is redefined and its type species, from the Virginia Miocene, is illustrated. Six known living species of the genus are treated. Two are from the Caribbean and four are from the eastern Pacific. Three new species are described: *B. acclivicosta*, from Guaymas in the Gulf of California; *B. clarionensis*, from Clarion Island, Mexico; and *B. margaritensis* from Venezuela.

The genus *Bellaspira* Conrad, 1868, type species *Mangelia virginiana* Conrad, 1862, from the Virginia Miocene, had served a need for a small group of American turrids showing rounded axial ribs, fine spiral sculpture and a closely constricted anal canal, not deeply notched as in most other clavinid genera. Conrad's original description of the genus was adequate and his illustration of the type species, although small, showed the diagnostic features in sufficient detail to allow Dall (1919) to associate with it a Recent west American species. Unfortunately, a specimen of some other species was mislabeled as the type of *B. virginiana*, causing Bartsch and Rehder (1939) to interpret it incorrectly. As a result, three Recent species, all of which had been associated with the genus *Bellaspira* at some time, have been without a satisfactory generic allocation until now.

Abbreviations for institutions cited in the text are as follows: AHF, Allan Hancock Foundation (on loan to LACM); AMNH, American Museum of Natural History, New York; ANSP, Academy of Natural Sciences, Philadelphia; CAS, California Academy of Sciences, San Francisco; LACM, Los Angeles County Museum of Natural History; SDNHM, San Diego Natural History Museum; SU, Stanford University, California; USNM, United States National Museum of Natural History.

ACKNOWLEDGMENTS

We are greatly indebted to Mrs. Virginia Orr Maes of the Academy of Natural Sciences, Philadelphia, for locating the type specimen of *Bellaspira virginiana* and providing us with photographs and helpful information about the western Atlantic species. Dr. Joseph Rosewater and Mr. Jack Byas of the U.S. National Museum kindly located and arranged the loan of specimens in

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that institution. Radula slides were prepared by Mrs. Ellen Brennan, Museum research assistant.

### **Bellaspira** Conrad, 1868

*Bellaspira* Conrad, 1868, p. 261; Dall, 1918, p. 323; Woodring, 1928, p. 162; Grant and Gale, 1931, p. 584.

Type species, by monotypy, *Mangelia virginiana* Conrad, 1862, Miocene, Yorktown, Virginia.

Non *Bellaspira* Conrad. Bartsch and Rehder, 1939, p. 133; Gardner, 1948, p. 271; Powell, 1966, p. 103.

Conrad (1868) described the genus as follows: "Subfusiform, longitudinally ribbed; canal very short, labrum obsolete and widely notched, curved outwards, simple; labium reflexed, entire; columella straight." With further reference to the type species, he added, "It is a beautiful and graceful shell with distant ribs and very minute, close revolving lines, which become gradually more distinct on the body whorl. The labium is slightly callous near the upper extremity."

The shell figured as the type of *Mangelia virginiana* by Bartsch and Rehder (1939), copied by Gardner (1948), and Powell (1966), in no way agrees with Conrad's description or illustration, and as Powell noted, the affinity of the specimen is "with the mangelias or eucitharids," in the subfamily Mangeliinae rather than the Clavinae.

Mrs. Virginia Maes has found that both the specimen figured by Bartsch and Rehder, ANSP 1610, and another specimen, ANSP 30737, are labeled "*Mangelia virginiana*" in Conrad's handwriting. There is no doubt that the latter specimen is the one figured by Conrad in 1868. There may have been another original specimen in lot 1610 which was subsequently lost. In order to avoid further confusion, the only extant specimen, ANSP 30737, is here considered the holotype. This specimen has seven postnuclear whorls, not five as stated in the original description.

Grant and Gale (1931) included two other genera in the synonymy of *Bellaspira*, the European *Atoma* Bellardi, 1875, and *Haedropleura* Bucquoy, Dautzenberg, and Dollfus, 1883, but these taxa, as treated by Powell, 1966, lack the features of *Bellaspira*. *Bellaspira* is therefore strictly an American genus, with Recent species in the Caribbean, Panamic, and Californian provinces.

Radulae of two west American species, *B. melea* and *B. acclivicosta*, new species, have been examined (Figs. 1, 2). The radula is of the prototypic type described by Powell (1966, p. 70) as occurring in many of the strongly ribbed, glossy shelled genera of Clavininae. The radula consists of a vestigial rachidian, comblike laterals and long, narrow marginals.



Figures 1-2. Radulae of *Bellaspira*, greatly enlarged. 1. *B. acclivicosta* sp. nov., Soladita Cove, Guaymas, Mexico. 2. *B. melea* Dall, San Carlos Bay, Guaymas, Mexico.

A new generic diagnosis, taking the features of the living species into account, follows:

Shell 7-19 mm in height, solid, spire elevated; outline concave below the suture, convex above; nuclear whorls two, smooth; axial sculpture of low rounded ribs, spiral sculpture of fine incisions or threads; anterior canal broad, only slightly notched, posterior notch constricted, mature specimens with a small deposition of callus at top of inner lip, immature specimens lacking a turrid sinus; lip of mature shell not greatly thickened, but penultimate axial rib thickened, producing a swelling as in other clavinid genera; color white to pink, some with darker spiral banding or markings on the axial ribs; operculum leaf-shaped, nucleus terminal; radula prototypic.

### ***Bellaspira virginiana* (Conrad, 1862)**

#### Fig. 3

*Mangelia virginiana* Conrad, 1862, p. 286.

*Bellaspira virginiana*, Conrad, 1868, p. 261, pl. 21, fig. 12.

Non *Bellaspira virginiana*, Bartsch and Rehder, 1939, p. 133, pl. 17, fig. 6;

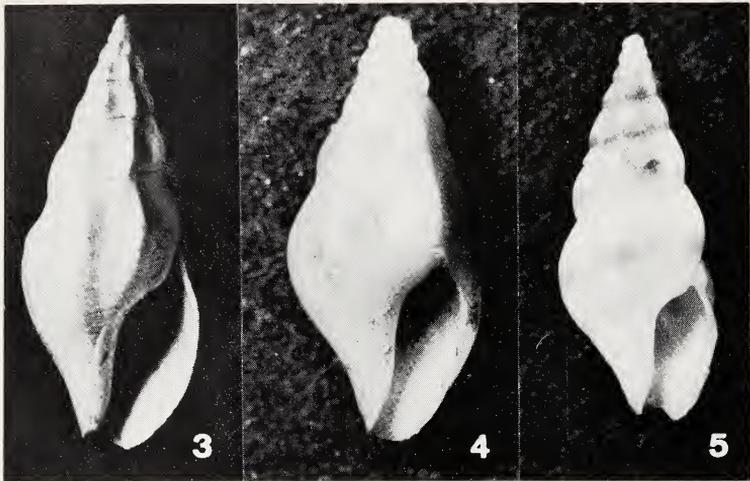
Gardner, 1948, p. 271, pl. 37, fig. 14; Powell, 1966, p. 103, pl. 16, fig. 6.

*Description*: Postnuclear whorls seven, axial ribs eight, continuous from whorl to whorl, spiral striae well spaced; height, 14 mm.

*Type locality*: Miocene of Yorktown, Virginia.

*Type material*: Holotype (here regarded as discussed above): ANSP 30737 (Fig. 3).

*Discussion*: We have no other information on the occurrence of the type species. Additional material is not represented in the Philadelphia Academy.



Figures 3-5. 3. *Bellaspira virginiana* (Conrad). Holotype, ANSP 30737. X 4. 4. *B. pentagonalis* (Dall). Holotype, USNM 9300. X 8. 5. *B. pentepleuræ* Schwengel (= *B. pentagonalis*). Holotype, ANSP 176450. X 5.

### ***Bellaspira pentagonalis* (Dall, 1889)**

Figs. 4, 5

*Drillia pentagonalis* Dall, 1889, p. 90.

*Bellaspira* (?) *pentepleuræ* Schwengel, 1940, p. 51, pl. 3, figs. 3, 3a; Powell, 1966, p. 104.

*Description:* Postnuclear whorls six, axial ribs five, continuous from whorl to whorl, color white with a peripheral row of squarish chestnut spots on the axial ribs, spiral striae weakly developed; height, 8-10 mm.

*Type material and type localities:* Holotype, *Drillia pentagonalis*, USNM 9300 (Fig. 4); 1 paratype, USNM 679297. Type locality: USFC sta. 2596, 17 miles east of Cape Hatteras, North Carolina, 49 fathoms. Holotype, *Bellaspira pentepleuræ*, ANSP 176450 (Fig. 5); 3 paratypes, ANSP 315786. Type locality: Off Palm Beach Florida, 45 fathoms, T. L. McGinty.

*Distribution:* Cape Hatteras, North Carolina, to Key West and Saint Petersburg, Florida, 20-60 fathoms. Approximately 80 lots are represented in the National Museum collection.

*Discussion:* Dall's early name *Drillia pentagonalis* has been overlooked, evidently because the type was never illustrated. The holotype is worn and faded, measuring 6.9 mm in height. This species has only five axial ribs and thereby differs from all the other species having more numerous ribs.

*Bellaspira margaritensis* sp. nov.

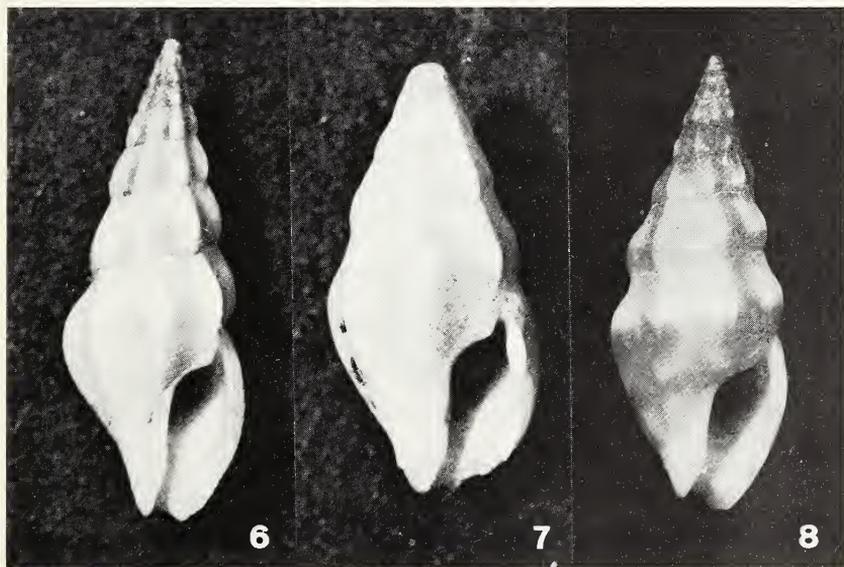
Fig. 6

*Diagnosis:* A relatively large species, having more numerous axial ribs and more deeply incised spiral striae than *B. pentagonalis*.

*Description of holotype:* Shell relatively large for the genus; nucleus of two smooth, rounded whorls; postnuclear whorls eight, axial ribs seven, continuous from whorl to whorl; suture simple, slightly undulating; axial ribs evenly rounded, no subsutural channel; spiral sculpture of well defined, broadly spaced spiral incisions, more crowded in the subsutural area, approximately 12 on the penultimate whorl. Color whitish except for a broad pinkish area about the periphery, weakly demarked and not extending over the rib surfaces. Parietal callus well defined, terminating in a small node in front of the anal sulcus. Edge of outer lip thin, with a shallow stromboid notch near the base, a minor axial rib slightly behind the edge; the penultimate rib more strongly developed than the others. Dimensions (in mm): height 15.0, diameter 5.5.

*Type locality:* Four to seven miles north of Margarita Island, Venezuela, 11° 08' N, 64° 17' W, 17-21 fathoms on sand, R/V *Velero* III Station A42-39, 21 April 1939, four specimens, two live-taken.

*Type material:* Holotype, LACM-AHF 1337 (Fig. 6); two paratypes, LACM-AHF 1338; one paratype, USNM 675964.



Figures 6-8. 6. *Bellaspira margaritensis* sp. nov. Holotype, LACM-AHF 1337. X 4.2. 7. *B. melea* Dall. Holotype, USNM 15952. X 4.5. 8. *B. melea* Dall. Off San Carlos Bay, Guaymas, Mexico. X 5.

*Discussion:* The only other species with roundly arched axial ribs is *B. pentagonalis*, from which *B. margaritensis* differs in having two additional axial ribs, more prominent and broadly spaced incised spiral sculpture, and a color band not developed across the rib surface.

***Bellaspira melea* Dall, 1919**

Figs. 7, 8

*Bellaspira melea* Dall, 1919, p. 29, pl. 19, fig. 8; Grant and Gale, 1931, p. 584.

*Elaeocyma melea*, Pilsbry and Lowe, 1932, p. 110.

*Clavus* (?*Cymatosyrinx*) *melea*, Keen, 1958, p. 448, fig. 736.

*Description:* Postnuclear whorls 7-8, axial ribs 6-8, continuous from whorl to whorl, first rib behind the lip greatly thickened; color whitish to flesh pink, with traces of darker banding, rib surfaces lighter in color; height, 13-19 mm.

*Type locality:* Panama, collected by Col. E. Jewett.

*Type material:* Holotype, USNM 15952 (Fig. 7).

*Distribution:* Tepoca Bay, Sonora, Mexico, to Port Utria, Colombia, 10-40 fathoms. Twenty-two lots are represented in the LACM collection. Intermediate stations in Mexico include Concepcion Bay, Baja California; Guaymas, Sonora; Cleopha Island, Tres Marias Islands; Sihauntanejo, Guerrero; Guatulco Bay, Oaxaca; and in Costa Rica, Port Culebra; indicating that the species is widely distributed throughout its range.

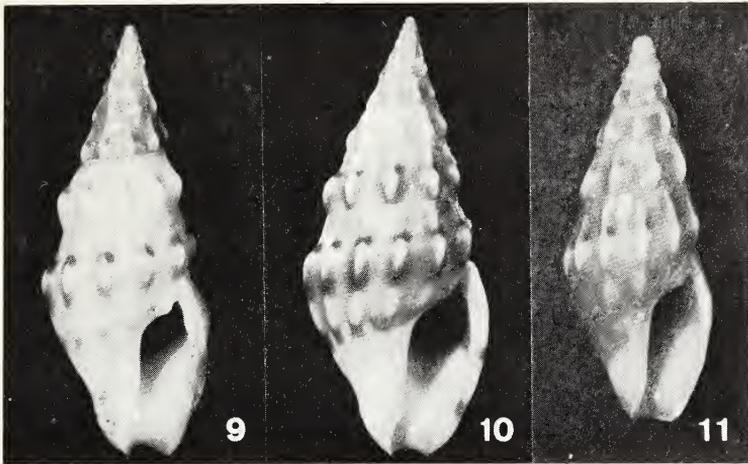
*Remarks:* Dall (1919) correctly assigned this species to *Bellaspira*, noting that it is "typical *Bellaspira*." It so resembles *B. virginiana* that it would undoubtedly be considered conspecific but for the discrepancies of age and distribution. The type specimen is a worn shell not showing spiral sculpture, but Dall observed that spiral sculpture could have been worn away. In fresh specimens (Fig. 8) the spiral sculpture is extremely minute and somewhat undulating. *Bellaspira melea* varies considerably in color. Some specimens are white and others have pink or flesh colored banding, the darkest band located at the periphery.

***Bellaspira acclivicosta* sp. nov.**

Figs. 9-11

*Diagnosis:* A relatively large species with a characteristic color pattern, having more numerous and more strongly crested axial ribs than *B. melea*.

*Description of holotype:* Shell large for the genus, pinkish white to flesh colored; nucleus of two smooth, rounded, glassy pink whorls; postnuclear whorls nine, axial ribs 10, not continuous from whorl to whorl; suture simple, slightly undulating at the base of the ribs; ribs weak on the shoulder, strong and nodulous at the periphery, becoming obsolete on the base. Entire shell



Figures 9-11. All *Bellaspira acclivicosta* sp. nov. 9. Holotype, LACM 1193. X 3. 10. Off Isla Candelero, Guaymas, Mexico, Poorman collection. X 3. 11. Pulmo Bay, Baja California, Mexico, LACM 66-19. X 5.5.

covered by microscopic, raised spiral threads, most numerous above the periphery and strongest on the base, crossed by incremental growth threads to form a minutely reticulated surface. Peripheral crests of ribs white, surrounded by red-brown, strongest above and below; a second and smaller row of dots on the ribs between the periphery and the anterior tip. Columella straight, parallel to axis of shell, twisting slightly to the left at the base. The parietal callus is well defined and terminates in a domelike pad in front of the anal sulcus. Outer lip thin, smooth within, nearly parallel to the columella, showing a shallow stromboid notch near the base and thickened by the final rib, which is preceded by an unusually wide valley and the penultimate rib that is stronger than all the others. Periostracum lacking; operculum with apical nucleus. Dimensions (in mm): height 18.1, diameter 6.8.

*Type locality*: One kilometer south of the east point at the entrance to Bahía San Carlos, Guaymas, Sonora, Mexico; 27° 56' N, 111° 03' W; 15-20 fathoms on rock and broken shell bottom, December, 1965, to April, 1967, Forrest and Roy Poorman, ten specimens.

*Type material*: Holotype, LACM 1193 (Fig. 9); one paratype, ANSP 315788, one paratype, AMNH 147999; one paratype, CAS 13159; one paratype, SDNHM 50000; one paratype, SU 9964; one paratype; USNM 679183; three paratypes, Poorman collection.

*Referred material*: Poorman collection, two specimens dredged at Isla Candelero, Guaymas (Fig. 10); LACM 68-27, four specimens, diving at 60 feet, Soladita Cove, Guaymas; LACM 66-19, one specimen, diving at 5-20

feet, Pulmo Bay, Baja California (Fig. 11); Shy collection (Westminster, California), one specimen dredged at Manzanillo, Colima, Mexico.

*Discussion:* Immature shells of *B. acclivicosta* do not show a turrid sinus and lack the callus deposition defining the anal sinus. Figure 10 shows a specimen slightly larger and broader than the holotype that has an immature lip. This specimen also is more distinctly colored than the holotype. The specimen from Pulmo Bay (Fig. 11) has six postnuclear whorls and measures 9.1 mm in height. It is evidently a miniature specimen of *B. acclivicosta* having a mature lip. It is similar to the type lot except for size.

The new species differs from *B. melea* in having about ten discontinuous axial ribs rather than seven continuous ribs per whorl. The spiral sculpture consists of fine raised spiral threads on *B. acclivicosta*, whereas the weak grooves on *B. melea* appear to be scratched into the surface.

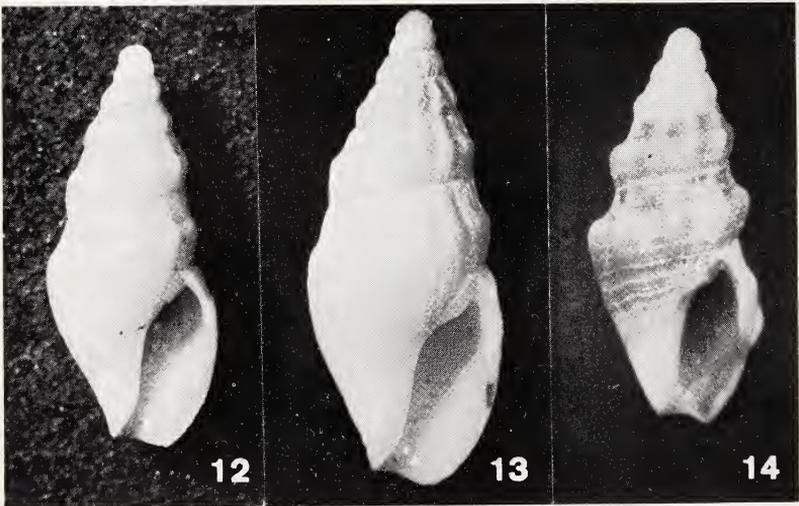
The name is derived from the Latin nouns *acclivis*, steep, and *costa*, rib, suggestive of the steep, concave slope of the ribs below the suture. The specific name is intended as a noun in apposition.

### **Bellaspira grippi** (Dall, 1908)

Figs. 12-15

*Bela grippi* Dall, 1908, p. 137.

*Lora grippi*, Dall, 1921, p. 74, pl. 3, fig. 8; Oldroyd, 1927, p. 100, pl. 7, fig. 6.



Figures 12-14. All *Bellaspira grippi* (Dall). 12. Holotype, USNM 200653. X 5.7. 13. San Martin Island, Baja California, Mexico, LACM 67-50. X 6.4. 14. Asuncion Island, Baja California, LACM 67-66. X 7.4.

*Bellaspira grippi*, Grant and Gale, 1931, pp. 514, 565; Burch, 1946, p. 19 ["grippii"].

*Description*: Relatively small, postnuclear whorls six, subsutural area markedly concave; axial ribs 12-14, not continuous from whorl to whorl, ribs obsolete at the base and often over the final whorl; color white to flesh pink, some with dark and light banding; height, 7-11 mm.

*Type locality*: Five miles south of the entrance to San Diego Bay, 15 fathoms, C. W. Gripp, collector.

*Type material*: Holotype, USNM 200653 (Fig. 12), one paratype, USNM 697389.

*Distribution*: Redondo Beach, California, to Asuncion Island, Baja California; Guadalupe Island, Mexico. Not uncommon on rocky bottoms under kelp and dredged on gravel bottoms to depths of 25 fathoms.

*Discussion*: Grant and Gale (1931) were the first to associate this species with the genus *Bellaspira*, a relationship missed by Dall, who had correctly assigned his *B. melea* in 1919.

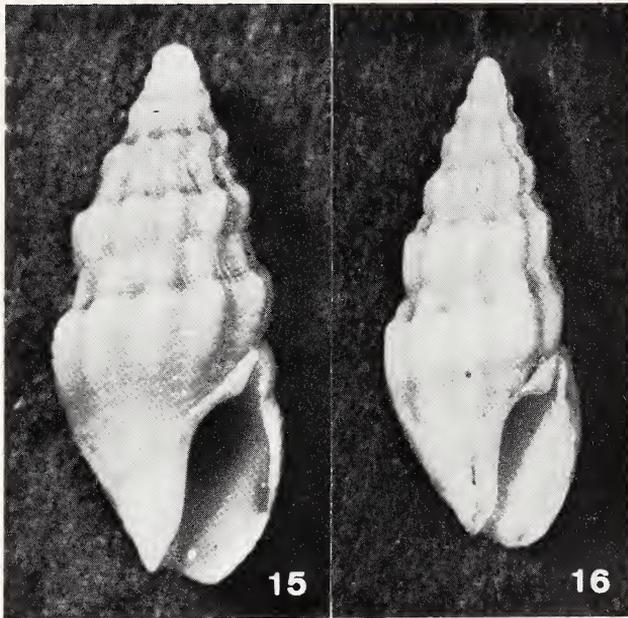
A wide range of variation is shown in this species. The typical southern Californian form, represented by the holotype (Fig. 12) and a specimen from San Martin Island, Baja California (Fig. 13), is whitish or flesh colored and usually shows a slightly darker band in the concave area of the shoulder. One specimen from Asuncion Island, outer coast of Baja California (Fig. 14), 6.9 mm in height, is dark rose colored, except on the siphonal fasciole, and the shoulder is more strongly tabulate, the axial ribs forming projecting nodes. Incised spiral sculpture is unevenly spaced on the body whorl. The largest of five specimens from Guadalupe Island (Fig. 15) is 7.5 mm in height. All are strongly tabulate and the spiral incisions are evenly spaced; two are dark flesh-colored and one is white.

### ***Bellaspira clarionensis* sp. nov.**

Fig. 16

*Diagnosis*: A medium sized species larger than *B. grippi* and having more numerous spiral striae.

*Description of holotype*: Shell of medium size for the genus, nuclear whorls two, rounded; postnuclear whorls seven, axial ribs 10, alternating in position on early whorls, but aligned from whorl to whorl on the final three whorls. Suture simple, slightly undulating; shoulder concave; axial ribs well defined across the shoulder, cresting at the periphery, extending across the body whorl and becoming obsolete on the base. Spiral sculpture of closely spaced spiral striae, more crowded upon the shoulder and overriding the axial ribs. Color whitish with a narrow band of flesh pink upon the shoulder and another uninterrupted narrow band across the base. Parietal callus projecting, anal sinus narrow. Lip edge thin, stromboid notch barely perceptible, the



Figures 15-16. 15. *Bellaspira grippi* (Dall). Guadalupe Island, Mexico, LACM 65-42. X 9.5. 16. *B. clarionensis* sp. nov. Holotype, LACM-AHF 1366. X 4.6.

second and third ribs behind the aperture coalesced and thickened. Dimensions (in mm): height 13.5, diameter 5.9 mm.

*Type locality*: Off Sulphur Bay, Clarion Island, Revillagigedo Islands, Mexico, 18° 20' N, 114° 44' W, 28-45 fathoms on sand, R/V *Velero III* Station 917-39, 16 March 1939, one specimen. Two additional paratype specimens were dredged at stations 136-34 and 921-39, Sulphur Bay, Clarion Island, 30-35 fathoms.

*Type material*: Holotype, LACM-AHF 1366 (Fig. 16), one paratype, LACM-AHF 1367; one paratype, USNM 675565.

*Referred material*: LACM A.375, five specimens, dredged by George Willett, 20-35 fathoms, Clarion Island, 24 March 1938.

*Discussion*: *Bellaspira clarionensis* differs from *B. grippi* in reaching a larger size, having a narrower shoulder area, elongate rather than nodular axial ribs, and more numerous spiral striae.

#### RESUMEN

El género clavínido túrrido *Bellaspira* Conrad se redefine y la especie tipo, del Mioceno de Virginia, se ilustra. Seis especies vivientes conocidas en este género son aquí tratadas. Dos de ellas son del Caribe y cuatro del Pacífico

Este. Se describen tres nuevas especies: *B. acclivicosta*, de Guaymas en el Golfo de California; *B. clarionensis*, de la Isla Clarión, México; y *B. margaritensis* de Venezuela.

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# CONTRIBUTIONS IN SCIENCE

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A NEW SPECIES OF FOSSIL KELLETIA (MOLLUSCA:  
GASTROPODA) FROM THE LOMITA MARL,  
LATE CENOZOIC OF SAN PEDRO, CALIFORNIA

By LEO G. HERTLEIN



LOS ANGELES COUNTY MUSEUM OF NATURAL HISTORY • EXPOSITION PARK  
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A NEW SPECIES OF FOSSIL KELLETIA (MOLLUSCA:  
GASTROPODA) FROM THE LOMITA MARL,  
LATE CENOZOIC OF SAN PEDRO, CALIFORNIA

By LEO G. HERTLEIN<sup>1</sup>

ABSTRACT: *Kelletia kanakoffi*, a new species of gastropod belonging to the family Neptuneidae, is described from strata of Late Pliocene or Early Pleistocene age in San Pedro, California.

INTRODUCTION

Numerous species of fossil mollusks have been reported from Hilltop Quarry and nearby localities (see Hanna, 1923; Schenck, 1945: 513-514; Woodring *et al.*, 1946: 49-52; Valentine, 1961: 411-413) in San Pedro, Los Angeles County, California. Intensive collecting in this area by George P. Kanakoff and his associates has yielded many interesting fossils now preserved in the Los Angeles County Museum of Natural History.

Recently Mr. Kanakoff sent the author two specimens of a large gastropod, referable to the genus *Kelletia*. Study of these fossils revealed that they represent an undescribed species here described as new.

The strata in which they were found have been considered to be of Late Pliocene age by some authors but as Early Pleistocene age by others. An age of three million years given by Obradovich (1965), based upon Potassium-Argon dating of glauconite, represents the most recent maximum age attributed to these sediments. This date would certainly place the Lomita Marl, a member of the lower San Pedro formation, in the Late Pliocene or very Early Pleistocene. Several species of mollusks reported from the Lomita Marl occur elsewhere only in strata believed by some authors to be of Pliocene age.

ACKNOWLEDGMENTS

I am grateful to Mr. George P. Kanakoff, Curator Emeritus of the Section of Invertebrate Paleontology, Los Angeles County Museum of Natural History, who lent the specimens of the new species described herein for study and description. Acknowledgment also is due Victor Zullo, Allyn G. Smith and Barry Roth, California Academy of Sciences, whose advice and criticism was particularly helpful during the preparation of the manuscript. Alan J. Galloway of the same institution, and Warren O. Addicott, United States Geological Survey, called my attention to certain literature concerning the geochronology of the Lomita Marl. The illustrations in the text are from photographs made by Maurice Giles, Staff Photographer, California Academy of Sciences.

<sup>1</sup>Curator (Emer.) of Invertebrate Paleontology, California Academy of Sciences; and Research Associate, Los Angeles County Museum of Natural History.

## CLASS GASTROPODA

## Family Neptuneidae Tryon

Genus *Kelletia* Bayle, in Fischer

*Kelletia* Bayle, in Fischer, 1884: 625. Sole species, "*S. Kelleti*, Forbes." Wenz, 1938 (reprint, 1962): 1166

*Type species: Siphonalia kelleti* Forbes [= *Fusus kelletii* Forbes (1852: 274, pl. 9, fig. 10)] "taken on the Californian coast."

This genus (and its type species) was named for Captain Kellett of the British Royal Navy. Some authors have used the orthography *Kellettia* but most recent authors have followed the original spelling given by Bayle for the genus and *kelletii* for the species as given by Forbes.

West American authors have placed *Kelletia* in either the family Neptuneidae or the Buccinidae. Powell (1929: 63) stated that the shell characters as well as the radula of this genus are very similar to *Austrosipho* Cossmann, and these genera he placed in the family Buccinulidae Finlay. Wenz (1962: 1151) placed both that family and the Neptuneidae as subfamilies under the Buccinidae. He considered *Austrosipho* Cossmann, 1906, and *Verconella* Iredale, 1914, to be synonyms of *Penion* Fischer, 1884.

Ruth (1942), in a monograph of *Siphonalia* in the Cenozoic of western North America, considered *Kelletia* a subgenus which included four species that he described and illustrated. The geologic range of the subgenus indicated by the included species was from Paleocene (Martinez) to Recent. Subsequent to Ruth's paper, one species, *Kelletia vladimiri* Kanakoff, was described from strata of Pliocene age in southern California. One species of *Kelletia* now lives in the region between Santa Barbara, California, and San Quintín, Baja California, from the intertidal zone to a depth of about 64 meters (35 fathoms). Another species, *Kelletia lischkei* Kuroda, lives in Japanese waters where it has been reported to range from 32° to 39° North Latitude on the Pacific coast and to 40° North on the Japan Sea coast.

In their catalogue of the Tertiary mollusks of Japan, 1952, Hatai and Nisiyama did not allocate any species to *Kelletia* but species assigned to *Kelletia* (considered to be a subgenus of *Siphonalia*) have been reported by others from strata of Late Tertiary age in Indonesia and in India.

Two species of Pliocene age from Ecuador, tentatively assigned to *Kelletia* by Olsson (1964: *K. ecuadoriana*, p. 165, pl. 24, figs. 2-2c and *K. rugosa*, p. 165, pl. 24, figs. 1, 1a), do not closely resemble species of that genus described from California.

Anderson (1964: 249) recently proposed a subgenus *Boreokelletia*, based upon *Kelletia* (*Boreokelletia*) *hosiusi* (Beyrich, 1856), from strata of Miocene age in Germany. The type species earlier was referred to the genus *Streptochetus* Cossman, 1889, by Kautsky (1925: 117), and others.

***Kelletia kanakoffi*, new species**

Figures 1, 2, and 3

*Diagnosis:* A new species of *Kelletia* which differs from other west American species of this genus in its large size, thick shell, coarse spiral sculpture and large umbilicus.

*Description:* Shell large, thick, fusiform, the spire elevated; whorls of spire five (the apex lacking), angulated near the middle, posteriorly slightly concave and extending over a little more than one half of the preceding whorl, the suture appressed; axial sculpture consisting of well developed, axially elongated nodes, seven on the uppermost, eight on the succeeding one, ten on the penultimate whorl and eight on the body whorl, followed by a low, carinate ridge at an angulation posterior to the middle, with vague vertical ridges outlined by lines of growth; the entire shell is sculptured with spiral ridges separated by deep grooves, about twenty on the penultimate whorl and about twenty-three on the body whorl, the anterior ones much coarser than the posterior ones; some ridges bear one to three spiral grooves and where eroded these separate small riblets; aperture ovate, outer lip not thickened, the interior lightly lirate corresponding to the exterior sculpture, pillar smooth, twisted, inner lip smooth; canal well developed, narrow, twisted and recurved, a large siphonal fasciole present, in front of which is a large, rather wide umbilicus.

*Dimensions:* The holotype, length (apex lacking), 181 mm, maximum diameter, 90 mm, length of aperture and canal, 102 mm; paratype, length, 178 mm, maximum diameter, 91 mm, length of aperture and canal, 104 mm.

*Type locality:* Loc. 435 LACMIP, Lomita Marl about 50 feet below the crossing of West Park Drive, Host Place and Coralmount Drive, San Pedro, California. Late Pliocene or Early Pleistocene. John Sutherland collector, July, 1966.

*Type specimens:* Holotype Catalog Number 2456, and Paratype Catalogue Number 2457, Los Angeles County Museum of Natural History, Invertebrate Paleontology Collection.

*Comments:* This new species differs from the Recent *Kelletia kelleitii* (Forbes, 1852: 274, pl. 9, fig. 10) in the larger size, coarser sculpture, very large umbilicus, the more angulated shoulder and slightly carinate body whorl, and in that the whorls on the spire overlap the preceding ones to a less extent posteriorly than do those of the well known living species (see Arnold, 1903: pl. 4, fig. 5; Ruth, 1942: pl. 48, fig. 5; Abbott: 1954, pl. 24, fig. W).

A large specimen of *Kelletia kelleitii* 161 mm long and 76 mm in maximum diameter, in the collections of the California Academy of Sciences, from Locality 31642 (CAS), from 3.7 miles off Huntington Beach, California, in 37 to 38 meters (20 to 21 fathoms), has only a short, narrow, shallow, umbilical groove in comparison to the large umbilicus of *K. kanakoffi*, new species. The largest specimen of *K. kelleitii* reported in the literature (Anon., 1959:

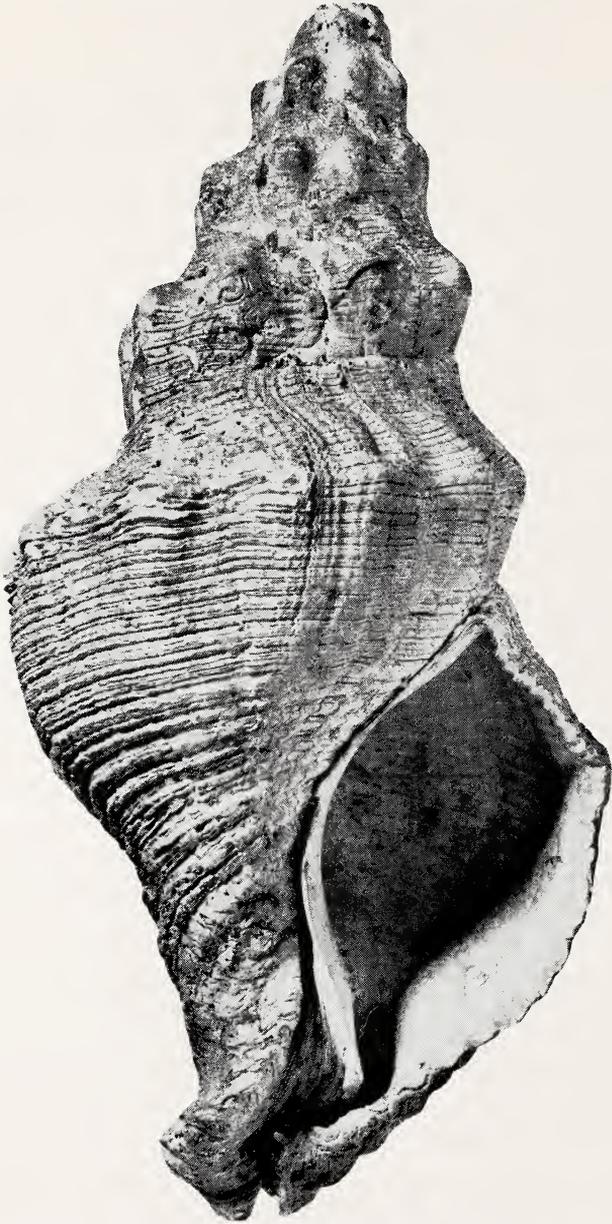


Figure 1. *Kelletia kanakoffi*, new species. Holotype, LACMIP 2456, from Lomita Marl, San Pedro, California; Late Pliocene or Early Pleistocene age. Approximately X 5/6; true length (apex lacking), 181 mm, maximum diameter, 90 mm.



Figure 2. *Kelletia kanakoffi*, new species. Dorsal view of holotype shown in figure 1.

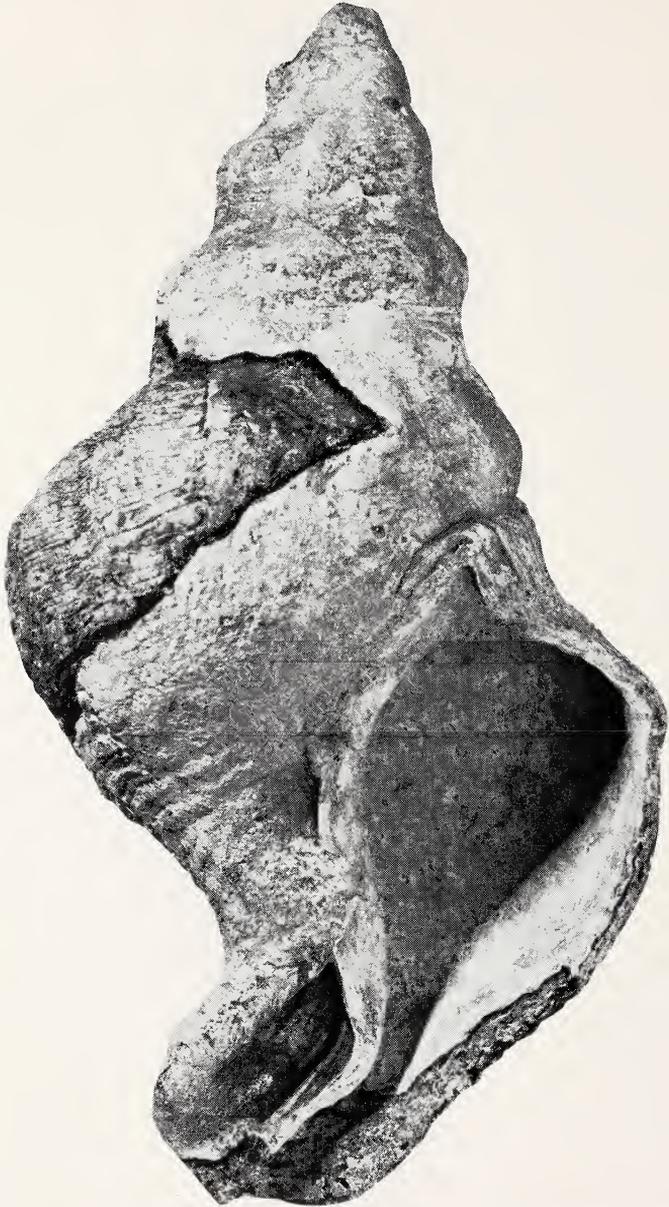


Figure 3. *Kelletia kanakoffi*, new species. Paratype, LACMIP 2457, from the same locality as the holotype shown in figure 1. Approximately X 5/6; true length, 178 mm, maximum diameter, 91 mm. Note the large umbilicus on this specimen.

19), from southern California, is 170 mm long and 87 mm in maximum diameter.

The same shell characters which serve to separate *Kellettia kanakoffi*, new species, from *K. kelletii* also differentiate it from *Kellettia vladimiri* Kanakoff (1954: 114, pls. 29, 30, 31), a smaller, more slender form described from the Pico formation, of Pliocene age, in Los Angeles County, California.

This species is named for Mr. George P. Kanakoff, Curator Emeritus, Los Angeles County Museum of Natural History, whose careful collecting has brought to light many interesting specimens.

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STUDIES ON THE FROGS OF THE GENUS *LEPTODACTYLUS*  
(AMPHIBIA: LEPTODACTYLIDAE). VI.  
BIOSYSTEMATICS OF THE MELANONOTUS GROUP

By W. RONALD HEYER



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BIOSYSTEMATICS OF THE MELANONOTUS GROUP

By W. RONALD HEYER<sup>1</sup>

ABSTRACT: Six species are recognized in the Melanonotus group: *dantasi*, *discodactylus*, *melanonotus*, *podicipinus*, *pustulatus*, and *wagneri*. A synonymy, diagnosis, summary of characteristics, and distributional summary are presented for each species. Series of *Leptodactylus* were analyzed from broad geographic and ecologic areas and situations for standard length, ventral pattern, ventrolateral gland development, posterior thigh pattern, and toe disk development. Correlations are evident between 1) larger size and more mesic habitats in *wagneri*, 2) darker ventral pattern and greater annual rainfall in *melanonotus*, 3) lighter ventral pattern and greater ventrolateral-gland extent in *wagneri*, and 4) greater ventrolateral-gland extent and greater annual rainfall in *wagneri*. The hypothesis is presented that character displacement is involved in the sharp differences in size and pattern between populations of *melanonotus* and *wagneri* as well as *podicipinus* and *wagneri* in sympatry.

*Leptodactylus melanonotus* is the most primitive of the species, while *discodactylus* and *pustulatus* are the most advanced.

*Leptodactylus melanonotus*, *podicipinus*, and *wagneri* are associated with old land masses and are species adapted for xeric conditions. *Leptodactylus dantasi* and *discodactylus* are limited to the Tropical Rainforest of the western Amazonian Basin. *Leptodactylus pustulatus* is distributed in the xeric regions of eastern Brasil.

#### INTRODUCTION

Since the frog genus *Leptodactylus* was proposed by Fitzinger in 1826, it has had an unstable systematic history. No one since Boulenger, in 1882, has treated the group as an entity. The present paper is the first of a projected series attempting to elucidate the biosystematics of each of the species groups within the genus. In the Melanonotus species group, characters of gross morphology and distribution are used to analyze the interspecific relationships, ecological distribution patterns, and geographical distribution patterns of the species.

#### METHODS

All adult specimens of the Melanonotus species group were examined for size, sex, ventral color pattern, ventrolateral gland development, posterior

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thigh pattern, and degree of toe-tip expansion. Analysis of these characters is the basis for the taxonomic conclusions. For convenience, taxonomic conclusions are presented first before discussing the variation of characters analyzed in detail.

All available adult individuals of *L. dantasi*, *discodactylus* and *pustulatus* were studied for variation in 34 characters. The same 34 characters were examined in a series of 15 males and 15 females for each of the other three species. Thirty specimens of *melanonotus*, *podicipinus*, and *wagneri* were chosen to represent the extremes in geographic origin and morphological variation. Details of the methods of examining individuals are the same as used previously (Heyer, in press). Percentages of standard length (SL) are presented as follows, 5-6.1-7, where the first number is the minimum, the second the mean, and the third the maximum percentage. The terminology follows Peters (1964) and Elias and Shapiro (1957). A dissecting microscope was used to examine the pattern of melanophore distribution on the ventral surfaces since melanophores in a contracted state are difficult to distinguish with the naked eye.

Prior to this study, five characters appeared adequate to define populations of the *Melanonotus* species group. Male and female sizes were recorded, and standardized forms were drawn which encompassed the range of variation for the ventral pattern, ventrolateral gland development, posterior thigh pattern, and toe-disk development. If a selected character appeared intermediate in any single frog, it was arbitrarily placed in the category it more closely resembled.

One to 100 individuals have been collected from each of 454 localities in Mexico and Middle America. As the status of the frogs in this geographic area was reasonably clear, samples for analysis were selected every 100 km along both coasts and in any inland area. In regions where faunal changes might be expected on the basis of other anuran distribution patterns more samples were analyzed. The samples, usually 10 frogs per locality, from 56 localities from Mexico through Panama and all available South American specimens of the *Melanonotus* species group were analyzed. The frogs were examined to determine how many distinctive morphotypes were present. Examples demonstrating the range of variation for individuals from each population were then recorded. Analyses of only the largest specimens of each distinct morphotype from each locality were recorded. Thus in the following analysis, size refers to the maximum for males and females for a given locality.

A series of mating call recordings were made in western Mexico in July 1967 on an Uher 4000 L portable tape recorder at 7.5 ips. The tapes were analyzed on a Kay Sonagraph 6061 B. Information on number of notes per call group, dominant frequency, harmonics, and frequency shifts was recorded from the sonagrams. The tapes are deposited at the University of Southern California, Department of Biological Sciences. Localities, tapes

(one individual per tape), and specimens on deposit at the Los Angeles County Museum of Natural History, respectively, are: COLIMA, Colima, WRH 67-12, LACM 37037; JALISCO, 5 km W Acatlán, 1400 m, WRH 67-20, LACM 37038, WRH 67-21, WRH 67-22, WRH 67-23, LACM 37039, WRH 67-24, WRH 67-25, LACM 37040; 7.7 km E La Huerta, 340 m, WRH 67-26, LACM 37041; 37.5 km SW Tecalitlan, 910 m, WRH 67-15, WRH 67-16, WRH 67-17; 0.5 km NE Tonila, 1300 m, WRH 67-18, LACM 37428; MICHOACÁN, 2.6 km N Capirio, 300 m, WRH 67-13, LACM 37427; NAYARIT, 13.2 km NE San Blas, WRH 67-31; Santa Cruz, 15 m, WRH 67-30, LACM 37043; Tepic, 950 m, WRH 67-27, LACM 37042, WRH 67-28; SINALOA, 36 km S Los Mochis turnoff on Mexican Highway 15, 10 m, WRH 67-2, LACM 37426, WRH 67-3, LACM 37036; SONORA, 3.1 km E Hermosillo, WRH 67-32.

Certain environmental parameters were chosen to evaluate as possible correlates with SL, gland development, ventral pattern, and posterior thigh pattern.

Total annual rainfall, number of months with less than 100 mm of rainfall (dry months), and elevation were recorded for each locality. The climatic data were taken from Espinal and Montenegro (1963) for Colombia; Holdridge (1964) for Middle America; Tosi (1960) for Peru; Vivo Escoto (1964) for Mexico; Walter and Lieth (1960-67) for South America and Lesser Antillean Islands. Elevational data were taken from museum catalogues or from the Millionth Map series (American Geographical Society).

The correlation coefficient used to compare categories was the product moment method for ungrouped data, as presented by Arkin and Colton (1966, pp. 80-82). Mary Nafpaktitis wrote a Fortran program for this formula suited to my data. Robert J. Lavenberg wrote a Basic program for a *t*-test, as presented by Fisher (1948, pp. 193-196). The correlation coefficients and *t*-tests were run on a General Electric Time Share Computer terminal, provided by the Los Angeles County Museum of Natural History. The *t* values were located on a table (Fisher, 1948, p. 174) to determine the level of statistical significance (*P* value) of the correlation coefficients. A *P* value of .05 or less was considered statistically significant.

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The curators of collections with which I worked were particularly gracious in providing information, lending large amounts of material and allowing dissections and skeletal preparations in certain cases (Museum abbreviations as used in the text in parentheses): James E. Böhlke, Academy of Natural Sciences, Philadelphia (ANSP); Werner C. A. Bokermann, São Paulo (WCAB); Antenor Leitao de Carvalho, Museu Nacional, Rio de Janeiro; Javier Castroviejo, Museo Nacional de Ciencias Naturales, Madrid; Doris M. Cochran and James A. Peters, United States National Museum (USNM and field series GOV and JAP); James R. Dixon, Texas A. & M. University (TCWC); William E. Duellman, Museum of Natural History, University of Kansas (KU); Josef Eiselt, Naturhistorisches Museum, Vienna; Alice G. C. Grandison, British Museum (Natural History) (BMNH); W. Hellmich, Zoologische Sammlung des Bayerischen Staates, Munich; B. Hubendick, Naturhistoriska Museet, Göteborg; Robert F. Inger and Hymen Marx, Field Museum of Natural History (FMNH); Alan E. Leviton, California Academy of Sciences (CAS); Clarence J. McCoy, Carnegie Museum (CM); Günther Peters, Institut für Spezielle Zoologie und Zoologisches Museum, Berlin; Hobart M. Smith, formerly of Museum of Natural History, University of Illinois (UIMNH); Robert C. Stebbins, Museum of Vertebrate Zoology, University of California at Berkeley (MVZ); Paulo E. Vanzolini, Departamento de Zoologia, São Paulo (DZ); Greta Vestergren, Naturhistoriska Riksmuseet, Stockholm; Charles F. Walker, Museum of Zoology, University of Michigan (UMMZ); Ernest E. Williams, Museum of Comparative Zoology, Harvard University (MCZ); John W. Wright, Los Angeles County Museum of Natural History (LACM); Richard G. Zweifel, American Museum of Natural History (AMNH). Field series from the University of Southern California collections are designated CRE (Costa Rica), JRM (Honduras),<sup>2</sup> and PAS (Colombia).<sup>2</sup>

Robert J. Lavenberg and Mary Nafpaktitis facilitated my use of the General Electric Time Share Computer service provided by the Los Angeles County Museum of Natural History.

I acknowledge the support from two National Science Foundation Summer Fellowships for Teaching Assistants (Summers of 1964 and 1965), an NDEA Dissertation Travel Fellowship administered by the University of Southern California for travel in the summer of 1967, and a National Science

<sup>2</sup>To be deposited in the herpetological collection of the Los Angeles County Museum of Natural History.

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For her constant encouragement and secretarial help, I thank my wife, Miriam.

#### SPECIES ACCOUNTS

Adult members of the *Melanonotus* species group may be confused only with those of the *Ocellatus* species group because members of both groups have extensive toe fringes as adults. The *Ocellatus* group members always have smooth dorsolateral folds, while members of the *Melanonotus* group usually do not have any indication of a dorsolateral fold, or, if such are present, they are weak and warty, never smooth.

Only brief synonymies are presented, including synonyms and generic reallocations of the valid species, as Gorham (1966) has recently published a bibliographic synonymy of the genus *Leptodactylus*.

#### *Leptodactylus dantasi* Bokermann

*Leptodactylus dantasi* Bokermann, 1959: 5-8, figs. 1-5 (Type locality, Brasil: Acre; Feijó. Holotype WCAB 1240, female).

*Diagnostic characters:* The only other species in the *Melanonotus* group with dark bellies with discrete light spots are *podicipinus* and *pustulatus*. *L. dantasi* has large light spots on the belly and lacks a metatarsal fold; *podicipinus* has small light spots on the belly and has a well developed metatarsal fold. *Leptodactylus dantasi* lacks light spots on the posterior face of the thigh; *pustulatus* has large, well defined light spots on the posterior face of the thigh.

*Summary of characteristics:* Snout rounded from above, rounded acute in profile; canthus rostralis indistinct; loreal slightly concave in cross section; tympanum distinct, horizontal diameter 0.5 eye diameter; vomerine teeth in slightly arched series, posterior to choanae; head length greater than width, 43 per cent SL; head width 39 per cent SL; interorbital distance 6 per cent SL; first finger much longer than second, first just shorter than third, second longer than fourth; no distinct ulnar ridge; back warty-pustulose, tibia with many, pronounced warts; supratympanic fold does not reach shoulder; ventrolateral glands present but not distinct; toe tips very slightly expanded, dorsal surfaces not grooved; toes with well developed lateral fringes; subarticular tubercles moderately well developed; metatarsal fold absent; tarsal fold distinct along distal two-thirds of tarsus, weakly continuous with toe fringe; tarsus and foot with many horny spicules, spicules dark on scattered warts; standard length of female holotype 68 mm; femur shorter than tibia, 37 per cent SL; tibia shorter than foot, 39 per cent SL; foot longer than femur, 48 per cent SL; upper lip barred; light outlined dark band from interorbit to sacrum; rest of back uniform; upper surfaces of limbs faintly barred; venter with large light spots on



Figure 1. Geographic distribution of *Leptodactylus dantasi*, *discodactylus*, *pustulatus*, and *podicipinus*. Dashed line indicates 2000 meter contour. Open symbols indicate sites of sympatry with *wagneri*.

a dark ground, spots not always regular, spots anastomosing on limbs; posterior thigh uniformly dark.

*Distribution:* Known only from the type locality (Fig. 1), 249 m.

*Remarks:* *L. dantasi* is at present known only from the holotype.

*Leptodactylus discodactylus* Boulenger

*Leptodactylus discodactylus* Boulenger, 1883: 637, pl. 58, fig. 3 (Type locality, Peru: Loreto; Yurimaguas. Holotype BMNH 84.2.18.44, female). Gorham, 1966: 128 (Literature list, synonymy).

*Leptodactylus nigrescens* Andersson, 1945: 57-58 (Type locality, Ecuador: Río Pastaza and Río Napo, Watershed. Type series, Naturhistoriska Riksmuseet, Stockholm, unnumbered. Gorham, 1966: 132 (Literature list, synonymy).

*Diagnostic characters:* The only other species in the *Melanonotus* species group that has disk-like swellings of the toe tips is *wagneri*. The upper disk surfaces of *discodactylus* have longitudinal grooves; if disks are present in *wagneri*, the upper surfaces are never grooved.

*Summary of characteristics:* Snout rounded, subovoid, or subelliptical from above, usually rounded or rounded-vertical in profile; canthus rostralis indistinct; loreal slightly concave in cross section; tympanum distinct, horizontal diameter 0.5-0.66 eye diameter; male vocal slits elongate, arise lateral to posterior 0.25-0.33 tongue and parallel jaw almost to the angle of the jaw; single internal vocal sac in males; vomerine teeth in transverse or very slightly arched series, posterior to choanae; head length greater than width, 37-39.1-43 per cent SL; head width 32-35.2-39 per cent SL; interorbital distance 8-9.5-11 per cent SL; finger tips swollen or not; first finger longer than second, first shorter than third, second longer than or rarely equal to fourth; no spines on thumb of male; arm of male not hypertrophied; no distinct ulnar ridge; back rarely smooth to scattered with conical apicalia; tibia especially scattered with conical apicalia; supratympanic fold extends to shoulder; gland present at corner of mouth or not; post-tympanic gland present or absent; ventrolateral glands if present, not extensive; glands usually not present on posterior face of thigh; no chest spines on males; toe tips expanded into disks, dorsal disk surfaces grooved; toes with well developed lateral fringes; subarticular tubercles well developed; metatarsal fold present, weakly to strongly developed; tarsal fold distinct along distal 0.5-0.66 tarsus, not continuous with toe fringe; tarsus scattered with conical apicalia; foot smooth, or outer sole scattered with conical apicalia; standard length of males to 35 mm, females to 35 mm; femur shorter than tibia, 38-43.6-48 per cent SL; tibia shorter than foot, 43-45.8-49 per cent SL; foot longer than femur, 48-52.0-56 per cent SL; upper lip uniform or barred; interorbital region usually with a light stripe bordered behind by a dark

triangle, the dark triangle may extend to the sacral region, or uniformly dark; rest of back usually uniform, may have faint large splotches; upper surfaces of limbs barred to uniform; venter with a profusion of melanophores anteriorly only, to profuse over the entire venter; posterior thigh mottled.

*Distribution*: Known elevational range: 150-1000 m.

Known from a few localities of the upper Amazonian drainage in Ecuador and Peru (Fig. 1).

*Nomenclature*: Boulenger described *L. discodactylus* from Peru in 1883. The subsequent use of the name in the literature has been only a citation of the original description. Dr. James A. Peters allowed me to send one of his specimens, JAP 6197, to the British Museum for comparison with the holotype of *L. discodactylus*. Specimen 6197 is from the upper known elevational range of the species, and its characteristics agree with those of other high elevation populations discussed in the remarks section. Dr. Alice G. C. Grandison of the British Museum (Natural History) compared specimen 6197 with the holotype of *L. discodactylus*. She noted the departures from the holotype characters associated with elevation (see remarks section, below), but concluded that in all other aspects, including the diagnostic toe fringe, toe disks, and upper toe disk surface grooves, the specimens were identical.

Andersson described *Leptodactylus nigrescens* on the basis of three specimens from east Ecuador in 1945. His description is based upon the largest specimen. I was able to examine the largest syntype of *L. nigrescens* at the United States National Museum where Dr. Peters' private collection was available for comparison. Mr. Werner C. A. Bokermann had previously borrowed the two smaller specimens and allowed me to examine them at the National Museum. The type series is composite. The largest syntype of *L. nigrescens* possesses the diagnostic combination of toe fringe and toe disks with grooved upper surfaces of *L. discodactylus*. The other two specimens have well developed toe disks, no finger disks, no toe fringe, no tarsal fold, and two rows (1 pair) of dorsolaterally arranged conical apicalia. I consider the smaller two syntypes of *L. discodactylus* to represent *Eleutherodactylus nigrovittatus* Andersson, described in the same paper as *L. nigrescens*. In a cursory literature review, I was unable to find a senior synonym for this distinct little frog, but one may exist. To avoid future confusion, I hereby designate the largest (35 mm) specimen (the specimen has no museum number) the lectotype of *L. nigrescens*. *Leptodactylus nigrescens* Andersson is a junior synonym of *L. discodactylus* Boulenger.

*Remarks*: The few individuals available have certain differences which correlate with elevation.

Contrasting the highland samples from Ecuador (1000 m) with the lowland samples from Ecuador and Peru (150-300 m), one finds the following consistent differences (lowland population characteristics in parentheses): 1) the finger tips are not swollen (finger tips swollen, forming small disks);

2) the tarsal fold is usually distinct along the distal 0.66 of the tarsus (tarsal fold usually distinct on distal 0.5 of tarsus); and 3) smaller adult size, males to 30 mm, females to 32 mm (both males and females to 35 mm). I assume that the differences noted are responses to different climatic parameters associated with differences in elevation.

*Leptodactylus discodactylus* has been taken in sympatry with *L. wagneri* at two localities, Ecuador: Pastaza; Puyo, 1000 m and Peru: Loreto; Río Tamaya, Sobral, 150 m.

*Leptodactylus melanonotus* (Hallowell)

*Cystignathus melanonotus* Hallowell, 1860: 485 (Type locality, Nicaragua. Type apparently lost).

*Cystignathus echinatus* Brocchi, 1877: 181-2 (Type locality, Guatemala: Río-madre Nieja. Syntypes Paris Museum 6322-3).

*Cystignathus microtis* Cope, 1879: 265 (Type locality, Mexico: Guanajuato; Guanajuato. Syntypes USNM 9906, 9908, 9909).

*Cystignathus perlaevis* Cope, 1879: 269-270 (Type locality, Mexico: Oaxaca; Japana. Holotype USNM 10041, female).

*Leptodactylus melanonotus*, Brocchi, 1881: 20 (Cites Hallowell's record). Gorham, 1966: 131 (Literature list, synonymy).

*Leptodactylus occidentalis* Taylor, 1937: 349-52, pl. 1, figs. 1, 2, 7 (Type locality, Mexico: Nayarit; Tepic. Holotype FMNH 100015, female). Gorham, 1966: 133 (Literature list, synonymy).

*Diagnostic characters:* There is no one character that immediately distinguishes *L. melanonotus* from the other members of the *Melanonotus* species group. The toe disks of *L. discodactylus* distinguish it from *L. melanonotus* (toe tips not expanded into disks). *Leptodactylus dantasi*, *L. podicipinus*, and *L. pustulatus* have dark bellies with discrete light spots; *L. melanonotus* may have a dark belly, but it is mottled and never distinctly spotted. Certain few individuals of *L. melanonotus* are difficult to distinguish consistently from *L. wagneri* (*L. melanonotus* characters in parentheses): *L. wagneri* may have the toe tips expanded into distinct disks (toe tips never disk-like); *L. wagneri* may have a light longitudinal stripe on the posterior face of the thigh (no distinct stripe); *L. wagneri* reaches a larger adult size, standard length of males to 63 mm, females to 81 mm (males to 46 mm, females to 50 mm). The only way to distinguish consistently *L. melanonotus* from *L. wagneri* is by geography. *Leptodactylus melanonotus* is distributed from Mexico through Middle America, and west of the Andes in South America. *Leptodactylus wagneri* is found east of the Andes in South America.

*Summary of characteristics:* Snout rounded-nearly semicircular, rounded, rounded-subelliptical, or rarely subovoid from above, rounded to rounded-vertical in profile; canthus rostralis indistinct; loreal slightly concave in cross section; tympanum distinct, horizontal diameter 0.5 to 0.75 eye diameter; male vocal slits elongate, arise lateral to mid-point of tongue to almost the angle of the jaw, usually parallel to jaw, rarely slightly oblique to the jaw; single internal vocal sac in males; vomerine teeth usually in transverse series, rarely very slightly arched, always posterior to the choanae; head usually longer than wide, rarely equal, or rarely head length shorter than wide, head length 30-36.3-41 per cent SL; head width 30-34.1-38 per cent SL; interorbital distance 5-7.2-9 per cent SL; finger tips not noticeably swollen; first finger just longer than or about equal to second, first shorter than third, second longer than fourth; finger ridges present, especially on second and third fingers; 2 spines on male thumb; male arm not hypertrophied; ulnar ridge not developed; head smooth or scattered with coni apicales; upper eyelids warty, glandular or smooth, usually lacking coni apicales; rest of back with scattered coni apicales, the coni may be on warts or not; upper femur and tibia scattered with coni apicales; supratympanic fold extends to shoulder, rarely indications of several warty dorsolateral folds; brown to orange ventrolateral glands poorly to extensively developed, same glandular material may or may not be on jaw angle, post-tympanic region, groin, posterior thigh, or inner tibia and along the tarsal fold; no chest spines on male; toe tips usually not expanded, sometimes slightly expanded, never disk-like, never with dorsal surfaces grooved; toes with well developed lateral fringes; subarticular tubercles well developed; metatarsal fold present, weakly to well developed; tarsal fold distinct along distal 2/3-5/6 tarsus, not continuous with toe fringe; tarsus with scattered coni apicales; foot smooth, with scattered coni apicales, or coni apicales on outer sole only; standard length of males to 46 mm, females to 50 mm; femur longer than, equal to, or usually shorter than tibia, 36-40.0-45 per cent SL; tibia shorter than foot, 37-42.7-47 per cent SL; foot longer than femur, 43-49.3-53 per cent SL; upper lip barred to uniform; interorbit with dark, light outlined triangle, a light and dark bar, or a light triangle reaching tip of snout anteriorly, bordered posteriorly by a dark triangle; rest of back brown to gray with darker indistinct spots, blotches, bands, stripes, or without pattern; upper limb surfaces barred to uniform; venter with few melanophores, appearing light to many melanophores profused especially anteriorly to rarely heavily profused over entire venter; posterior thigh mottled.

*Distribution:* Elevational range: sea level—1440 m. The species is known from both coasts of Mexico—Hermosillo, Sonora and the Gómez Farías region, Tamaulipas in the north, extending southward throughout Middle America. The species is known only from the western lowlands of South America to mid-Ecuador. (Figs. 2-4.)

*Nomenclature:* The holotype of *Cystignathus melanonotus* Hallowell is



Figure 2. Geographic distribution of *Leptodactylus melanonotus* in Mexico.

apparently lost. The late E. R. Dunn noted (Dr. Dunn's notes presently on deposit in the library of Dr. Jay M. Savage) that the type was originally deposited in the National Museum as specimen number 6264 and that it was missing. The specimen is not listed in the catalog of type specimens of reptiles and amphibians in the U.S. National Museum (Cochran, 1961). In recent visits to the U.S. National Museum, although aided by the late Dr. Cochran and by Dr. Peters, I was unable to locate the type. The evidence indicates that the original holotype is lost.

*Leptodactylus melanonotus* is very closely related to both *L. wagneri* and *L. podicipinus*. *L. melanonotus* is found in Mexico and Middle America, where there is relatively little question as to what the species is. *L. melanonotus* is found west of the Andes and some individuals are very difficult to differentiate consistently from some individuals of *L. wagneri*, an Amazonian species. For nomenclature stability, the name *L. melanonotus* should be applied to a single specimen from the population found in Nicaragua, the type locality of the original, now lost, holotype. I therefore designate specimen number 84848 in the collection at the University of Kansas, an adult male, from Nicaragua, Zelaya, Bonanza, as the neotype of *Cystignathus melanonotus* Hallowell.

I have examined the holotype and two paratypes of *Cystignathus microtis*

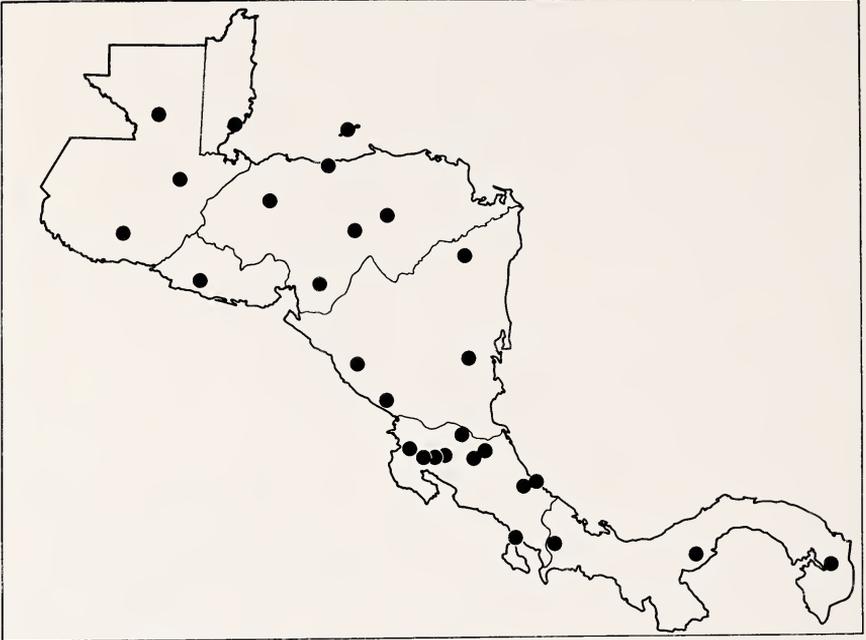


Figure 3. Geographic distribution of *Leptodactylus melanonotus* in Middle America.

Cope. Only two species of *Leptodactylus* (*labialis* and *melanonotus*) occur in Mexico; they are quite distinct from each other. Members of the type series of *C. microtis* agree with *L. melanonotus* in having fringed toes and mottled thighs; both characters differentiate *L. melanonotus* from *L. labialis*. There is no morphological reason for retaining *C. microtis*. The status of *C. microtis* has always been questioned, because the type locality was given as Mexico: Guanajuato; Guanajuato. Guanajuato is well above the elevational limits of *L. melanonotus*. No other specimens of *L. melanonotus* have since been taken from Guanajuato. I think the locality data are in error and probably represent the shipping point from which the specimens were sent to the U.S. National Museum rather than the collecting site.

I have examined numerous paratypes of *Leptodactylus occidentalis* Taylor and have collected topotypic specimens which correspond closely with the type series of *L. occidentalis*. As is shown in the character analysis portion, *L. occidentalis* does not differ in any consistent way from *L. melanonotus* and is therefore considered a junior synonym of the latter.

I have examined the holotype of *Cystignathus perlaevis* Cope and concur with the numerous workers who have placed it in synonymy with *L. melanonotus*.

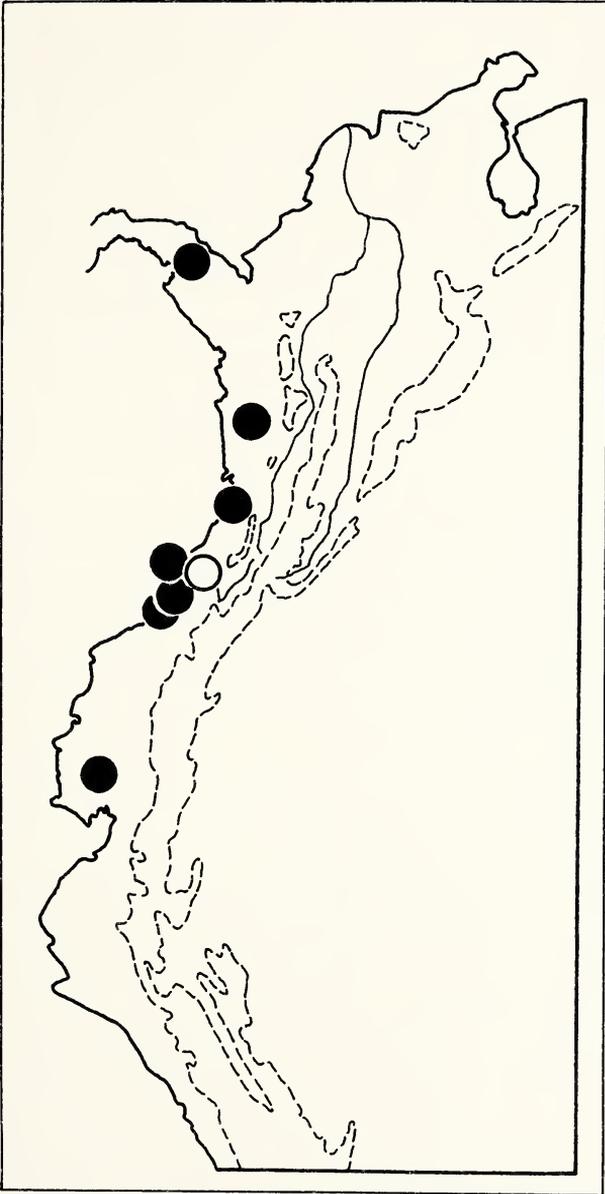


Figure 4. Geographic distribution of *Leptodactylus melanonotus* in South America. Dashed line indicates 2000 meter contour. Open symbol indicates site of sympatry with *wagneri*.

*Remarks:* A single specimen of *L. melanonotus* is recorded from Starr County, Texas, in the United States. I have examined the specimen (UIMNH 29817); it is a juvenile *L. melanonotus*. This single record is about 400 km north of the next recorded locality, from which several samples are known. The locality data for the Texas specimen is possibly in error, and for that reason I have not included the record in the range of *L. melanonotus*.

*Leptodactylus melanonotus* has been taken in sympatry with *L. wagneri* at one locality in western Colombia (Nariño, La Guayacana). This instance of sympatry is not too surprising, as the sources of the rivers Cauca and Patia interdigitate at about 1600-1800 m within the range of *L. wagneri*. *Leptodactylus wagneri* is found throughout the Valle de Cauca. Apparently *L. wagneri* follows the Río Patia into the west-coast lowlands of Colombia.

*Leptodactylus podicipinus* (Cope)

*Cystignathus podicipinus* Cope, 1862: 156 (Type locality, Paraguay. Holotype ANSP 14539).

*Leptodactylus podicipinus*, Boulenger, 1882: 248 (Catalogue, synonymy). Gorham, 1966: 135-6 (Literature list, synonymy).

*Leptodactylus nattereri* Lutz, 1926: 1011-2 (Type locality, Brasil: São Paulo; Itapura, Ilha Seca. Syntypes AL 1314-1315).

*Leptodactylus podicipinus podicipinus*, Gans, 1960: 305-6 (List). Gorham, 1966: 136 (Literature list, synonymy).

*Diagnostic characters:* The only other species in the *Melanonotus* species group with a dark belly with discrete light spots are *L. dantasi* and *L. pustulatus*. *L. dantasi* has large light spots on the belly and lacks a metatarsal fold. *L. podicipinus* has small light spots on the belly and has a well developed metatarsal fold. *L. pustulatus* has large, light discrete spots not only on the belly, but on the entire ventral surface of the leg and on the posterior surface of the thigh. *L. podicipinus* has small spots which, if on the leg, are only on the ventral surface of the thigh. The males of *L. podicipinus* have thumb spines, the males of *L. pustulatus* lack thumb spines.

*Summary of characteristics:* Snout rounded, subelliptical to subovoid from above, rounded in profile; canthus rostralis indistinct; loreal slightly concave in cross section; tympanum distinct, horizontal diameter  $\frac{1}{2}$ - $\frac{3}{4}$  eye diameter; male vocal slits elongate, arise lateral to middle of tongue, parallel jaw almost to angle of jaw; single internal vocal sac in males; vomerine teeth usually in transverse series, rarely in very slightly arched series, always posterior to choanae; head length greater than width, 34-37.0-41 per cent SL; head width 32-34.6-38 per cent SL; interorbital distance 7-8.2-10 per cent SL; finger tips not swollen; first finger usually longer than second, sometimes

equal, first finger much shorter than, shorter than, or about equal to third, second longer than fourth; finger ridges present, especially on second and third fingers; 2 spines on male thumb; male arm not hypertrophied; ulnar ridge usually not developed, sometimes a glandular ridge or 4 conical apices in a row; dorsum smooth, glandular, or warty, scattered with conical apices, especially on posterior dorsum and upper leg surfaces; supratympanic fold extends to shoulder, may or may not be faint indication of several warty dorsolateral folds; ventrolateral glands orange-brown, small to large or absent, glands present or absent on angle of jaw, dorsolateral folds, posterior thigh, inner tibia, and along tarsal fold; no chest spines on male; toe tips not expanded; toes with well developed lateral fringes; subarticular tubercles well developed; metatarsal fold well developed; tarsal fold distinct along distal 2/3-5/6 tarsus, usually not continuous with toe fringe, rarely weakly continuous with toe fringe; tarsus scattered with conical apices; foot smooth or outer sole with scattered conical apices; standard length of males to 38 mm, females to 44 mm; femur usually shorter but sometimes longer than tibia, 35-40.9-48 per cent SL; tibia shorter than foot, 38-42.9-48 per cent SL; foot longer than femur, 44-50.7-56 per cent SL; upper lip barred or uniform; interorbital region with light and dark stripe, or light outlined dark triangle extending to sacrum or not; rest of back uniform or with indistinct darker bands; upper limb surfaces uniform or with indistinct dark bars; throat, chest, belly dark with small light spots, rest of venter dark, but not with distinct light spots, posterior portion of belly occasionally with limb pattern rather than light-spotted; posterior thigh usually mottled, rarely with a moderately distinct light longitudinal line.

*Distribution:* Elevational range: 18-550 m.

*Leptodactylus podicipinus* is found south of the Amazonian drainage region in the following river drainages: São Francisco, Parana, Paraguay. The species is absent from the narrow coastal lowland strip along eastern Brazil from the States of Rio Grande do Norte to Rio de Janeiro. The species follows the Serras de San José, Santiago, and Sunsas in Bolivia, and the Serras dos Parecis and Pacaás Novos in western Brasil. (Fig. 1).

*Nomenclature:* In his description of *Cystignathus podicipinus*, Cope designated as type(s) "Mus. Smithsonian, (No. 5831) Philada. Acad." Dr. James A. Peters informed me that in the catalog under 5831 is a later remark stating that the specimen had been sent to the Academy of Natural Sciences in Philadelphia. Apparently there was only one specimen upon which Cope based *C. podicipinus*. I have examined the holotype of *C. podicipinus* from the Academy of Natural Sciences. The specimens I have examined from Paraguay are morphologically similar to the holotype in all diagnostic features.

Lutz described *Leptodactylus nattereri* on the basis of specimens collected in the state of São Paulo, Brasil, and included the specimens figured by Steindachner (1864) from the collection of Natterer. The figures in Steindachner

(Plate XI, figs. 1 a-d) show the two spines per thumb and dark belly with small light spots characteristic of *L. podicipinus*.

*Remarks:* *Leptodactylus podicipinus* has been taken in sympatry with *L. wagneri* at two localities: Bolivia (Santa Cruz: Buenavista, 500 m) and Brasil (Rondônia: Forte Príncipe da Beira, 100-200 m). At both localities the species are very distinct, markedly differing in size, belly pattern, and posterior thigh pattern. There is apparently a narrow band of sympatry between *L. podicipinus* and *L. wagneri*, with character displacement occurring in the band of sympatry.

*Leptodactylus pustulatus* (Peters)

*Entomoglossus pustulatus* W. Peters, 1870: 647, Pl. 2, fig. 1 (Type locality, Brasil: Ceará. Type apparently lost).

*Leptodactylus pustulatus*, Boulenger, 1882: 239 (Catalogue, synonymy); Gorham, 1966: 137 (Literature list, synonymy).

*Diagnostic characters:* The only other species in the *Melanonotus* species group with a dark belly with discrete light spots are *L. dantasi* and *L. podicipinus*. *Leptodactylus pustulatus* has large, light discrete spots on the posterior surface of the thigh. *Leptodactylus dantasi* and *L. podicipinus* do not have spots on posterior surface of the thigh. The males of *L. pustulatus* lack thumb spines, the males of *L. podicipinus* have thumb spines.

*Summary of characteristics:* Snout rounded to subovoid from above, rounded to rounded-obtuse in profile; canthus rostralis indistinct; loreal slightly concave in profile; tympanum distinct, horizontal diameter 2/3 eye diameter; male vocal slits elongate, parallel to jaw, extend from mid-tongue almost to angle of jaw; single internal vocal sac in male; vomerine teeth usually in transverse series, rarely very slightly arched, always posterior to choanae; head length greater than width, 35-36.4-38 per cent SL; head width 33-34.0-35 per cent SL; interorbital distance 5-6.7-8 per cent SL; finger tips not expanded; first finger longer than second, first shorter than third, second greater than fourth; finger ridges present, especially on fingers two and three; no spines on male thumb; male arm not hypertrophied; ulnar ridge not developed; dorsal texture pustulose, with scattered conical apices; supratympanic fold extends to shoulder, may or may not be indications of 6-8 warty dorsolateral folds; brown ventrolateral glands extend onto belly, or entire frog appears glandular; no chest spines on males; toe tips not expanded; toes with well developed lateral fringes; subarticular tubercles well developed; metatarsal fold present; tarsal fold distinct along distal 1/2-3/4 tarsus, usually continuous with toe fringe, occasionally weakly continuous; tarsus with scattered conical apices; foot usually with scattered conical apices, rarely smooth; standard length of males to 38 mm, females to 51 mm; femur shorter than tibia, 37-39.0-41 per cent SL; tibia shorter than foot, 39-41.8-44 per cent SL; foot longer than femur, 45-

51.3-55 per cent SL; dorsum uniform or patterned, if patterned, a light inter-orbital triangle originating at tip of snout bordered behind by a dark triangle, rest of back with darker longitudinal lines; upper limb surfaces faintly barred to uniform; venter dark with large light spots extending onto lower leg surfaces and groin; posterior thigh with light spots as on venter.

*Distribution:* Known elevational range: 100-200 m.

The few localities from which *L. pustulatus* have been collected are all low Amazonian. The major river drainages for which accurate locality data are available include the Paranaíba, Araguaia, and Tocantins. (Fig. 1).

*Nomenclature:* *Entomoglossus pustulatus* was described by W. Peters on the basis of a single female from Ceará, Brasil, in the collection of the Royal Zoological Museum, Berlin. Dr. Peter Beurton of the Berlin Museum states that he was unable to locate the type in the collections there. Dr. Hellmich of the Munich Museum informed me that the type of *Entomoglossus pustulatus* is not and has never been in the Munich collection, the likely alternative depository for the type. This suggests that the type is lost. The identity of *L. pustulatus* has been very unclear because of the rarity of specimens in collections. Because of this confusion and because there appears to be no other Ceará (topotypic) material in collections, I have selected an individual representative of the population that I consider to be *L. pustulatus*. The nearest locality to the type locality is the Rio Poti in Piauí. The specimen from this locality is only in a fair state of preservation, but it still retains the pattern diagnostic of *L. pustulatus*. I designate this specimen, MCZ 373, from the collection of the Museum of Comparative Zoology, Harvard University, as the neotype of *Entomoglossus pustulatus* Peters.

*Remarks:* *L. pustulatus* has been taken in sympatry with *L. wagneri* at one locality (Brasil: Mato Grosso: São Domingoes, Rio das Mortes, 200 m).

#### *Leptodactylus wagneri* (Peters)

*Plectromantis wagneri* W. Peters, 1862: 232-3 (Type locality, Ecuador, west side of the Andes. Type formerly at Munich Museum, destroyed in World War II).

*Platymantis petersii* Steindachner, 1864: 254-6, Pl. 16, fig. 2, 2 a-c (Type locality, Brasil: Amazonas; Marabitanas. Type lost).

*Leptodactylus brevipes* Cope, 1887: 51-2 (Type locality, Brasil: Mato Grosso, Chupada, 30 mi. NE of Cuyata, near the headwaters of the Xingu. Holotype ANSP 11270, female).

*Leptodactylus validus* Garman, 1887: 14 (Type locality, West Indies: St. Vincent; Kingston. Syntypes ANSP 26108, MCZ 2185).

*Leptodactylus wagneri* Nieden, 1923: 479 (Literature list, synonymy). Gorham, 1966: 140 (Literature list, synonymy).

*Leptodactylus pallidirostris* A. Lutz, 1930: 25-6, Pl. 1, fig. 3 (Type locality, British Guiana: Essequibo; Kartabo).

*Leptodactylus natalensis* A. Lutz, 1930: 26-7, Pl. 1, figs. 7-7a, Pl. 3, figs. 1-2 (Type locality, Brasil: Rio Grande do Norte; Rio Bahu. Syntype USNM 81130, male).

*Leptodactylus intermedius* A. Lutz, 1930: 27-8, Pl. 3, fig. 6 (Type locality, Brasil: Amazonas; Manacapuri near Manaus).

*Eleutherodactylus leptodactyloides* Andersson, 1945: 43-4, fig. 15 (Type locality, Ecuador: Pastaza; Río Pastaza. Holotype Stockholm Royal Museum, male).

*Leptodactylus podicipinus petersii*, Rivero, 1961: 47 (Redescription, synonymy). Gorham, 1966: 136 (Literature list, synonymy).

*Diagnostic characters:* *Leptodactylus wagneri* may have expanded toe tips, but the upper surface of the toe tip is never with longitudinal grooves, distinguishing *wagneri* from *discodactylus*, which has well developed toe disks with the upper disk surfaces grooved. *Leptodactylus wagneri* may have a dark belly, but it is mottled, and not with distinct light spots, distinguishing it from the dark-bellied, light-spotted *dantasi*, *podicipinus*, and *pustulatus*. Some individuals of *wagneri* are difficult to distinguish consistently from *melanonotus* (*melanonotus* characters in parentheses); *wagneri* may have the toe tips expanded into distinct disks (toe tips never disk-like); *wagneri* may have a light longitudinal stripe on the posterior face of the thigh (no distinct stripe); *wagneri* reaches a larger adult size, standard length of males to 63 mm, females to 81 mm (males to 46 mm, females to 50 mm). The only consistent way to distinguish *melanonotus* from *wagneri* is by geography. *Leptodactylus melanonotus* is distributed from Mexico through Middle America, and west of the Andes in South America. *Leptodactylus wagneri* is found east of the Andes in South America.

*Summary of characteristics:* Snout usually rounded, rarely subelliptical or subovoid from above, rounded to rounded-vertical in profile; canthus rostralis indistinct; loreal slightly concave in cross section; tympanum distinct, horizontal diameter  $\frac{1}{2}$ - $\frac{3}{4}$  eye diameter; male vocal slits elongate, arise lateral to tongue, parallel jaw and extend almost to the angle of the jaw or slightly oblique to jaw; single internal vocal sac in male; vomerine teeth in transverse to arched series, posterior to choanae; head length greater than, equal to, or less than width; head length 33-36.8-42 per cent SL; head width 32-34.9-39 per cent SL; interorbital diameter 6-7.8-9 per cent SL; finger tips not noticeably swollen; first finger longer than second, first shorter than or equal to third, second longer than or equal to fourth; fingers with lateral ridges, especially on second and third fingers; two spines on male thumb; male arm

slightly hypertrophied only in largest specimens; no ulnar ridge; dorsal texture smooth to glandular, posterior portion of back and legs with scattered conical apicalia; supratympanic fold extends to shoulder, may or may not be indication of 2-4 faint dorsolateral folds; orange-brown ventrolateral glands moderately developed or absent; gland at angle of jaw developed or not; post-tympanic gland developed or not; posterior thigh gland present or absent; no chest spines on male; toe tips not expanded to moderately expanded and disk-like, never with longitudinal grooves on dorsal surface; toes with well developed lateral fringes; subarticular tubercles well developed; metatarsal fold present; tarsal fold distinct along distal  $4/7$ - $3/4$  tarsus, not continuous with toe fringe; tarsus with scattered conical apicalia; foot smooth, with scattered conical apicalia, or outer sole with scattered conical apicalia; standard length of males to 63 mm, females to 81 mm; femur shorter than tibia, 35-42.4-48 per cent SL; tibia shorter than foot, 41-46.9-51 per cent SL; foot longer than femur, 49-52.4-57 per cent SL; upper lip usually barred, sometimes uniformly patterned; light and dark interorbital bar, dark bar may extend posteriorly as a triangle or band as far as sacrum; rest of back uniformly patterned or indistinctly spotted or striped, warts on sides may be darker than ground color; upper limb surfaces barred to uniform; ventral pattern of scattered melanophores, melanophores may be profuse anteriorly only, or profuse over entire venter; posterior thigh with distinct light longitudinal stripe to mottled.

*Distribution:* Elevational range: sea level—1900 m.

The species is widely distributed throughout northern and central South America east of the Andes. There is a single record west of the Andes in Colombia. The species occurs in the Cauca and Magdalena valleys of west-central Colombia, and throughout the greater Amazonian Basin; the species is also distributed along the narrow eastern coastal strip of Brasil from the States of Rio Grande do Norte to Rio de Janeiro. The species occurs on the islands of Bequia, Granada, St. Vincent, Tobago, and Trinidad. (Fig. 5).

*Nomenclature:* Wilhelm Peters (1862) described *Plectromantis wagneri* from Ecuador on the basis of a single male specimen. Peters listed the type as "von Dr. Moritz Wagner an den Westseite der Anden in Ecuador . . . im zoologischen Cabinet du München." Dr. Richard Etheridge kindly looked for the type when he was at the Munich museum. He writes (personal communication), ". . . the old museum had one specimen, No. 1080/0, from 'Pastassa' collected by Wagner. This may or may not have been the type, there is no indication in the record that it was, but in any event the specimen was destroyed during World War II." It is likely that specimen number 1080/0 was the unique type of *Plectromantis wagneri*. Pastassa is a geographically more reasonable locality than the west side of the Andes. Peters' description is quite good, and the secondary sexual characteristics of spines on the thumb of the male leave no doubt as to the identity of the frog described by Peters. It is the population herein called *L. wagneri*. The only *Leptodactylus* west of the



Figure 5. Geographic distribution of *Leptodactylus wagneri*. Dashed line indicates 2000 meter contour. Open symbols indicate sites of sympatry with other species of the Melanonotus group.

Andes in Ecuador with thumb spines on the male is *L. melanonotus*. The males of *L. melanonotus* reach 40 mm SL in Ecuador; the type of *P. wagneri* was 68 mm SL. I consider that Peters' locality is probably incorrect, and the data as recorded for Munich specimen 1080/0 are correct. The name *L. wagneri* has never been used in association with a *Leptodactylus* population in the literature since the original description. The status of the northern South American population of the *Melanonotus* group has always been uncertain. To stabilize the nomenclature I hereby designate the holotype of *Eleutherodactylus leptodactyloides* Andersson in the Stockholm Royal Museum of Natural History (no number), an adult male, from the Río Pastaza, as the neotype of *Plectromantis wagneri* Peters.

Steindachner described *Platymantis petersii* on the basis of a single male specimen from Marabitanas, Amazonas, Brasil. Dr. Josef Eiselt of the Vienna Museum has been unable to find the unique type of *Platymantis petersii*. The type has been searched for several times and is most likely lost. *Leptodactylus petersii* has been used in various combinations for various populations of frogs of the *Melanonotus* species group. I consider *P. petersii* to be a junior synonym of *L. wagneri*, and that nomenclatural stability would be served by designating a neotype which conforms with my analysis. I have not examined any material from Marabitanas, nor do I know of any material from there. The closest record that I know of to Marabitanas is in Venezuela. This specimen, AMNH 23182, is in very good condition. The locality is Venezuela: Amazonas; Río Pescado, approximately 150 m. The specimen is a female. I hereby designate AMNH 23182 as neotype of *Platymantis petersii* Steindachner.

Cope described *Leptodactylus brevipes* on the basis of a single specimen from Chupada, Mato Grosso, Brasil. The name has been cited in literature lists based upon the original description but not upon the basis of recent material. I have examined the type, and find it the same as *wagneri*. The belly has very few melanophores, so that no confusion is possible with either *podicipinus* or *pustulatus*, the only other members of the *Melanonotus* species group with which it could possibly occur or be confused. *Leptodactylus brevipes* is regarded as a junior synonym of *L. wagneri*.

*Leptodactylus validus* was described by Garman from a series of specimens from the island of St. Vincent. I have found no differences between any of the island populations and the mainland population of *wagneri*, as shown below in the character analysis section. No holotype was designated by Garman. I hereby designate MCZ 71920, an adult male, from Kingston, St. Vincent, as the lectotype of *Leptodactylus validus* Garman.

Lutz described three species of *Leptodactylus* of the *Melanonotus* group in the same paper in 1930. The first, *pallidirostris*, was described from British Guiana: Essequibo; Kartabo. I have not been able to examine the type, but have examined numerous examples of the *Melanonotus* group from the type locality. All specimens represent a single species and conform with the type

description of *pallidirostris*. The specimens from Kartabo are not distinct from *wagneri*. Thus, *L. pallidirostris* is considered a junior synonym of *L. wagneri*.

*Leptodactylus natalensis* is the second species described by Lutz. I have examined one syntype of the type series and find it the same as other specimens examined in this study from the type locality (vicinity of Natal). The syntype has a lightly pigmented venter and marbled posterior thigh surfaces. I consider *L. natalensis* Lutz to be a junior synonym of *L. wagneri*. No holotype was designated. I designate the specimen I have examined, USNM 81130, a male, as the lectotype of *Leptodactylus natalensis* Lutz.

The third species of the Melanonotus group described by Lutz is *L. intermedius*. As in the case of *pallidirostris*, I have not seen the types, but have examined material from the type locality. The topotypic material I have examined from Manaus agrees with the description of *intermedius*. I consider the material from Manaus to be *wagneri*; hence *intermedius* is a junior synonym of *L. wagneri*.

Andersson described *Eleutherodactylus leptodactyloides* on the basis of a single specimen from Ecuador. I have been able to examine the type specimen. It is a *Leptodactylus* as suggested by the specific name, rather than an *Eleutherodactylus*. I have designated this specimen, above, as the neotype of *Plectromantis wagneri*, thereby making *Eleutherodactylus leptodactyloides* a junior synonym of *L. wagneri*.

*Remarks:* *Leptodactylus wagneri* has been taken in sympatry with *discodactylus*, *melanonotus*, *podicipinus*, and *pustulatus*.

#### KEY TO ADULT MEMBERS OF THE MELANONOTUS SPECIES GROUP

- 1a. Toe tips expanded into disks, dorsal surfaces with longitudinal grooves ..... *discodactylus*
- 1b. Toe tips usually not expanded into distinct disks, dorsal surfaces never grooved ..... 2
- 2a. Ventral surfaces of legs and posterior surface of thigh with large, light, distinct spots ..... *pustulatus*
- 2b. Ventral surfaces of legs light or dark, if large spots present, spots not distinct; posterior surface of thigh light or dark, never with large, light, distinct spots ..... 3
- 3a. Belly dark with distinct, light spots, spots usually distinct over entire belly, but sometimes anastomosing on posterior belly..... 4
- 3b. Belly light or dark; if dark, no distinct light spots..... 5
- 4a. Belly with large light spots; no metatarsal fold.....*dantasi*
- 4b. Belly with small light spots; well developed metatarsal fold.....*podicipinus*
- 5a. Moderate sized frogs, males to 46 mm SL, females to 50 mm; posterior thigh never with light longitudinal stripe; toe tips never noticeably expanded; Mexico, Middle America, South America west of the Andes to Ecuador ..... *melanonotus*

- 5b. Moderate to large frogs, males to 63 mm SL, females to 81 mm; posterior thigh may have a light longitudinal stripe; toe tips often noticeably expanded; South America east of the Andes.....*wagneri*

CHARACTER ANALYSIS

*Standard length:* Two broad geographic patterns are evident in male *L. melanonotus*. The coastal populations vary between 30 and 40 mm. Modal sized individuals (36 mm Hermosillo, Sonora, Mexico) or smaller specimens (34 mm Gómez Farías region, Tamaulipas, Mexico; 33 mm Ecuador) are associated with the extreme northern and southern geographic range. The largest specimens are associated with two lowland pass regions in the montane backbone of the Americas: the lowland pass at Tehuantepec, Mexico; and the Arenal pass in Costa Rica. The geographic pattern of female *L. melanonotus* size parallels the male geographic pattern, but the trends are not as pronounced. In addition to the Tehuantepec and Arenal passes harboring the largest females (47-50 mm), the Yucatan Peninsula and eastern lowlands of Costa Rica also have females of large size (46-48 mm). The range of adult female size is approximately 35-50 mm.

*Leptodactylus wagneri* males attain greatest size along the eastern slopes of the Andes in Colombia, Ecuador, and Peru, ranging from about 40-60 mm. Along the northern coast of South America, on the islands, and in the Amazonian basin, the sizes range from 30-40 mm. The geographic pattern of *L. wagneri* female size exactly parallels the male adult size with the exception of the ranges. The east Andean slope populations most frequently range in size from 50-80 mm; the north coast, island, and Amazonian populations usually range from 40-60 mm.

Adult male *L. podicipinus* range from about 28-38 mm in length, with a trend towards smaller size at the southern end of the geographic range. Adult female *L. podicipinus* range in size from 36-44 mm also with a trend towards smaller size at the southern end of the geographic range.

The geographic pattern of size variation is basically the same in males and females, the only difference being that the females average larger than the males.

The relationship between size and rainfall, number of dry months, and elevation are statistically significant only in the case of *L. wagneri*. In *L. wagneri* males, a statistically significant correlation is present between greatest size of adults and mesic habitats ( $r = .28, P = <.01$ ). This correlation appears to be biologically valid for both males and females, as a statistically significant correlation was found with smaller size in more xeric habitats as measured by number of dry months (males  $r = -.50, P = <.01$ , females  $r = -.27, P = <.01$ ). A statistically significant correlation was found for greatest size and increasing elevation for both males and females in *L. wagneri* (males

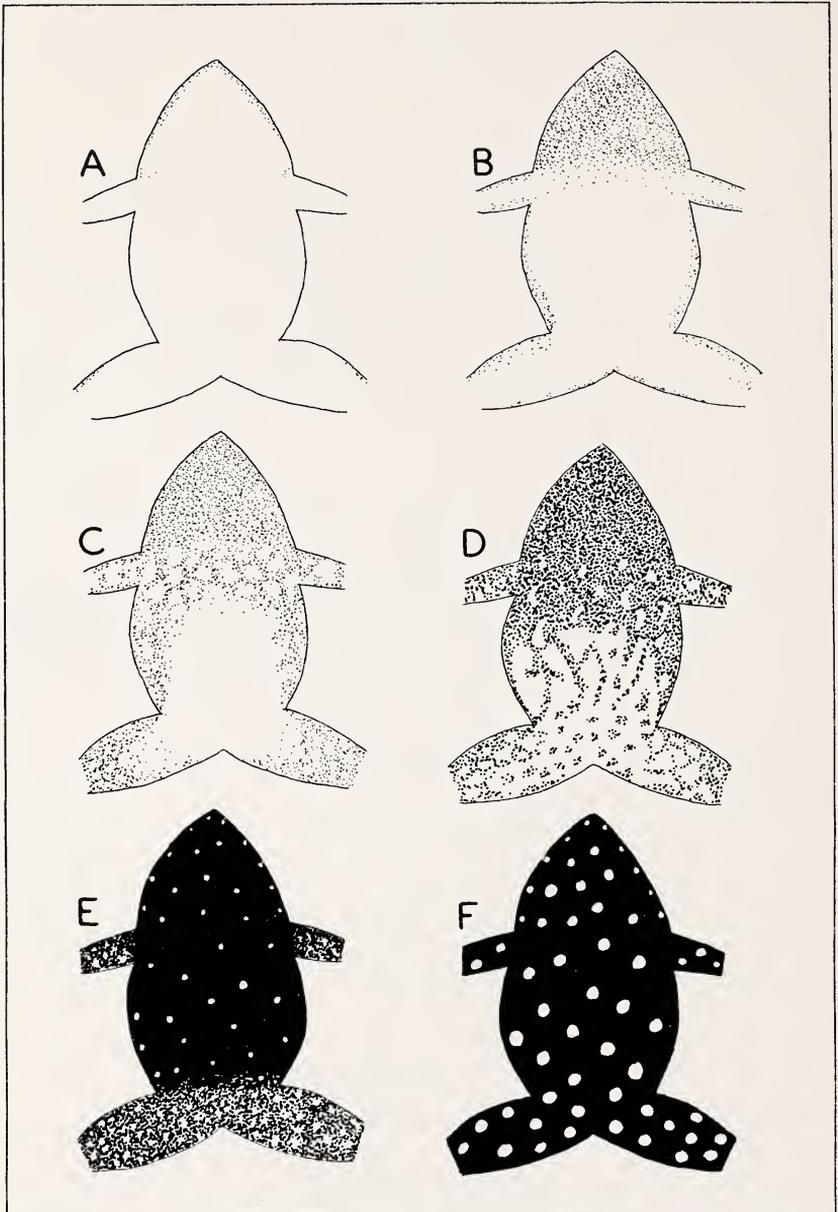


Figure 6. Ventral color pattern standards. Note that pattern F is restricted to *Leptodactylus pustulatus*.

$r = .38$ ,  $P = < .01$ , females  $r = .42$ ,  $P = < .01$ ). The elevational effects producing size differences in these frogs are probably associated with rainfall differences also.

Character displacement apparently occurs in the narrow bands of sympatry between *L. melanonotus*, *podicipinus*, and *wagneri*. At La Guayacana in Colombia, a female *melanonotus* (mature) measures 38 mm, and a female *wagneri* measures 59 mm. Two instances of sympatry are known for *wagneri* and *podicipinus*. At Buenavista, Bolivia, a female *podicipinus* measures 40 mm, and a female *wagneri* 46 mm. At Forte Principe da Beira, Brasil, a female *podicipinus* measures 34 mm, a female *wagneri* 43 mm, and a male *podicipinus* 29 mm, and a male *wagneri* 38 mm.

*Ventral pattern*: Five categories were used in scoring the ventral pattern. These ranged from A, in which the throat and belly do not have any melanophores, to E, in which the throat and belly are heavily covered with melanophores, leaving light spots (Fig. 6).

The distribution of ventral pattern is variable throughout most of the geographic range of *L. melanonotus*. In many localities, conditions ranging from B to D, encompassing the variation encountered in this species, are found. The populations at the northern and southern extremes of the geographic range lack much of the variability as in other populations, and are lighter in ventral coloration. Northwestern Mexican and South American populations are average in pattern density. There is a weak trend of darker pattern in Atlantic lowland populations.

No clear geographic trend in ventral pattern in *L. wagneri* is evident. The usual range for the species is B to D, with a few populations having an intermediate condition between D and E. Most adequate samples (10 or more individuals) show a variation through only two categories, either B-C or C-D. The occurrence of individuals with pattern B seems to be random with perhaps more B category individuals throughout the northern part of the species range, including the populations of islands off northern South America.

There is no geographic trend of ventral color pattern in *L. podicipinus*. Almost all populations fall in the E category, with a few individuals in D or between D and E.

A correlation between a darker ventral color pattern and greater annual rainfall is present in *L. melanonotus* ( $r = .17$ ,  $P = .05$ ). There is no correlation between ventral pattern and glandular extent, number of dry months, or elevation in *melanonotus*. No correlations between ventral color pattern and glandular extent, annual rainfall, number of dry months, or elevation are present in *podicipinus*. A correlation is found between a lighter ventral color pattern and greater ventrolateral gland extent in *wagneri* ( $r = -.14$ ,  $P = .05$ ). This is most certainly not a cause-effect relationship, but it may indicate that the genes responsible for these two characters are on the same chromosome or are co-functional in some other way. No correlations between ventral color

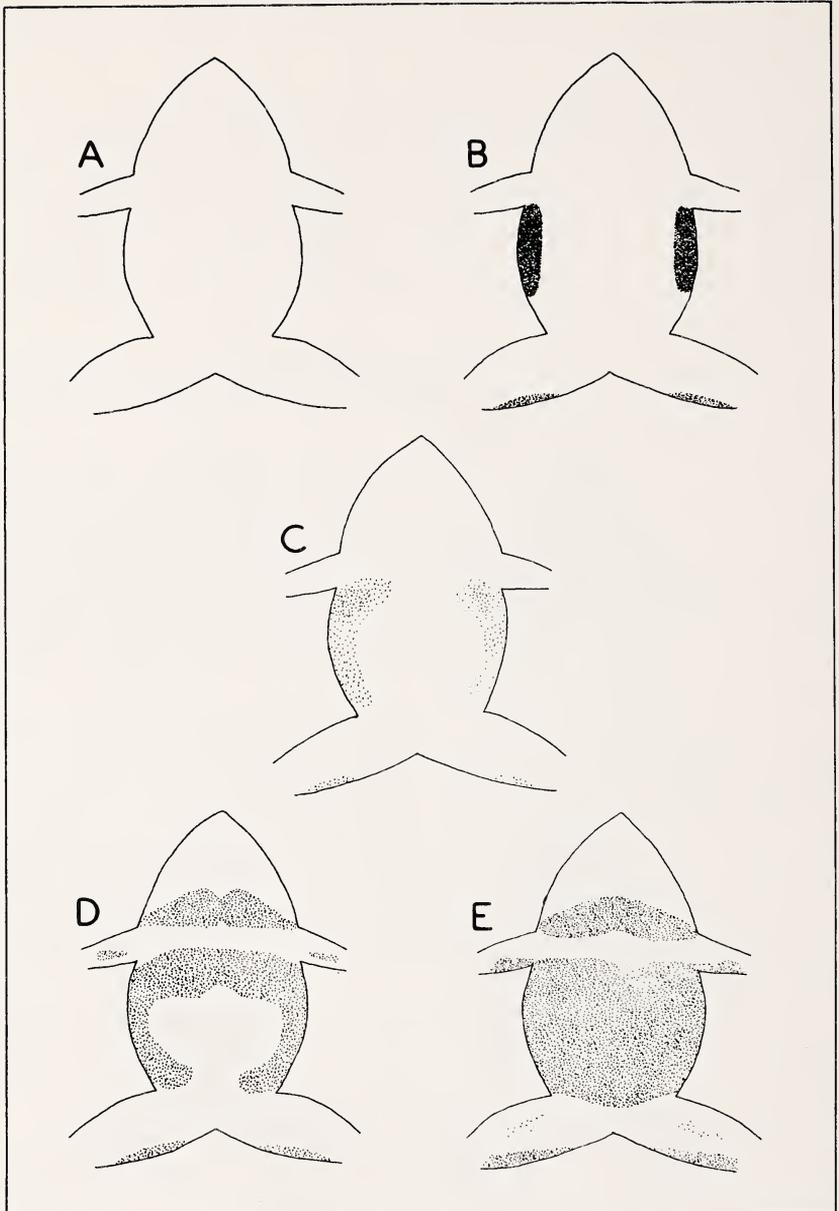


Figure 7. Ventrolateral gland standards.

pattern and annual rainfall, number of dry months, or elevation are found for *wagneri*.

Ventral color pattern is a character that has apparently undergone character displacement in the area of sympatry between *L. podicipinus* and *wagneri*. Certain individuals of *wagneri* closely approach the pattern of *podicipinus*. In the two known instances of sympatry of *podicipinus* and *wagneri*, the ventral color patterns are clearly distinct; *wagneri* individuals have a light belly; *podicipinus* individuals have a dark, light spotted belly. *Leptodactylus discodactylus* and *wagneri* have basically the same ventral color patterns. *Leptodactylus pustulatus* is very distinct from *wagneri* with respect to ventral pattern. *Leptodactylus pustulatus* has a distribution allopatric to those of *dantasi* and *podicipinus*, the species it most closely resembles in ventral color pattern.

*Ventrolateral glands*: Five categories of ventrolateral gland extent were established, ranging from no glands, A, to the entire belly, and most other ventral surfaces covered with glands, E (Fig. 7). In addition, five categories of gland color were noted in preserved animals: 1—brown; 2—gray; 3—black; 4—orange-brown; and 5—yellow-orange.

The geographic distribution of ventrolateral gland extent and coloration in *L. melanonotus* is a mosaic. The ventrolateral glands are very compact and brownish to orange-brown (B—1,4) in populations from northwest Mexico and Panama. The greater degree of glandular extent is found in populations from the Isthmus of Tehuantepec, Yucatan Peninsula, Atlantic coastal British Honduras and Honduras, and the Arenal pass region in Costa Rica. These generalities are complicated in that individuals from a single locality 1) have or lack glands and 2) demonstrate a range of variation of glandular extent which encompasses the range of the entire species.

Most populations of *L. wagneri* either have no ventrolateral glands or have orange-brown diffuse glands of moderate extent (C—4). A few *wagneri* specimens from the southern part of their geographic range have more extensive glandular extent. Where moderate samples (10 or more individuals) are available, the specimens at any single locality demonstrate categories A and C—4. There is no geographic trend.

Many individuals of *L. podicipinus* lack ventrolateral glands. When ventrolateral glands are present, they are of moderate extent and orange-brown in preservative (C—4, D—4). Individuals from a single locality usually encompass the range of variation found within the species. No clear geographic trend is evident.

There are no correlations between ventrolateral gland extent and annual rainfall, number of dry months, or altitude in *L. melanonotus* and *podicipinus*. A correlation is present between greater ventrolateral gland extent and greater annual rainfall in *wagneri* ( $r = .13$ ,  $P = .05$ ). Such a correlation is more suggestive of a causal relationship than the correlation between ventral color pattern and ventrolateral gland extent in *wagneri*. There are no correlations

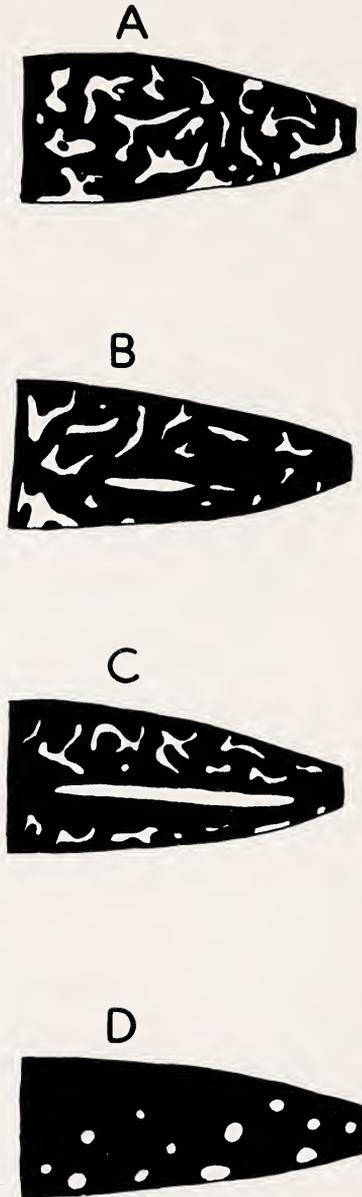


Figure 8. Posterior surface of thigh color pattern standards. Note that pattern D is restricted to *Leptodactylus pustulatus*.

between ventrolateral gland extent and number of dry months or elevation in *wagneri*.

Changes of extent of ventrolateral glands may occur seasonally, but there are no collections made at all seasons from a single locality. In the summer of 1967 when breeding was just beginning, Dr. James R. Dixon and I collected several series of *L. melanonotus* from western Mexico. We noticed that no glands were evident on living animals. After a few days in preservative, however, the ventrolateral glands on the animals were dark brown in color and distinct. The function of ventrolateral glands is not known.

*Color pattern of posterior surface of thigh*: Four categories were distinguished: A) mottled; C) with a light longitudinal stripe; B) intermediate between A and C; D) with distinct light spots on a dark background (Fig. 8).

Almost all *L. melanonotus* have a mottled posterior thigh, although a few individuals from scattered localities show some indication of a light stripe (category B).

In large series of *L. wagneri* from one locality, character states A, B, and C are represented. This is true throughout the geographic range of *wagneri*, with the exception of the Cauca Valley (Colombia) population.

Few large samples from *L. podicipinus* demes were available for this study, but, on the basis of the series available, the distribution of the thigh pattern appears to parallel the situation in *wagneri*. That is, categories A, B, and C are represented within any deme.

There is no correlation between the posterior thigh pattern and the climatic and elevational parameters used. It appears likely that the light stripe in *L. wagneri* and *podicipinus* is genetically controlled by very few genes, perhaps one. The scattered B categories in *melanonotus* populations indicate that the gene potential for a posterior thigh light stripe is present. The D category is found only in *pustulatus*.

The light stripe on the posterior thigh is another feature that shows character displacement in the instances of sympatry between *L. podicipinus* and *wagneri*. At both sites of known sympatry, *wagneri* individuals have well developed stripes. The *podicipinus* at the sites of sympatry either have a mottled thigh (Buenavista, Bolivia), or only an indication of a light stripe (Forte Principe da Beira, Brasil). At this latter locality, the differences in thigh pattern are very striking. The light stripe in *wagneri* individuals is completely bordered with black and is very distinct from the thigh pattern of sympatric *podicipinus*.

*Toe-disk size*: Three categories were used (Fig. 9): A) toe tips not expanded at all; C) Toe tips expanded into definite disks; B) intermediate condition.

There is a gradient of toe-tip size in *L. melanonotus*. In the northern part of the range, Mexico to Costa Rica, most are in category A, only 3 demes among those examined within this area had individuals with B condition. Many

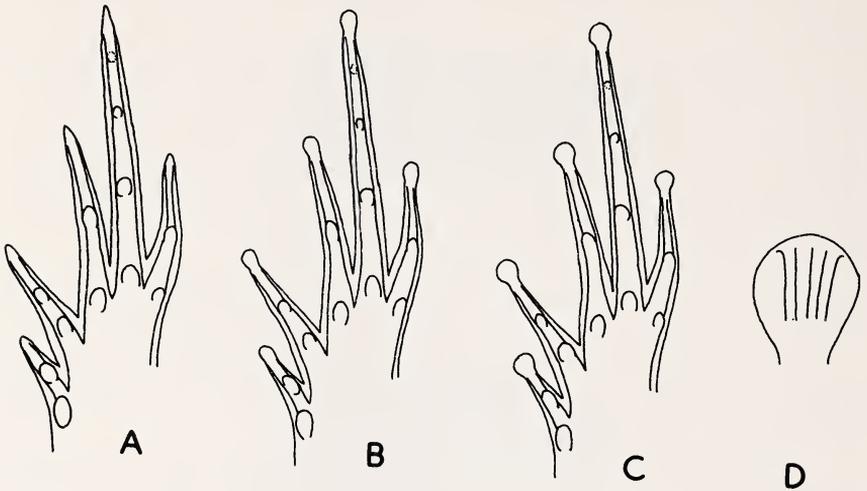


Figure 9. Toe tip standards. Pattern D is the upper disk surface of *Leptodactylus discodactylus* showing longitudinal grooves.

individuals from Costa Rica have intermediate disks, B. In the South, from Panama through Ecuador, all populations have B disks. In no case is the toe tip expansion developed into a distinct disk as found in *L. discodactylus*.

A distinct geographic gradient in toe tip expansion is also seen in *L. wagneri*. The Cauca Valley (Colombia) population is marked by non-expanded toe tips. The rest of the Andean slope and upper Amazonian populations of Colombia, Ecuador, Peru, and Bolivia have categories A and B, with B predominant. The frogs associated with the rivers draining northward, those upon the islands, and probably those of the eastern Amazon region are either B or C; that is, many individuals from these areas have distinct toe disks such as are found in *L. discodactylus*.

No distinct geographic gradient in toe tip expansion is evident in *L. podicipinus*. Most specimens lack expanded toe tips, A, but a few individuals from scattered demes have slightly expanded toe disks, B.

The possible role of character displacement in toe-tip expansion is evident at the two sites of sympatry between *L. podicipinus* and *wagneri*. At both sites, the toe tips of *podicipinus* are not expanded, A, and the toe tips of *wagneri* are slightly, but noticeably, expanded, B.

*Mating call:* Mating call samples were chosen to answer the specific status concerning *L. occidentalis*. Demes were sampled in lowlands throughout the latitudinal geographic range of *occidentalis* from Sonora through Nayarit. Lowland samples of *melanonotus* from Jalisco, Colima, and Michoacán were

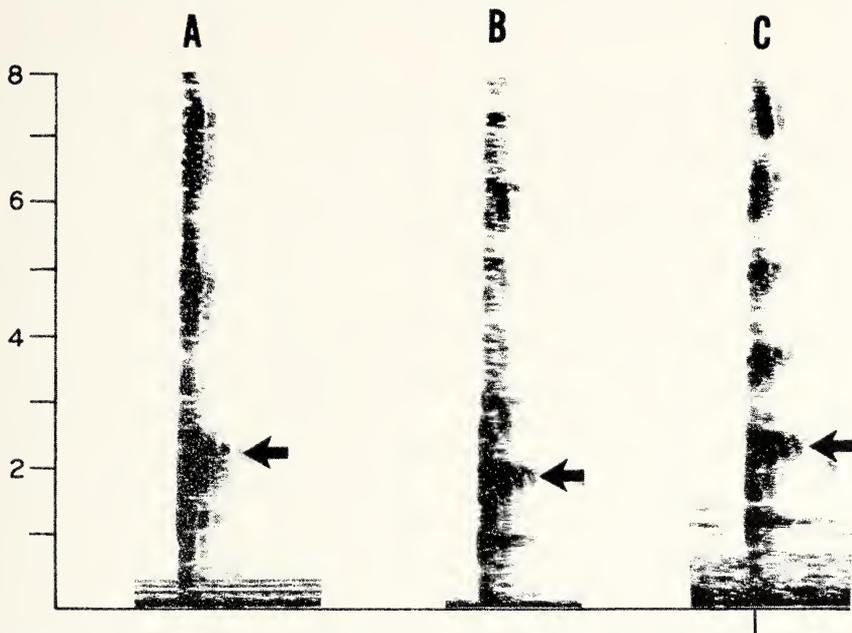


Figure 10. Mating calls of *Leptodactylus melanonotus* in western Mexico. Vertical scale in kilocycles per second, horizontal scale in seconds. Arrows indicate dominant frequency band. A—Call specimen from Sinaloa, 36 km S Los Mochis turnoff on Mexico Highway 15. B—Call specimen from Jalisco, 0.5 km NE Tonila. C—Call specimen from Jalisco, 7.7 km E La Huerta.

also taken. Demes along elevational transects were sampled in the states of Jalisco and Nayarit.

All of the calls have a basic similarity when heard and when viewed on sonagrams. All calls consist of quite short notes, with a very wide frequency range. The call components are difficult to compare with calls of other species in which the components are very distinct. I consider the dominant frequency the darkest, widest portion of the sonagram of the call, as substantiated in sections, measuring the call duration at that point (Fig. 10A). Any other noticeably prominent frequency below the dominant is taken as the fundamental frequency (Fig. 10B). Any periodic emphasized frequencies above the dominant are considered harmonics, even though they may not be sharply differentiated (Fig. 10C). The duration of the call is from .04 to .09 seconds, the range .05 to .08 seconds being common in the call of a single individual. Call duration does not correlate with temperature in the samples at hand. The most striking differences among the calls are: 1) one or two notes per call group; 2) the fundamental frequency is dominant or not; 3) the dominant frequency values; 4) whether harmonics above the dominant are distinct or

not; 5) whether the note is straight on the paper, or components are displaced to the right.

Most of the calls are characterized by having a single note per call group. Only in the state of Nayarit did individuals have calls consisting of two notes per call group. One of the calls recorded at Tepic has a call consisting of both one and two notes, as does the individual recorded from near San Blas. The specimen recorded from Santa Cruz has a call consisting of two notes.

The calls recorded from near Acatlán, Jalisco, Tepic, Nayarit, and Hermosillo, Sonora, show the fundamental to be the same as the dominant. One call from near Los Mochis, Sinaloa, has a fundamental distinct from the dominant; another call has the fundamental equal to the dominant. All other calls have fundamentals distinct from the dominant. Where fundamental frequencies are present, they approximate one half the frequency of the dominant.

The dominant frequencies usually range from 2000 to 2500 cycles per second. A range of 2000 to 2400 cycles per second is recorded in the deme from Tepic, Nayarit. The only dominant differing from the range is from a call recorded from Santa Cruz, Nayarit, which has a dominant of 3000 cycles per second. The higher frequency can not be accounted for by differences in temperature or elevation.

Three categories are used to distinguish whether harmonics above the dominant are evident: 1) not present; 2) some indication of presence; 3) present. Calls from Colima, Michoacán, and near La Huerta and Tecalitlan, Jalisco, have harmonics. The call from near Tonila, Jalisco, has some indication of harmonics. The calls from near Acatlán, Jalisco, show all three states. The calls from Tepic, Nayarit, either lack harmonics, or show some indications of harmonics. The calls from Santa Cruz, Nayarit, show harmonics present or absent. All calls recorded north of Santa Cruz lack harmonics above the dominant frequency.

Notes with certain components displaced to the right on the sonagram are found in calls from localities that also have straight notes on the sonagram. These localities demonstrating both types of notes are near Los Mochis, Sinaloa, Santa Cruz, Nayarit, and near Acatlán, Jalisco.

Two of the call characteristics are gradually clinal in nature; the relation of the fundamental to the dominant, and the presence or absence of harmonics above the dominant. Two of the call characteristics are largely variable within demes, and not constant on any geographic basis: number of notes per call group; and whether the call is displaced to the right on the sonagram or not. A call from a single deme shows a higher dominant frequency than the others.

*Discussion:* Physical size appears to be a major, pre-mating isolating mechanism between *L. melanonotus* and *wagneri*. Additional collecting around the northern end of the Andes in Colombia is necessary to determine the interactions or lack of interactions between these two species.

Character displacement is most noticeable in sympatric demes of *L. podi-*

*cupinus* and *wagneri*, where respective adult sizes, ventral color patterns, posterior thigh color patterns, and toe tip expansions are very distinct. Expression of certain of these characters are similar in other populations of *podicipinus* and *wagneri*. Ventral color pattern in particular shows the effects of character displacement. Certain demes along the slopes of the Andes in Bolivia and southern Peru have ventral color patterns that closely approach the pattern of some *podicipinus*. The ventral patterns of *wagneri* and *podicipinus* are distinct at points of sympatry; the specimens do not exhibit gradation of ventral pattern D to E.

The status of the population of frogs in northwest Mexico (*L. occidentalis* Taylor) has been particularly uncertain. The main characters used to distinguish the population are adult size and extent and color of the ventrolateral glands. The size of the population fits into a larger pattern discussed above and is not peculiar to a series of demes in northwest Mexico. The ventrolateral gland condition (B) is characteristic of the population in northwest Mexico, but the same condition is found in certain demes in Panama. The mating call data indicate that the extreme northwestern demes are differentiated from the lowland demes in Colima and Michoacán, but that the differences are connected by a series of demes demonstrating intermediate call types. The lowland demes in Colima and Michoacán are separated geographically from the highland demes of Jalisco and Nayarit by terrain with virtually no standing water; water is either cascading or nonexistent. The population from northwest Mexico appears to be isolated at present from the coastal demes of Colima and southward. Morphological differentiation of the northwest Mexican population is slight, and the same differentiation is repeated in other demes of *L. melanonotus* throughout its geographic range.

The island demes of *L. wagneri* are in no way distinguishable from mainland *wagneri*; in fact, the presence of expanded toe disks and the adult size indicate that the demes originated from the population found in northern Venezuela and Guyana.

I follow an earlier statement on the value of the subspecies concept (Savage and Heyer, 1967). I believe the methods treating variation within a species, as here presented, reveal more of the populational trends than does the arbitrary practice of designating subspecies. It is nearly impossible to fragment the three widespread species on the basis of any combination of characters.

It is appropriate to interject a comment on my evaluation of the taxonomic decisions at this point. Most of the study was based on morphology; I did not have the benefit of any biological data for most of the specimens; I regard the taxonomic decisions as conservative. With the evidence available for this study, my best judgment is that the *Melanonotus* species group is composed of six species.

*Relationships*: Four characters shared by members of the *Melanonotus*

group are useful in determining the degree of evolutionary advancement of the species. More adequate justification for determining primitive and advanced character states is presented elsewhere (Heyer, 1968). The presence of toe disks is considered an advanced condition, and the presence of grooves on the upper disk surfaces is considered a further advancement. Absence of thumb spines in males, a striped or distinctly spotted pattern on the posterior thigh surface, and a ventral pattern of light spots on a dark background are considered advanced conditions.

Certain trends among the species are clear. *Leptodactylus melanonotus* is primitive in all four characters, and is probably most like the ancestral *Melanonotus* group stock which gave rise to the six extant species. *Leptodactylus discodactylus* and *pustulatus* are the most specialized. *Leptodactylus discodactylus* has the most advanced disks, and the males lack thumb spines. *Leptodactylus pustulatus* has an advanced ventral and thigh pattern, and the males also lack thumb spines. *Leptodactylus dantasi*, *podicipinus*, and *wagneri* are intermediate. *Leptodactylus dantasi* has the advanced ventral pattern. The male is unknown for this species. *Leptodactylus podicipinus* and *wagneri* have individuals with the advanced thigh stripe. *Leptodactylus podicipinus* has a spotted belly and *wagneri* has individuals with toe disks. Based on only these four characters, a graphic representation is very difficult as evolution appears to have produced a mosaic pattern. *Leptodactylus melanonotus*, *podicipinus*, and *wagneri* are the most closely related. I think *dantasi* and *pustulatus* are more closely related to these three species than they are to *discodactylus*. *Leptodactylus dantasi*, *pustulatus*, and *podicipinus* resemble each other in general appearance, and the distinctive patterns of *dantasi* and *pustulatus* could have been derived from a species very much like that of *podicipinus*. For the present, I regard the loss of thumb spines to be a case of parallel loss in *discodactylus* and *pustulatus*. The relationships are presented as a dendrogram (Fig. 11).

#### DISTRIBUTIONAL ANALYSIS

Although some areas of Latin America have been studied moderately intensively, the geology, climate, soil types, and vegetation of many parts of Middle and South America are known poorly or not at all. Savage (1966) has recently given an excellent synthesis on the origins and history of the Central American herpetofauna, but no such synthesis has been attempted for South America. Only the broadest generalizations can be made with respect to the distribution of the components of the Latin American herpetofauna and the following remarks must be considered as provisional.

To discuss the distribution of the *Melanonotus* group, it is necessary to review briefly the broad geographic, paleogeographic, climatic, and vegetational patterns of Latin America.

*Geography:* The great American Cordillera forms a distributional barrier

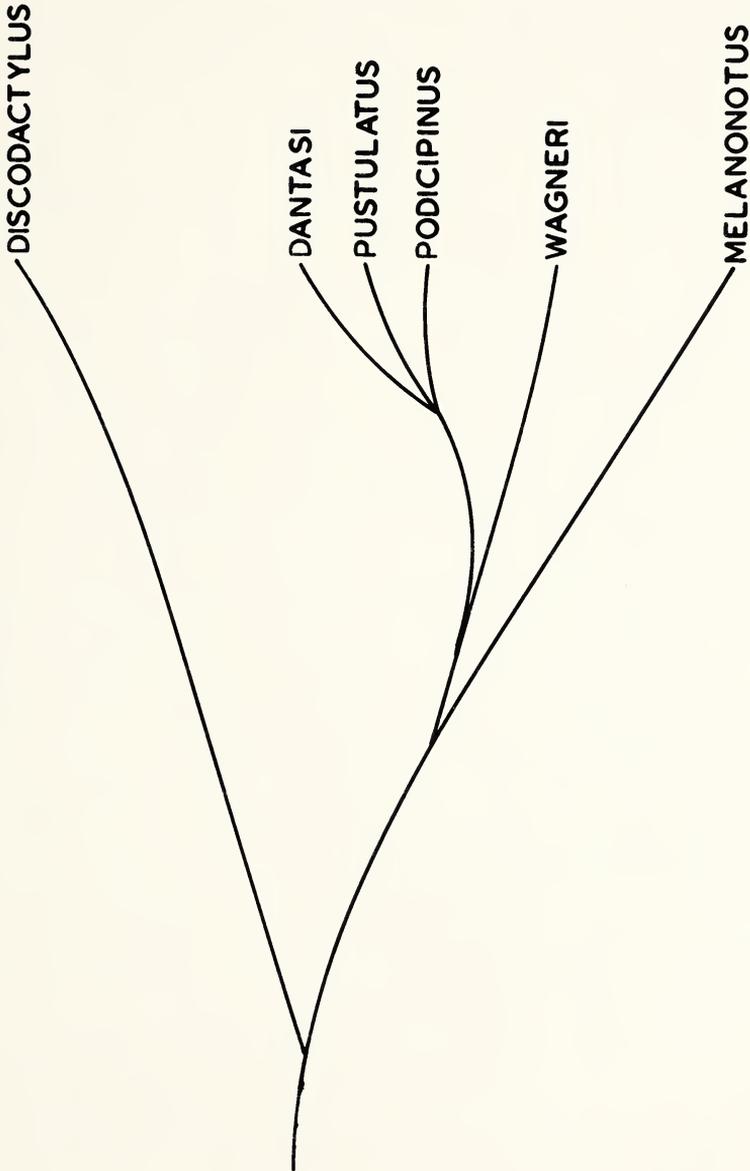


Figure 11. Proposed phylogeny of members of the Melanonotus group.

to frogs of the *Melanonotus* species group; the upper elevational limit for any species is about 1800 meters. Breaks in the montane chain where faunal interchange occurs are: the Isthmus of Tehuantepec in Mexico; the region around Lake Managua in Nicaragua; the Arenal pass in Costa Rica; and an extensive area including most of Panama and northernmost Colombia. The Andes of South America pass along the western outline of the continent, abut against the sea, or leave a very narrow lowland coastal strip to the west.

In South America, there are three major upland regions in addition to the Andes. These are the Guiana shield, the central Brazilian shield, and the coastal Brazilian shield. These upland regions do not form an elevational barrier to the distribution of frogs of the *Melanonotus* group. The Guiana shield is somewhat continuous from eastern Colombia, extending through central and southern Venezuela, to and including almost all of the Guianas and part of Brasil just below the Guianas. The central Brazilian shield is of irregular outline bordering Bolivia on the west and extending as a band eastward along the southern edge of the Amazon basin. The coastal Brazilian shield extends from the easternmost tip of South America in the state of Rio Grande do Norte along the coast southward to the state of São Paulo.

*Paleogeography:* The Cordillera of Latin America is geologically young, its present form attained in the very vigorous orogenesis from Mid to Late Tertiary, especially in Miocene and Pliocene times. Orogenesis continues in some parts of the Cordillera. (For a more detailed account and further references, see Childs and Beebe, 1963; Harrington, 1962; and Savage, 1966).

The Guiana, central Brazilian, and coastal Brazilian shields date from the Early Precambrian and have probably been land positive since then (Harrington, 1962). The history of the present land areas amidst the shields is poorly known, particularly since Mid-Tertiary to present, comprising, probably, the whole of the history of the *Melanonotus* species group. The Amazon basin has had a recurrent history of continental sediment deposition and marine embayment. Continental deposition has definitely occurred in the Late Tertiary, but whether any marine embayment alternated with continental deposition during or following this time is not known (Harrington, 1962). No precise information on the isolation or continuity of the shields with relation to each other exists, and it is impossible to comment on the isolation of the ancestral stocks of the frogs of the *Melanonotus* species group.

*Climate:* Comments are limited to climates affecting the distribution of members of the *Melanonotus* group. The coasts of Mexico and Middle America are characterized by seasonal rainfall patterns. A very pronounced hot and dry season is found along the western Mexican coast southward to the middle of Costa Rica. Similar conditions are found along the east coast of Mexico south to Nicaragua. The Atlantic coastal area of Costa Rica is wet the year around, but a seasonality in rainfall occurs. The only place in Middle America with a nearly continuously wet tropical rainforest is the Osa peninsula region

of Pacific Costa Rica. A wet climate with no cool season and basically no dry season occurs in four restricted areas in South America. The first such area is the Chocó region along the western coast of Colombia extending into north-west coastal Ecuador. The second and largest region is amidst the upper tributaries of the Amazon in southern Colombia, eastern Ecuador, most of eastern Peru, and northwestern Brasil. The third extends from coastal Guianas to the Brazilian coast just south of the mouths of the Amazon. The fourth area extends along a sometimes very narrow coastal strip of eastern Brasil from the states of Bahia south to Rio de Janeiro. All the other regions in South America occupied by the *Melanonotus* group have a pronounced dry season from one to nine months in duration. The driest regions in South America, also four, appear to limit the distribution of the *Melanonotus* group. The first runs along the western lowlands of middle Ecuador southward the length of the western lowlands of South America. The second lies along the north coast of Colombia and Venezuela, penetrating inland various distances. The third is in northeastern Brasil including the states of Maranhão, Piauí, and Ceará. The fourth is the Gran Chaco of northern Argentina, southeastern Bolivia, and southwestern Brasil (James, 1959; see also Walter and Lieth, 1960-1967).

*Vegetation:* The vegetation of Latin America is very complex and very inadequately studied. Many different systems have been used to define and describe the vegetation of Latin America. For the present I use the broad vegetational maps found in James (1959) and Wagner (1964) as the basis for discussion.

True tropical rainforests are found in the Osa peninsula region of Costa Rica; along western coastal Colombia and northwestern coastal Ecuador; along upper drainages of the Amazon characterized by high, continuous rainfall; and along the narrow coastal strip of Brasil from the states of Rio Grande do Norte to Rio de Janeiro. Tropical and subtropical rainforests which have a definite seasonal rainfall distribution are found in a continuous belt along the east coast of Mexico through Panama. Coastal patches of deciduous forest are found within the tropical and subtropical rainforests along the Caribbean coast of Mexico, the tip of the Yucatán peninsula, easternmost British Honduras, easternmost Honduras and northeastern Nicaragua. Seasonal tropical rainforest is continuous with the tropical rainforest of the upper Amazon and covers almost all of the Amazon basin not covered by the tropical rainforest. Tropical deciduous forests are found along the west coast of Mexico from the state of Jalisco southeast to the middle of the Pacific coast of Costa Rica; along the periphery of the Guiana shield; in eastern Brasil from the north coast of the state of Rio Grande do Norte to middle Bahia, excluding the narrow eastern coastal strip; and in the Gran Chaco. Thorn forests are found along the northern coasts of northeast Colombia and Venezuela. Savannas cover the Guianan and central Brazilian shields, and most of the coasts ad-

acent to the Brazilian shields. A palm forest is found in northeast Brasil in the states of Piauí and Maranhão.

*Distribution of the Melanonotus Species Group:* Most of the species are known from scattered localities. *Leptodactylus melanonotus* has been most thoroughly sampled, and moderately accurate distributional data are available for at least Mexico and Costa Rica. Records for *dantasi*, *discodactylus*, and *pustulatus* are very spotty, and more distributional data are needed to define the geographic limits of the species. *Leptodactylus podicipinus* has been moderately well collected in Argentina, but inadequate distributional data are available for the rest of its geographic range. Distributional data of *wagneri* are most adequate for Ecuador, parts of Colombia and Guyana. Throughout the rest of the geographic range of *wagneri*, records are so spotty that it is impossible to determine whether it has a broadly continuous range or if it is composed of many isolated populations.

The limited information gives the following patterns of occurrence:

*Leptodactylus melanonotus*, *wagneri*, and *podicipinus* form a series of closely related, basically allopatric species ranging throughout low and moderate elevations of tropical Latin America. All three species are found in areas having a definite dry season. Judged by collections, *melanonotus* is not common along the continuously wet lowlands of Colombia and Ecuador. Only *wagneri* is commonly associated with the tropical rainforests of eastern Colombia, Ecuador, and Peru. The foam nest formed by these species appears to be an adaptation to a definite dry season.

In some more xeric portions of its range (southern Sonora and northern Sinaloa, Mexico), *melanonotus* is found only in association with permanent bodies of water, such as persisting springs or irrigation water. The northernmost locality for *melanonotus* on the west coast of Mexico is a dam seepage by Hermosillo, Sonora. In more mesic areas, it is often associated with temporary bodies of water, such as rain filled ditches along roadsides.

*Leptodactylus melanonotus*, *podicipinus*, and *wagneri* are found in regions with old land masses in South America: *melanonotus* with an old land mass in western Colombia and Ecuador (land positive at least during Late Mesozoic and Tertiary time, Harrington, 1962:1780); *podicipinus* with the Brazilian shields; and *wagneri* with the Guiana shield. If one assumes that the three species had a common, widespread ancestor, isolation of the land masses in the Cenozoic could account for the fragmentation of the stock that gave rise to *melanonotus*, *podicipinus*, and *wagneri*.

Individuals of *melanonotus* in the region from the Isthmus of Tehuantepec to the Arenal Pass of Costa Rica are characterized by having a larger size, a more variable ventral pattern, and a greater ventrolateral gland extent than individuals to the north or south. Such character gradients suggest that the major dispersal point of *melanonotus* has been from this land bloc in Middle America. Secondary dispersal in Middle America by a species which had its

evolutionary origin in South America has also been hypothesized for the hylid frog *Phrynohyas venulosa* by McDiarmid (1968). Dispersal into Middle America by a species from western South America is consistent with Savage's (1966) scheme of historical herpetofaunal dispersal. He suggested that an assemblage of species, termed the Western South American Herpetofaunal Complex, evolved during the separation of nuclear Middle America from South America from Eocene through Miocene. When Middle America and South America were joined again at the beginning of the Pliocene, members of the Western South American Complex invaded Middle America.

*Leptodactylus wagneri* today is found in a variety of climates and associated vegetation types, but is found consistently in more mesic situations than either *melanonotus* or *podicipinus*. Throughout most of its range, *wagneri* is found in tropical or subtropical rainforest with either a short or no dry season. An exception occurs in the northern part of the range, particularly along the extreme north coasts of Colombia and Venezuela. *Leptodactylus wagneri* is not recorded from the palm forest or tropical deciduous forest of eastern Brasil in the states of Maranhão through Rio Grande do Norte. Records are so scattered for eastern Brasil that it is hard to tell whether its absence in any region is a collecting artifact.

The islands of Trinidad and Tobago are on the continental shelf and were probably connected to the mainland during glacial maxima. The presence of *wagneri* on these islands is to be expected. The islands of Grenada, Bequia, and St. Vincent are not on the continental shelf; they probably have been always isolated from the continent of South America. Grenada and Bequia are on the same bank. Currently, Bequia lies only 10 km from St. Vincent and possibly was separated by no more than 5 km of water during glacial maxima. The distance from the 100 fathom contour outside of Tobago to the 100 fathom line surrounding Grenada is at most 100 km, and these two points are directly connected by westerly surface ocean currents. All island populations are indistinguishable from mainland populations of northeast Venezuela, suggesting either that dispersal to the Lesser Antilles has been a rather recent event or that Lesser Antillean populations have been populated repeatedly from the mainland stock. A single dispersion of *wagneri* from South America (including Trinidad and Tobago) could account for all of the populations on the Lesser Antilles. Other members of the genus *Leptodactylus* are more successful island colonizers, especially *mystaceus* which has apparently hopped from island to island along the Lesser Antilles to as far as Haiti. As judged from the similarity of the island and mainland populations, it is reasoned that *wagneri* dispersed to the Lesser Antilles during the glacial maxima of the Pleistocene.

*Leptodactylus podicipinus* is associated with the southern river drainages and the São Francisco drainage system. All of the regions, such as the Gran Chaco, where *podicipinus* has been found have a very distinct dry season. *L. podicipinus* is generally adapted to more xeric conditions than *wagneri*.

This may be seen where the two species occur close together, most notably with *wagneri* along the thin mesic coastal strip of east Brasil, and *podicipinus* close by in the dry parts of the São Francisco drainage system.

*Leptodactylus dantasi*, *discodactylus*, and *pustulatus* are known from spotty distributional records, which suggest a distribution associated with climatic and vegetational factors. *Leptodactylus dantasi* has been taken only from the tropical rainforest in western Brasil. *Leptodactylus discodactylus* is apparently limited to the tropical rainforest of southeastern Colombia, eastern Ecuador, most of eastern Peru, and western Brasil. *Leptodactylus pustulatus* is apparently limited to the more xeric conditions in the palm forest, tropical deciduous forest, and savannas of eastern Brasil.

The total distribution of members of the *Melanonotus* species group indicates that three species have broad ecologic tolerances and are distributed in extensive geographic regions and that three of the species have much narrower ecologic tolerances and have restricted geographic distributions.

#### SPECIMENS EXAMINED

*Leptodactylus dantasi* (N = 1): BRASIL. TERRITORIO DO ACRE: Feijó, 249 m—WCAB 1240 (Holotype).

*Leptodactylus discodactylus* (N = 15): ECUADOR. NAPO: Payamino, 304 m—GOV 7238; PASTAZA: Puyo, 1000 m—GOV 2062, JAP 6197-8; 6333; Veracruz, 1000 m—JAP 6151, 6153-6, 6164. PERU. LORETO: Estirón, Río Ampiacu, 200 m—CAS 93316, 7; Río Itaya, 150 m—AMNH 43217; Río Tamaya, Sobral, 150 m—AMNH 42680.

*Leptodactylus melanonotus* (N = 520): BRITISH HONDURAS. STANN CREEK: Mango Creek, 120 m—MCZ 37884; 4.8 km S Waha Leaf Creek, 120 m—MCZ 37875-6. COLOMBIA. CHOCÓ: Río San Juan, Playa de Oro, 400 m—FMNH 54374; NARIÑO: La Guayacana, 230 m—PAS 44; Río Mataje, 200 m—USNM 147393; Valle de Cauca: Río Raposo Virology Field Station, 20 m—USNM 151463. COSTA RICA. Alajuela: Cariblanco, 800 m—CRE 2928 (10); 0.5 km S Cariblanco, 820 m—CRE 694; Los Chiles, 70 m—AMNH 54638, 54641-3, CRE 7217, 7219; Punta Cortéz, 70 m—CRE 7218; CARTAGO: Cervantes, 1441 m—KU 28189; IICA, Turrialba, 600 m—CRE 575, 2808 (2), 7074 (2), 7079 (7); GUANACASTE: Arenal, 520 m—CRE 6251, 6258 (4), 6259, 6260 (2); 4.8 km NW Arenal—CRE 2901 (3); Bebedero, 6 m—CRE 7162; Cañas, 88 m—CRE 7164; 9.6 km S La Cruz—CRE 8091; Río Lagarto at Inter. Am. Hiway, 100 m—CRE 7122 (2); 2 km W Liberia—CRE 728 (4); 9 km N and 4 km E Liberia on Inter. Am. Hiway on Río Colorado—CRE 714 (2); 14.8 km S Liberia, 90 m—CRE 8168; 45 km SW Liberia, Hwy #21—CRE 8216; Hacienda La Norma, 5 km N and 4.5 km W Liberia on Río Colorado, 150 m—CRE 105 (2), 106 (6), 107, 251 (2); 3-11 km E Playa del Coco, 45 m—CRE 8012 (2); Finca San Bosco de Tilarán, 640 m—CRE 6273, 6278; 3.2 km W Santa Cruz on the

Playa del Tamarindo rd.—CRE 8233; Santa Cruz, 50 m—CRE 7128, 8232 (3); Silencio de Tilarán, 825-850 m—CRE 6217 (8), 6225 (2), 6228 (2); 0.5 km NW Tilarán, 530 m—CRE 520 (7); 3 km NE Tilarán—CRE 524; 5 km NE Tilarán, 600 m—CRE 8021; 5.5 km NE Tilarán, 560 m—CRE 8022; 6 km NE Tilarán, 550 m—CRE 523 (3), 8020 (9); Finca Taboga, 9.6 km S and 8.0 km W Cañas, 4 m—CRE 2902; HEREDIA: Puerto Viejo, 100 m—KU 65683; 6.5 km W Puerto Viejo—KU 91798; 7.5 km W Puerto Viejo—KU 86293; LIMÓN: Batán, 15 m—KU 34146-51; 2.4 km E Los Diamantes, 260 m—CRE 8049; El Tigre, 680 m—CRE 290 (2); PUNTARENAS: 9.6 km ESE Golfito, 10 m—CRE 7105; junction of road and rail line (Base of Peninsula), 5 m—CRE 238 (2), 253-4. ECUADOR. ESMERALDAS: San Javier, 200 m—JAP 9077-82; Cacnauí, 20 m—JAP 2889-9; Río Bogotá, 200 m—GOV 6398; LOS RIOS: Vinces, 150 m—UMMZ 55587 (7). EL SALVADOR. SAN SALVADOR: San Salvador, 620 m—FMNH 65071-86. GUATEMALA. EL PETÉN: N of La Libertad—UMMZ 75367 (12); 5.2 km S La Libertad—MCZ 21454; Toocog, 15 km SE La Libertad, 170-200 m—KU 58959; ESCUINTLA: Río Guacalate, nr. Masagua, 100 m—USNM 125246-51, 125253, 125261-3; ZACAPA: 8 km ENE Río Hondo, 175 m—KU 58960; 23 km NE Zacapa—ANSP 22165-6; 23 km W Zacapa, 240 m—TCWC 16403, 16406. HONDURAS. ATLÁNTIDA: Corozál, 15 km E La Ceiba, 10 m—JRM 2316, 2328-33, 2335, 2337-8, 2341, 2343; CHOLUTECA: 1.5 km NW Choluteca, 170 m—KU 65676; 5 km S Choluteca, 80 m—MCZ 26460-2; CORTÉS: Agua Azul, Laguna Yogoá, 700 m—AMNH 54778; FRANCISCO-MORAZÁN: 31 km S Guaimaca, Santa Clara, 1000 m—AMNH 54884-5, 54887; ISLAS DE LA BAHIA: Isla de Guanaja, SE shore opposite Guanaja, 10 m—JRM 1938, 1961-6; Isla de Roatán, .5-4 km N Roatán, 10-30 m—JRM 1828-9, 1896, 1916; OLANCHO: Escuela Nacional de Agricultura, 4.5 km SE Catacamas, 400 m—JRM 1660-2. MEXICO. CAMPECHE: Chuina, 46 km S Champotón, 50 m—KU 75017-26; CHIAPAS: 4 km NW La Esperanza, 100-300 m—USNM 114372-6, 114381-2, 114385, 114388; Tonalá, 55 m—USNM 114338-44; Tuxtla Gutierrez—UMMZ 115530; 9.8 km W Tuxtla Gutierrez, 520 m—UMMZ 119147 (2); COLIMA: 25.9 km N Manzanillo, 10 m—CAS 97111-8, 97155-7; GUERRERO: 12.9 km SW Tierra Colorada, 300 m—TCWC 8323-6, 8333-9; JALISCO: 5.2 km W Acatlán, 1400 m—LACM 37381-408; MICHOACÁN: Apatzingan, 540 m—FMNH 38835, 38837, 38853-5, 38859-60, 38862, 38865-6, 38873; NAYARIT: San Blas, 3 m—UMMZ 110892 (7), 115543 (3); Tepic, 1000 m—LACM 37042-3; OAXACA: Cacahuatpec at river, 150 m—UIMNH 52854-8; 8.3 km N Pochutla, 100 m—UMMZ 123982 (8); 5.2 km N Matías Romero, 150 m—UMMZ 115522 (3); 7.8 km S Matías Romero, 150 m—UMMZ 113804 (4); Tehuantepec, 35 m—FMNH 123248-50, 123253, 123256, 123264, 123267-9; Tolosa, 50 m—AMNH 53610; QUINTANA ROO: 3 km E Caobas, 5-10 m—KU 75033; 4 km WSW Puerto Juárez, 5 m—KU 71117-

8; SAN LUIS POTOSÍ: 5.1 km NE Tamazunchale, 150 m—TCWC 7285-91; 5.1 km SW Tamazunchale, 150 m—UIMNH 16802-3; SINALOA: Culiacán, 45 m—AMNH 58382-91; 18.9 km SW Mazatlán, 48 m—KU 78259-61; 5.2 km W Villa Union—KU 29901-7; SONORA: Alamos, 300 m—AMNH 51356-65; Hermosillo, 28 m—AMNH 62737, MVZ 26066; TABASCO: Teapa, 40 m—UMMZ 119148 (2); 20.7 km N Teapa—UMMZ 119901 (2); 33.7 km N Teapa—UMMZ 119903 (6); 57 km N Villahermosa, 30 m—AMNH 69007-8; TAMAULIPAS: Paño Ayuctle, 12.9 km NE Gómez Farías, 100 m—UMMZ 98947 (2), 101185 (5), 102263, 102912; VERACRUZ: 5 km SW Boca del Río—KU 23700; Cuatotolapam, 13 m—UMMZ 41640-3, 41646-7, 41649; 1 km E Mecayucán, 30 m—KU 24084, 24086, 24091-4; 25.9 km WNW Temapache, 50 m—KU 60225-8; YUCATÁN: 31 km N Tizimín, 5 m—CM 40108-10; 16.2 km S Yaxcopoil, Aguada Xcamal, 5 m—CM 45233-43; Yuncu, 25-50 m—UMMZ 73155, 73158 (2). NICARAGUA, MANAGUA: 15.5 km NW Managua, 55 m—KU 43030-39; RIVAS: San Jorge, Shore of Lake Nicaragua, 50 m—MCZ 28980-89; ZELAYA: Bonanza, 260 m—KU 84839-41, 84843-48; 10.4 km SW Bonanza, 300 m—KU 84842; 25.9 km above Recreo, Río Mico, 30 m—UMMZ 79734, 79735 (4). PANAMA. CHIRIQUÍ: Las Lagunas,  $\pm$  6 km W El Volcán,  $\pm$  1200 m—KU 76522; Finca Palosanto, 6 km WNW El Volcán, 1230 m—KU 76520-1; COCLÉ: El Valle, 560 m—KU 76523-32; DARIÉN: Río Canclón, 60 m—UMMZ 125008, 125009 (10). UNITED STATES, TEXAS: Starr County, 5.1 km SE Rio Grande City—UIMNH 29817.

*Leptodactylus podicipinus* (N = 154): ARGENTINA. CHACO: Resistencia, 60 m—KU 84732-4; CORRIENTES: 30 km W Itati, 60 m—CAS 100504; Manantiales, 50 m—MCZ 35589-90; FORMOSA: Esteros Laguna Oca, 65 m—MCZ 32775-6; SANTA FÉ: Bañados Monteiro, 15 km N Santa Fé, 20 m—CM 38011; Bañados del Rincón, 20 m—CM 37981-3, 38003, 38005; Santa Fé, 18 m—CM 39181, 39194. BOLIVIA. BENI: Ivon, 150-200 m—UMMZ 64099 (7); Puerto Almacén, 260 m—AMNH 72245-53; SANTA CRUZ: Buenavista, 500 m—AMNH 39538; El Carmen, 212 m—CM 36234-7; Naranjal, 5 km from Montero, 350 m—USNM 146551; El Porton, 550 m—CM 36248; Robore, 330 m—MCZ 30032-6; 3 km S Robore, 330 m—CM 36238-41; San José de Chiquitos, 350 m—CM 36164, MCZ 30028-9. BRASIL. BAHIA: Barreiras, 500 m—UMMZ 109986; Rio Grande at São José, 450 m—UMMZ 109989; MATO GROSSO: Agua Clara, 304 m—FMNH 67088; Conceicao, Paraguay River, 150 m—FMNH 9161; Corumbá, 115 m—CM 2429, 36165, UMMZ 104225 (2); 40 km from Corumbá, Urucum Mts., 200-300 m—CM 2430; Descalvados, 142 m—FMNH 9097, 9100-14; 1 day's run below Descalvados, 150 m—USNM 132736-7; Maracajú, 385 m—USNM 107705-8, 107710-11; Pôrto Esperança, 120 m—UMMZ 104232 (11), USNM 133005-8; Salobra, 190 m—UMMZ 104227 (2); MINAS GERAIS: Januaria, 454 m—UMMZ 109984; Pirapora, 472 m—UMMZ

109982 (10), USNM 98535, 99801-3; PARANA: Andira, 480 m—MCZ 32725-6; RONDÔNIA: Forte Príncipe da Beira, 100-200 m—WCAB 8330, 8982; Pôrto Velho, 60 m—KU 92933-37; SÃO PAULO: Anhembi, 500 m—WCAB 30880-1; Baurú, 499 m—DZ 53-4; Cachoeira de Emas, Pirassununga, 650 m—DZ 4636-42; Lins, 396 m—DZ 9024; Pôrto Marcondes, Parapanema, 250 m—DZ 19979, 19999 (10 total). PARAGUAY. CAAGUAZJU: Pastorea nr. Caaguazú, 250 m—MCZ 17902-11; CORDILLERA: Villeta, 110 m—AMNH 50654; PRESIDENTE HAYES: Río Pilcomayo, 38.8 km W Río Paraguay, 80 m—MCZ 25827-33.

*Leptodactylus pustulatus* (N = 7): BRASIL. GOIÁS: Aruaña, 200 m—DZ 4992, 8109; MATO GROSSO: São Domingoes, Río das Mortes, 200 m—DZ 986-7, 996, 1069; PIAUÍ: Río Poti—MCZ 373.

*Leptodactylus wagneri* (N = 711): BOLIVIA. BENI: Cachuela Esperanza, 150 m—UMMZ 64102 (2); nr. Guauará-mirim, Río Marmorí, 160 m—CM 2666; Swamp along Río Guaporé, San Antonio de Guaporé, 150 m—USNM 115973; Huachi, 250 m—UMMZ 64103 (3), 64104; Puerto Almacén, 260 m—AMNH 72251, 72254, 72398-402; Lake Rogoagua, 200 m—UMMZ 64100 (7); Rurrenabaque, 227 m—UMMZ 64097 (3); Villa Bella, 120 m—CM 2659; COCHABAMBA: Puerto Chipiriri, 300 m—AMNH 72242-3; PANDO: in front of Placido de Castro, Acre, Brasil—DZ 6529-31; SANTA CRUZ: Buenavista, 500 m—CM 4331, 4353, UMMZ 64028-29, 64030 (2), USNM 118688-9, 146523-4. BRASIL. ALAGOAS: Fazenda Canoas, Río Largo, 60 m—DZ 9279; Mangabeiras, 50 m—DZ 11982-3; São Miguel, 20 m—DZ 9250; AMAZONAS: Manacapuró, 50 m—USNM 103621-2; BAHIA: Salvador, 15 m—DZ 9131, 9550-1; GOIÁS: km 47 Estrada Goiás-Aruaña, 350 m—DZ 1518; MARANHÃO: Carolina, 168 m—DZ 21664-5; MATO GROSSO: Dumbá, 200 m—DZ 1448; Banks of center of Río Guaporé, 250 m—CM 2508-9; Confluence of Río Araguaia and Río Tapirape, 190 m—AMNH 68093; São Domingoes, Río das Mortes, 200 m—DZ 10891-2, 10894-900, USNM 148677-91; PARÁ: Belem, 20 m—FMNH 83264-5, MCZ 36010-1, USNM 154068; Cachimbo, 500-600 m—DZ 21656-61; Río Mapuera at the Equator, 80 m—AMNH 46181; Santarem, betwn Río Tapajos and Río Amazonas, 16 m—CM 2641; RIO DE JANEIRO: km 31 on Estrada Mage-Estrada Río Petropolis, 100 m—DZ 12034-5; RIO GRANDE DO NORTE: Natal, 120 m—AMNH 36261, MCZ 15847, UMMZ 68791; TERRITORIO DO ACRE: Iquiri, 150 m—DZ 6588-92; TERRITORIO DO RIO BRANCO: Río Urariquera, 100-200 m—WCAB 18792; TERRITORIO DO RONDÔNIA: Forte Príncipe da Beira, 100-200 m—WCAB 10690, 10703. COLOMBIA. AMAZONAS: Falls of Engano—MCZ 28063; Leticia, 275 m—CM 36081-2, USNM 142179-86, 142187-94, 146252, 147031; ANTIOQUIA: Envigado, 1600 m—AMNH 39265, 39274, 39281; Medellín, 1500 m—AMNH 38785, 38808-15, 39465; Sonsón, 2500 m—AMNH 39631; BOYACÁ: Muzo, 1240 m—FMNH 69744, MCZ 24920;

CAUCA: Popayán, 1700 m—FMNH 54377-83; CUNDINAMARCA: Anolaima, 1500 m—USNM 147054-5; Bogotá, 2600 m—AMNH 13471; Fusagasugá, 1700 m—AMNH 71581; La Mesa, 1000-1300 m—USNM 144892-3; META: Buenavista, 1200 m—MVZ 63067-73; Menegua, upper Río Meta, 260 m—USNM 147273-4; 46 km S, 22 km W San Martín, 490 m—MVZ 63076; Villavicencio, 500 m—ANSP 25765, FMNH 30571, 81788-9, MCZ 16277, MVZ 63074-5, 63738-9, UMMZ 74811, USNM 144848-66, 147056-62; 7 km NE Villavicencio, 500-700 m—USNM 146382-4; NARIÑO: La Guayacana, 100 m—FMNH 61754; NORTE DE SANTANDER: Astillero, 100-200 m—USNM 147063; E of Cucuta 200-500 m—ANSP 25758; PUTUMAYO: Río Putumayo, 5 km N Puerto Asís, 260 m—PAS 47; Rumiayaco, 1000 m—FMNH 54376; SANTANDER: nr. Lebrija, 1086 m—USNM 144883-8, 146250; San Gil, 1095 m—CM 7938, UMMZ 74799; TOLIMA: Guindío Mtns.—MCZ 8217; VALLE DE CAUCA: Buenaventura—USNM 147076; 2 km S Cali, 950 m—USNM 148800-23; VICHADA: Puerto Carreño—CM 17122. ECUADOR. NAPO: Lagarto Cocha, 200 m—GOV 9208; Loreto, 400 m—GOV 9205, WCAB 36541; Río Napo, Avila, 300 m—UMMZ 92145-6; PASTAZA: Upper Bobonaza—JAP 8732; Canelos, 530 m—MCZ 17950; Cerros de Abitagua, 1100 m—FMNH 25789, 26899, UMMZ 92147; Chichirota, 300 m—GOV 9207; Upper Río Curaray—GOV 9210; Upper Río Oglán, 500 m—GOV 9206; Río Pindo, 190 m—GOV 9195-7; Puyo, 940 m—JAP 1958-71, 1973-2005, 2036, 2038, 6182, 6186-7, 6191-5, 6289-99, 6303-5, 6329-32, 6334, GOV 8021-2; Shell Mira, 1064 m—GOV 8503, JAP 2177; Don Tomás, 340 m—GOV 9209; Río Villano, 300-400 m—GOV 7731-6, JAP 3776; ZAMORA-CHINCHIPE: Copal, 910 m—JAP 6747-8; Limón, 1550 m—JAP 6937, 6964-5; Río Llushin—GOV 9198-201, 9203, JAP 3751; Mendez, 580 m—JAP 2037, 6805, 6870, 6872-5, 6880, 6832-4, 6837, 6845-6, 6855-6, 6936; Plan de Milagro, 1700 m—JAP 7008, 7014-6, 7018-23, 7027, 7057; Plan Grande, 880 m—JAP 6903; NE of Riobamba—FMNH 23509 (8); Sucua—JAP 2186, 2225. FRENCH GUIANA. Sophie, on trail leading S from St. Elie Gold Pits, 200 m—MCZ 44564. GUYANA. DEMARARA: Atkinson, McKenzie Trail, 50 m—USNM 162872-3; Dunoan, Demerara Riv., 20 m—UMMZ 50183-9; Georgetown, 5 m—UMMZ 80497; Wismar, 50 m—AMNH 45750, UMMZ 77517, 80417; ESSEQUIBO: Isheraton, 250 m—AMNH 53435-7; Karanambo, 100 m—AMNH 53438; Kartabo, 10 m—AMNH 10377, 10379-83, 11659, 13518-9, 25233, CM 5443-4, USNM 118059-62; Kuyuwini Landing, 250 m—AMNH 46281, 49352, 49355 (5); Lethem, 100 m—MCZ 50708; Marudi, 250 m—AMNH 46238 (2); Moku Moku, 100-200 m—USNM 146366-7; Oko Mts., 115 m—FMNH 26691; Santa Rosa Is., Moruca Riv., 7 m—UMMZ 55833 (2), 80417; Shudikarwan, 200-300 m—AMNH 46274 (9). PERU. AYACUCHO: Candalosa,  $\pm$  1400 m—FMNH 39727-32, 39734-46; La Mar,  $\pm$  760 m—FMNH 39725; La Mar, Ayna  $\pm$  1900 m—FMNH 39726; HUAN-

UCO; Ganzo Azul, 150 m—FMNH 45144; JUNÍN: Satipo, 500 m—MCZ 24424-8, UMMZ 89476 (7); Tarma, Palmapata, 1200-1400 m—FMNH 36827-30; Tarma, Valley of Vitoc River, 1200-1400 m—FMNH 36817-26; LORETO: Río Marañón, mo. of Río Pastaza, 150 m—AMNH 42221-3, 42225-7; Pampa Hermosa, 176 m—AMNH 42142-4, 42661; Roabaya, 100 m—AMNH 42823-4; Río Tamaya, Sobral, 150 m—AMNH 43238; Río Alto Tapiche, mo. R. Contaya, 200 m—AMNH 42988; Tibi Playa, 150 m—AMNH 42783; Río Ucayali, Pacapa, 150 m—FMNH 56322; Upper Utoquina, 200 m—AMNH 42599; PASCO: Iscozazin Valley, Chontilla, 780 m—LACM 40660-5; Río Pachitea, Monte Alegre, 150 m—AMNH 43013; SAN MARTÍN: Tocache, 450-750 m—AMNH 42627. SURINAM. MARO-WIJNE: Kaiserberg airstrip, Zuid R., 200-300 m—FMNH 128925, 128927-8, 128933-7, 128939-40. VENEZUELA. AMAZONAS. Río Pescado—AMNH 23182; ARAGUA: Colonia Tuvar, 1830 m—CM 7729; Cumboto, 150 m—UMMZ 113975 (2); Rancho Grande, nr. Maracay, 450 m—AMNH 70687; BOLÍVAR: Arabopo, 1280 m—UMMZ 85197 (5); Mt. Roraima, Paulo, 1216 m—AMNH 39753, 39758-9; DELTA AMACURO: 140 km NE Barrancas, 5-10 m—LACM 31382-97; DISTRITO FEDERAL: Cotiza, Camino de Calipan, 900 m—USNM 117526, 128837; El Limón, 577 m—CM 7676-7, 7697, 7699, USNM 121146; FALCÓN: Cerro Cosme, 100-200 m—MCZ 26144-6; Lagoon, Palma Sola, 50 m—UMMZ 55551; MÉRIDA: Mérida, 1641 m—MCZ 2640, USNM 118176; Río Albirregas nr. Mérida, 1640 m—AMNH 10517-9; MIRANDA: Petare, 885 m—CM 7769-71, 7791; USNM 121147; MONAGAS: Caripito,  $\pm$  50 m—AMNH 70669-86, USNM 117088-9; SUCRE: Cumanocoa, 300 m—CM 9055-76; Latal, Hacienda Mirasol, 975 m—CM 9099, 9101; San Rafael, nr. Cumanocoa, 200-400 m—CM 8972; El Yaque, 800 m—CM 9108-9; TÁCHIRA: La Fría, Rt. Fork Río Oropito, 110 m—UMMZ 55552-3; ZULIA: Chama, 10 m—AMNH 10685-8. WEST INDIES: BEQUIA: north end—USNM 103976-8; GRENADA: Grand Etang—MCZ 2963-71, 2974-6; no specific locality—AMNH 18961, 18970-2, 18992, USNM 67183-4, 67186-94; ST. VINCENT: Botanical Garden—USNM 144246; Brighton—USNM 79068-75; Mt. St. Andrews—USNM 79076-7; TOBAGO: Bacolet River—AMNH 55873; Buccoo Bay—AMNH 55863-5; nr. Speyside, 180 m—MCZ 27788-9; TRINIDAD: Nariva: Brickfield—FMNH 49656-60; Upper Tucker Valley—USNM 119055-60; St. Andrew: Mount Harris—FMNH 49654-5; Sangre Grande—MCZ 3295-8; San Rafael—FMNH 49664-5; St. George: St. Augustine—CM 5466.

#### RESUMEN

En el grupo *Melanonotus* se reconocen las siguientes seis especies: *dantasi*, *discodactylus*, *melanonotus*, *podicipinus*, *pustulatus*, y *wagneri*.

Para cada especie se ofrecen: sinonimia, diagnóstico, sumario de caracte-

terísticas y distribución. Series de *Leptodactylus* procedentes de amplias áreas geográficas y ecológicas fueron analizadas para estudiar largo normal, apariencia ventral, desarrollo de las glándulas ventrolaterales, apariencia de las extremidades posteriores, y desarrollo de los discos digitales. Se encontraron correlaciones evidentes entre: tamaño grande y habitats húmedos en *wagneri*, 2) apariencia ventral más oscura y una cantidad mayor de lluvia anual en *melanonotus*, 3) apariencia ventral pálida y una mayor extensión de las glándulas ventrolaterales en *wagneri*, y 4) mayor extensión de las glándulas ventrolaterales y mayor cantidad anual de lluvia en *wagneri*.

Se postula la hipótesis de que existe desplazamiento de caracteres en la estricta diferencia en tamaño y apariencia tanto entre poblaciones de *melanonotus* y *wagneri* como entre *podicipinus* y *wagneri* las cuales viven simpatricamente.

*Leptodactylus melanonotus* es la especie más primitiva, mientras que *discodactylus* y *pustulatus* son más avanzadas.

*Leptodactylus melanonotus*, *podicipinus*, y *wagneri* están asociadas con regiones antiguas y son especies adaptadas a condiciones xéricas. *Leptodactylus dantasi* y *discodactylus* están limitados al bosque tropical húmedo del valle al oeste del Amazonas. *Leptodactylus pustulatus* se encuentra en las regiones orientales xéricas de Brasil.

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SYSTEMATICS OF THE LIZARDS OF THE GEKKONID GENUS  
PHYLLODACTYLUS OF MAINLAND SOUTH AMERICA

By JAMES R. DIXON AND RAYMOND B. HUEY



LOS ANGELES COUNTY MUSEUM OF NATURAL HISTORY • EXPOSITION PARK  
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# SYSTEMATICS OF THE LIZARDS OF THE GEKKONID GENUS PHYLLODACTYLUS OF MAINLAND SOUTH AMERICA

By JAMES R. DIXON<sup>1</sup> AND RAYMOND B. HUEY<sup>2</sup>

**ABSTRACT:** A brief description of the habitat of species of *Phyllodactylus* of mainland South America is presented. Microhabitat preferences are given for each species where possible. Little or no microhabitat information is available for *P. heterurus*, *sentosus*, and *clinatus*. Four species, *P. angustidigitus*, *gerhopygus*, *microphyllus*, and *sentosus* are primarily terrestrial and allopatric in distribution. Nine species, *P. clinatus*, *dixonii*, *inaequalis*, *interandinus*, *johnwrighti*, *kofordi*, *lepidopygus*, *pumilus*, *reissi*, and *ventralis* are scansorial and only *johnwrighti*, *ventralis*, and *dixonii* are not found sympatric with one or more of the other scansorial species. Where three or more species are sympatric, there is little overlap in daytime retreats and foraging areas.

One egg is laid per clutch by most species of *Phyllodactylus* of mainland South America except *reissi*, which lays two eggs. Information on clutch size is not available for *P. heterurus*, *sentosus*, and *clinatus*. Communal egg laying appears to be common among most species, including such sympatric species as *P. interandinus* and *reissi*, *kofordi* and *reissi*.

Species of *Phyllodactylus* appear to have specific adaptations to their microhabitat. Enlarged terminal digital lamellae, dorsoventrally compressed head and body, and lateral nostrils characterize species of *Phyllodactylus* from a boulder microhabitat; small terminal digital lamellae, round body and head, dorsolateral valvular nostrils for species from a sand microhabitat; small terminal digital lamellae with enlarged claw, slim body and head, dorsolateral valvular nostrils for species from shell beaches. Depending upon the degree of scansorial or terrestrial behavior some species of *Phyllodactylus* are intermediate in the above adaptations.

Distribution maps and photographs are given for each species, except *P. heterurus*, and a gazetteer of important localities is presented.

Of the holotypes and syntypes for species described from the mainland of South America, ten (*dixonii*, *inaequalis*, *lepidopygus*, *magister*, *microphyllus*, *nigrofasciatus*, *phacophorus*, *pumilus*, *reissi*, and *ventralis*) are extant and eight have been examined. Seven new species (*angustidigitus*, *clinatus*, *interandinus*, *johnwrighti*, *kofordi*, *pumilus*, *sentosus*) are described herein and nine older names (*abrupteseriatus*, *baessleri*, *guayaquilensis*, *lobensis*, *magister*, *nigrofasciatus*, *phacophorus*, *underwoodi*, *variegatus*) are relegated to the synonymy of other species.

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## INTRODUCTION

The leaf-toed geckos, genus *Phyllodactylus*, form two distinct geographic units in South America, a northeastern group in Colombia, Venezuela and the Caribbean Islands, and a western group in Ecuador (including the Galapagos Islands), Peru, and Chile. A study of the northeastern representatives was completed by Dixon (1962, 1964a). The present work treats the systematics and biology of the mainland South American *Phyllodactylus*. Although the Galapagos Islands species are evolutionarily close relatives to the mainland species of western South America, they are a special problem and will be reported on at a later date.

The earliest description of a species for the mainland of South America was by Wiegmann (1835) for *P. gerrhopygus* and the most recent by Rivero-Blanco and Lancini (1968) for *P. dixonii*. A total of 19 species have been described, ranging from the coast and mountain areas of Ecuador to Chile, including the upper Amazon Basin of northwestern Peru in western South America; from the lowlands and foothills of eastern Colombia to central Venezuela in eastern South America.

A common Mexican and Central American species, *P. tuberculosus*, described by Wiegmann (1835), has also been reported in the literature from Ecuador, Peru, the Galapagos Islands, and the Greater Antilles. The distribution of this species is Mexican and Central American (Dixon, 1960), and specimens on the mainland and islands of South America to which this name has been misapplied represent populations of *P. reissi*, *P. darwini*, and *P. wirshingi*.

Individual species were studied and described by Wiegmann (1835), Tschudi (1846), W. Peters (1862), Cope (1876, 1877), Werner (1901, 1907, 1910, 1912), and Noble (1924). Short notes on distribution, habitat and taxonomy of mainland South American species were given by Parker (1935), Taylor (1942), Codoceo (1950), Titschack (1951), Yañez (1951), Dixon (1962, 1964a), J. Peters (1967), Donoso-Barros (1966), and Rivero-Blanco and Lancini (1968).

As a group, the mainland South American species were studied by Boulenger (1885) and Werner (1912), both of whom published a key to the arid and tropical American species known at the time. Burt and Burt (1933) published a preliminary checklist of lizards of South America. Wermuth (1965) published a world checklist of the genera, species, and subspecies of the family Gekkonidae, and Vanzolini (1968a) published a paper on the geographic distribution of South American Gekkonidae. Vanzolini (1968b) also published a key and list of Gekkonidae known to occur in Brazil, and included a list of the species of *Phyllodactylus* known to occur in South America. Mechler (1968) published a key, descriptions, and maps for all gekkonids in Colombia.

Some of the latter studies contain errors in species determination, through the uncritical acceptance of publications of earlier workers who did not have

adequate knowledge of the distribution and ecology of the species. With some of these problems in mind, a study of the genus was initiated by one of us (Dixon) in 1957. Recent collections of *Phyllodactylus* by Huey in 1967 and 1968, and by Dixon and Wright in 1968, from the coast and upper Amazon Basin of Peru and an examination of extant syntypes and holotypes of South American species has provided the necessary material to complete this study.

A detailed study of the sympatric relations of *P. kofordi*, *P. microphyllus*, *P. reissi*, and *P. clinatus* will be presented by one of us (Huey) at a later date.

#### TYPE MATERIAL

Of the 19 available names for mainland South American species of *Phyllodactylus*, only nine have extant type material that has been examined by us: *lepidopygus*, *phacophorus*, *reissi*, *inaequalis*, *microphyllus*, *nigrofasciatus*, *magister*, *ventralis*, and *dixonii*.

The remaining 10 typical series are either definitely destroyed or lost. The museums in Hamburg and Dresden were seriously damaged during the fire bombings of the second world war. Among type material destroyed in the Dresden Museum were the nine syntypes of *P. variegatus* and the holotype of *P. baessleri*. The Hamburg Museum lost two syntypes each of *P. abruptereriatus* and *P. guayaquilensis*, and type material (if any existed) of *P. lobensis* (nomen nudum). The syntypes of *P. gerrhopygus*, reported to be housed in the Berlin Museum, are lost (Wermuth, pers. comm.). The holotype of *P. heterurus*, housed in the School of Medicine, University of Chile, was destroyed by a fire in the early 1950's (Capurro, pers. comm.).

Fortunately, Donoso-Barros (1947) was able to examine the type of *P. heterurus* in detail prior to its destruction by fire. However, some of the early type descriptions by Werner (1912) were brief and failed to give a detailed description that could be used to identify his species with certainty. Therefore, our analyses of his original descriptions and our subsequent synonymies based on these descriptions may be in error.

A problem related to the loss of types is knowledge of the exact type locality for some species. Werner (1912) gives the type locality for *P. abruptereriatus* as "probably Brazil." Members of this genus have never been found in Brazil and we assume, as have earlier workers (e.g. Burt and Burt, 1931), that the type series probably came from Ecuador or northern Peru. The type description clearly describes individuals of *Phyllodactylus reissi* Peters in these areas. Tschudi's (1846) original descriptions of *P. lepidopygus* and *P. phacophorus* gave only the type locality for the former species (Chorillos, Peru). The only statement made on the type locality of the latter species was "a wooded region." Werner's (1901) description of *P. baessleri* gave the town of Chanchamayo, Peru, as the type locality. Several towns of that name were located in west central and southern Peru. Most of these towns are sufficiently low in elevation to sustain populations of *Phyllodactylus*, but only two species are known to occur in the above areas, *P. gerrhopygus* and *P. lepidopygus*.

The only known populations fitting Werner's description are found 1600 km NW of the nearest town named Chanchamayo. Therefore, the type locality of *P. baessleri* is presumed to be in error.

These and other problems have been responsible for the misapplication of species names in a number of publications on *Phyllodactylus* over the past 100 years. Consequently, we present the following table of the chronological synonymy of sixty-one specific names proposed for North, Central, and South American species.

TABLE 1

Chronological synonymy of sixty-one specific names proposed for the genus *Phyllodactylus* from North, Central and South America

<i>Date, original name and author</i>	<i>present name</i>
1830 <i>pulcher</i> Gray	<i>pulcher</i>
1835 <i>tuberculosis</i> Wiegmann	<i>tuberculosis</i>
1835 <i>gerrhopygus</i> (Wiegmann)	<i>gerrhopygus</i>
1836 <i>gymnopygus</i> Dumeril & Bibron	<i>gerrhopygus</i>
1846 <i>lepidopygus</i> (Tschudi)	<i>lepidopygus</i>
1846 <i>phacophorus</i> (Tschudi)	<i>lepidopygus</i>
1862 <i>reissi</i> Peters	<i>reissi</i>
1862 <i>spatulatus</i> Cope	<i>pulcher</i>
1862 <i>julieni</i> Cope	<i>julieni</i>
1863 <i>unctus</i> Cope	<i>unctus</i>
1863 <i>xanti</i> Cope	<i>xanti</i>
1869 <i>galapagoensis</i> Peters	<i>galapagoensis</i>
1875 <i>ventralis</i> O'Shaughnessy	<i>ventralis</i>
1876 <i>inaequalis</i> Cope	<i>inaequalis</i>
1876 <i>microphyllus</i> Cope	<i>microphyllus</i>
1877 <i>nigrofasciatus</i> Cope	<i>lepidopygus</i>
1887 <i>martini</i> Van Lidth de Jeude	<i>martini</i>
1889 <i>leei</i> Cope	<i>leei</i>
1892 <i>bauri</i> Garman	<i>bauri</i>
1900 <i>variegatus</i> Werner	<i>lepidopygus</i>
1900 <i>baessleri</i> Werner	<i>reissi</i>
1903 <i>gilberti</i> Heller	<i>gilberti</i>
1907 <i>heterurus</i> Werner	<i>heterurus</i>
1910 <i>mentalis</i> Werner	<i>xanti</i>
1910 <i>guayaquilensis</i> Werner	<i>reissi</i>
1910 <i>lobensis</i> Werner	<i>microphyllus</i>
1912 <i>abrupteseriatus</i> Werner	<i>reissi</i>
1912 <i>barringtonensis</i> Van Denburgh	<i>barringtonensis</i>
1924 <i>magister</i> Noble	<i>reissi</i>
1935 <i>mulleri</i> Parker	<i>ventralis</i>
1935 <i>homolepidurus</i> Smith	<i>homolepidurus</i>
1935 <i>lanei</i> Smith	<i>lanei</i>
1936 <i>delcampi</i> Mosauer	<i>delcampi</i>
1940 <i>magnatuberculatus</i> Taylor	<i>lanei</i>

1940 <i>muralis</i> Taylor	<i>muralis</i>
1940 <i>rutteni</i> Hummelinck	<i>rutteni</i>
1942 <i>darwinii</i> Taylor	<i>darwinii</i>
1942 <i>bordai</i> Taylor	<i>bordai</i>
1942 <i>magnus</i> Taylor	<i>tuberculosus</i>
1952 <i>eduardofischeri</i> Mertens	<i>tuberculosus</i>
1955 <i>wirshingi</i> Kerster & Smith	<i>wirshingi</i>
1960 <i>duellmani</i> Dixon	<i>duellmani</i>
1960 <i>paucituberculatus</i> Dixon	<i>paucituberculatus</i>
1960 <i>insularis</i> Dixon	<i>insularis</i>
1962 <i>underwoodi</i> Dixon	<i>ventralis</i>
1964 <i>davisi</i> Dixon	<i>davisi</i>
1966 <i>angelensis</i> Dixon	<i>angelensis</i>
1966 <i>partidus</i> Dixon	<i>partidus</i>
1966 <i>tinklei</i> Dixon	<i>tinklei</i>
1966 <i>bugastrolepis</i> Dixon	<i>bugastrolepis</i>
1966 <i>santacruzensis</i> Dixon	<i>santacruzensis</i>
1966 <i>apricus</i> Dixon	<i>apricus</i>
1968 <i>palmeus</i> Dixon	<i>palmeus</i>
1968 <i>dixoni</i> Rivero-Blanco & Lancini	<i>dixoni</i>
1970 <i>kofordi</i> new species	<i>kofordi</i>
1970 <i>interandinus</i> new species	<i>interandinus</i>
1970 <i>johnwrighti</i> new species	<i>johnwrighti</i>
1970 <i>angustidigitus</i> new species	<i>angustidigitus</i>
1970 <i>clinatus</i> new species	<i>clinatus</i>
1970 <i>sentosus</i> new species	<i>sentosus</i>
1970 <i>pumilus</i> new species	<i>pumilus</i>

#### MATERIALS AND METHODS

Approximately 1,800 specimens of *Phyllodactylus* were examined from mainland South America. The material is housed in the American Museum of Natural History (AMNH); Academy of Natural Sciences, Philadelphia (ANSP); Berlin Museum (BM); British Museum (Natural History) (BMNH); California Academy of Science (CAS); Escuela Politecnica Nacional, Quayaquil (EPN); Field Museum of Natural History (FMNH); Hamburg Museum (HM); Los Angeles County Museum of Natural History (LACM); Museo de Ciencias Naturales, Caracas (MCNC); Museo de Biología de la Universidad Central de Venezuela (MBUCV); Museum of Comparative Zoology (MCZ); Museo "Javier Prado," Peru (MJP); Museum of Vertebrate Zoology (MVZ); Neuchatel Museum, Switzerland (NM); San Diego Society of Natural History (SDSNH); Senckenberg Museum, Frankfurt am Main (SMFM); Texas Cooperative Wildlife Collection (TCWC); University of Illinois Museum of Natural History (UIMNH); University of Michigan Museum of Zoology (UMMZ); United States National Museum (USNM); private collections of Charles M. Fugler (CMF), and Raymond B. Huey (RBH).

Descriptions of habitat, behavior, ecology, and color notes of living specimens were obtained in the field by Huey during July, August, and September, 1967 and 1968 and by Dixon and Wright during November and December, 1968. Climatological data were obtained from Robinson (1964) and details of the vegetation were obtained from Macbride (1936). Measurements and analysis of squamation were made by methods described by Dixon (1964b). Sex was determined by the presence of cloacal bones and enlarged postanal tubercles in males, or by dissection.

When we present a description of a species, it will describe all individuals except those covered in the sections on variation.

#### GENERAL DESCRIPTION OF THE HABITAT OF WESTERN SOUTH AMERICA

The Andes of western South America divide the coastal countries of Ecuador and Peru into three relatively distinct geographic and biological units: the narrow Pacific coast, the Andes and associated valleys, and the tropical forests of the east. Species of *Phyllodactylus* and other lizard genera such as *Tropidurus*, *Dicrodon*, and *Callopistes* are restricted primarily to the arid coast of western South America and to the northwestern interandean basins of Peru.

The coastal zone, buttressed by the moist Chococoan forests in northern Ecuador (Peters J., 1960), passes south from the thorn scrub and mangrove forests of Ecuador to the barren deserts of Peru and northern Chile. With the exception of a few low passes in northern Peru the Andes to the east form a high barrier generally more than 4,250 meters in areas relevant to discussion.

The deciduous thorn scrub forests extend from the Pacific coast and Andean foothills of Ecuador to the extreme northwestern corner of Peru in the Department of Tumbes, east to the base and foothills of the Andes in the Department of Piura, and then south along the foothills of the Andes into the Department of Lambayeque. Some of the dominant plants of this region include species of *Loxopterygium*, *Caesalpinia*, *Bursura*, *Bombax*, *Capparis*, *Mimosa*, and *Cereus* (Weberbauer, 1936).

The junction of the Ecuadorian thorn scrub and the Peruvian deserts in Tumbes is very narrow and has been attributed to the climatic changes associated with the boundary between the cold waters of the Humboldt Current and the warmer Equatorial Counter Current (Dawson, 1963). The coast of Peru below Tumbes to northern Chile is a barren, arid desert. This desert is not induced by excessively high temperature regimes; rather, it is apparently the result of the aridity associated with the cold Humboldt Current and a rainshadow produced by the Andes (Dawson, 1963; Kendrew, 1961; Murphy, 1948). Rainfall is very low and sporadic throughout much of the area. Most of the water available to plants comes from rivers penetrating the coast from the western slopes of the Andes, high water tables in the Quebradas, and fault zones of northern Peru and fog.

Weberbauer (1936) recognizes two major plant zones in the Peru and Chile deserts. The first runs from Tumbes to a latitude of about 8° south. This area is essentially rainless, except for stormy El Niño years, and extremely barren. Encompassed are such areas as the Sechura Desert in the Department of Piura. Plants tend to be widely scattered and grow as shrubs rather than trees. The substratum is sandy throughout much of the region with a few rocky cerros and the rocky, hard soils of the Quebrada zones. Characteristic features are shifting barchan dunes intermingled with large hummock-like dunes stabilized by *Capparis scabrida* (Koford, 1968). Major plants inhabiting this region include species of *Cryptocarpus*, *Prosopis*, *Capparis*, and *Acacia* (Weberbauer, 1936).

The second zone follows the narrow coast to northern Chile and contains the famous Lomas and *Tillandsia* plant formations. The Lomas are chiefly seasonal carpets of herbs and occasional low trees in areas where the coastal foothills of the Andes rise to heights sufficient to intercept the winter and spring clouds. The increased elevation and lowered temperatures produce considerable condensation in the form of mists making the existence of vegetation possible in an otherwise arid climate. The average annual precipitation recorded in the open is 201 mm for 29 years at Lomas de Lachay in the Department of Ancash (elevation 450 m) compared with only 46 mm for 18 years at nearby Lima (Holdridge, 1964). Major Lomas plants include species of *Aniantum*, *Bowlesia*, *Astrephia*, *Sicyos*, and abundant lichens, mosses and ferns (Weberbauer, 1936).

Unlike the Lomas, the *Tillandsia* association is not dependent on seasonal changes and appears to survive upon atmospheric moisture. *Tillandsia* is most often found on the leeward side and at a lower elevation of hills covered with Lomas vegetation, in drier valleys inland from the coast, and along the coastal plain where no other plants survive. There are large expanses of the deserts where even *Tillandsia* is not found and one is confronted only with barren sand reaching from the Pacific tides to several thousand feet up the Andean foothills.

The deserts of northern Chile extend south to a latitude of about 27°. Extremely barren and arid, much of these deserts are colonized only by *Tillandsia*. South of 27°, the desert is bordered by brush and savanna (Mann 1960). To the east the height of the Andes has apparently prevented invasion by species of *Phyllodactylus* into the *Larrea* deserts of western Argentina.

The northern interandean basins, lying between latitudes 4° to 6° south and longitudes 78° to 80° west (Weberbauer, 1936), are loosely connected with the Peruvian coast by the relatively low passes in the Department of Piura (e.g. Porculla Pass at 2,160 m). These low passes have served as an invasion route for species of *Phyllodactylus* and other species of coastal lizards into a portion of the Amazon drainage.

Surrounded by the higher Andean passes to the north and south and by the Amazonian forests to the east, the interandean basins are limited in extent

and similar in appearance to the coastal foothills of northwestern Peru. The general aridity of these basins, less pronounced than the coast, apparently results from a rain-shadow produced by the eastern chain of the Andes cutting the basins off from the Amazonian moisture.

The interandean basins vary considerably in species composition and physiognomy but are somewhat uniform in vegetative cover with cacti and deciduous plants covering the basin floors except along water courses. The higher slopes are generally matted with dense growths of woody plants (Weberbauer, 1936).

Further details of the habitat of Ecuador, Peru, and Chile can be obtained from Weberbauer (1936), MacBride (1936), Tosi (1960), Koepcke, M. (1954), Koepcke, H. (1961), Dawson (1963), Murphy (1948), Mann (1960), Robinson (1964), Kendrew (1961), Donoso-Barros (1966), and Verdoorn (1945).

Details of the arid and semiarid habitats of Colombia and Venezuela may be obtained from Ruthven (1922) and Shelford (1926).

#### KEY

The following key is based upon approximately 2,000 specimens of 15 species of *Phyllodactylus* from mainland South America.

The size, shape, and number of scales in the median row beneath the tail is variable within some species but it is generally consistent if a careful examination of the entire, original tail is made. Regenerated tails do not have tubercular scales even if they were present on the original tail. In some instances, the width of the scales of the median row beneath the regenerated tail may be about the same size as those of the original tail.

#### KEY TO THE SPECIES OF *PHYLLODACTYLUS* OF MAINLAND SOUTH AMERICA

- 1a. Preanal scale single, greatly enlarged, 10-20 times larger than belly scales ..... 2
- 1b. Preanal scales small, equal in size to other belly scales ..... 4
- 2a. Tail smooth, without enlarged rows of lateral tubercles ..... 3
- 2b. Tail keeled, with four rows of lateral tubercles (northern Chile) *heterurus*
- 3a. Digits short, fourth toe lamellae 12-15 (13.1), terminal lamellae large (southern Peru to northern Chile) ..... *gerrhopygus*
- 3b. Digits long, fourth toe lamellae 15-20 (16.8), terminal lamellae very small (coastal south central Peru) ..... *angustidigitus*
- 4a. Dorsal tubercles small, rounded, sometimes slightly keeled, not arranged in regular rows; ventral surface of tail with all scales of equal size... 5
- 4b. Dorsal tubercles large, trihedral, arranged in regular rows; ventral surface of tail with or without enlarged scales in median row ..... 6
- 5a. Terminal lamellae of digits much enlarged, most of claw hidden when viewed from above; nostril not swollen (extreme northwestern Peru and probably southwestern Ecuador) ..... *inaequalis*

- 5b. Terminal lamellae of digits very small, most of claw exposed when viewed from above; nostril greatly swollen (central to extreme northwestern Peru) . . . . . *microphyllus*
- 6a. Dorsal surface of tibia without enlarged tubercles . . . . . 7
- 6b. Dorsal surface of tibia with enlarged tubercles . . . . . 9
- 7a. Dorsal surface of tibia with very small granular scales; ventral surface of tail with all scales of median row enlarged, rectangular (northwestern Peru) . . . . . *clinatus*
- 7b. Dorsal surface of tibia with round, elevated scales; ventral surface of tail with or without some enlarged, rounded scales in median row . . . 8
- 8a. Tubercles in paravertebral row from head to base of tail 44-53; no scales on ventral surface of tail enlarged (coastal foothills of central Peru) . . . . . *lepidopygus*
- 8b. Tubercles in paravertebral row from head to base of tail 65-81; some scales in median row of ventral surface of tail enlarged, rounded (Maranon Basin, northwestern Peru) . . . . . *interandinus*
- 9a. Tubercles present on dorsal surface of forearm . . . . . 10
- 9b. Tubercles absent on dorsal surface of forearm . . . . . 13
- 10a. Terminal lamellae of digits much enlarged; claw mostly hidden when viewed from above; ventral surface of tail with all scales of median row enlarged, rectangular . . . . . 11
- 10b. Terminal lamellae of digits small, narrow; claw mostly exposed when viewed from above; ventral surface of tail with a few scales of median row enlarged, rounded (Lima, Peru) . . . . . *sentosus*
- 11a. Large species, average snout-vent length of 64 mm; 19-26 paravertebral tubercles between axilla and groin . . . . . 12
- 11b. Small species, average snout-vent length of 38 mm; 16-21 paravertebral tubercles between axilla and groin; (northwestern Peru and probably southwestern Ecuador) . . . . . *kofordi*
- 12a. Distal one-third of tail with at least two or more rows of tubercles; scales across venter 18-24; (northern Venezuela and Colombia) . . . *ventralis*
- 12b. Distal one-third of tail without tubercles; scales across venter 26-28; (central Venezuela) . . . . . *dixoni*
- 13a. Scales of supraocular region largest of interorbital scales; enlarged tubercles usually present on dorsal surface of thigh; maximum snout-vent length 51 mm . . . . . 14
- 13b. Scales of supraocular region smallest of interorbital scales; enlarged tubercles usually absent on dorsal surface of thigh; maximum snout-vent length 75 mm (northwestern Peru and west central Ecuador) . . . *reissi*
- 14a. Scales on proximal one-fourth of tail homogeneous; internasals usually separated along median edges (Huancabamba Basin, northwestern Peru) . . . . . *johnwrighti*
- 14b. Scales on proximal one-fourth of tail heterogeneous; internasals usually in contact along median edges (west central Ecuador) . . . . . *pumilus*

## SPECIES ACCOUNTS

***Phyllodactylus heterurus* Werner**

*Phyllodactylus heterurus* Werner 1907. Ann. Univ. Chile, 121:149.

*Holotype*. Adult male, (lost in a fire), collected by C. Reiche 1902. Type-locality. Oasis de Pica (Desierto de Tarapaca), Department of Tarapaca, Chile.

*Definition and Diagnosis*. This species is known only from the holotype that was destroyed by a fire. *Phyllodactylus heterurus* is a small gecko with a maximum snout-vent length of 38 mm; dorsal surfaces of head and body smooth, without tubercles; tail with four rows of tubercles, two on each lateral surface; preanal plate present; terminal lamellae of digits moderately large.

This species is distinguished from all other species of *Phyllodactylus* except *gerrhopygus* and *angustidigitus*, by the presence of an enlarged preanal plate; from *gerrhopygus* and *angustidigitus* by the presence of four rows of tail tubercles, with anteriorly projecting tips.

*Description of holotype*. Since the holotype is no longer extant, we submit a translated version of Werner's (1907) original description: Head ovoid, very much longer than wide; snout longer than the distance from the posterior corner of eye to ear and two times the length of eye; frontal region not concave; ear opening small, horizontal and elliptical; body decidedly thin; inferior aspect of digits similar on anterior and posterior limbs, with wide plates whose distal ends are visibly wider than their proximal portion; dorsal aspect of body with small scales that are ovoid, smooth, somewhat convex; rostral scales pentagonal, somewhat concave posteriorly, with a groove beginning on posterior border; nasal opening surrounded by rostral, supralabial and three nasals; nine supralabials and seven infralabials; nasal (internasals) scales separated on median line by an azygous scale; mental two times longer than wide with posterior border rounded, lateral sides parallel; chin without enlarged scales (postmentals absent); scales in gular region very small; ventral scales small, smooth, circular and overlapping; tail cylindrical, with transverse series of robust, conical tubercles whose points are directed anteriorly.

Color and pattern on dorsum lead gray with black irregular spots and lines; lines unite on dorsal side to form transverse bands with obscure outlines; tubercles on tail brick red.

Total length 71 mm, head 12 mm in length by 7.5 mm in width; tail 30 mm in length.

*Comments*. Donoso-Barros (1947) redefined the holotype prior to its destruction and further distinguished the species from *gerrhopygus* by its large, round eye, ovoid head with sharply pointed snout, and gave preservation colors that differed from those given by Werner (1907).

As far as we can determine, no additional specimens have been taken since 1902, therefore data are not available on its habits, habitat, or natural history.

*Distribution*. Known only from the type locality (fig. 5).

**Phyllodactylus gerrhopygus** (Wiegmann)

*Diplodactylus gerrhopygus* Wiegmann 1835. Nova Acta Leop.-Carol., 14:242.

*Phyllodactylus gymnopygus* Dumeril and Bibron 1836. Erp. Gen., 3:394.

*Phyllodactylus gerrhopygus*, Boulenger 1885. Cat. Liz. Brit. Mus., 1:95.

*Phyllodactylus inaequalis*, (part) Burt & Burt, 1931. Bull. Amer. Mus. Nat. Hist., 61(7):250.

*Holotype*. Lost, formerly in Berlin Museum, collector and date of collection unknown. Type-locality. Chile.

*Definition*. An average size gecko with a maximum known snout-vent length of 56 mm; large preanal plate present; dorsal tubercles absent; tibia and femur tubercles absent; ear denticulate on anterior and posterior margins; median row of scales beneath tail equal in size to other ventral scales; tail about 50 percent of total length; mental much longer than wide and postmentals absent; terminal lamellae of digits large, longer than wide; claws of digits large, usually extending slightly beyond tip of terminal lamellae; dorsal markings present or absent, if present, consisting of broad bands or blotches; tail usually banded (fig. 8a).

*Diagnosis*. This species may be distinguished from all other species, except *angustidigitus* and *heterurus*, by the presence of an enlarged preanal plate; from *heterurus* by the absence of enlarged lateral tubercles on the tail; from *angustidigitus* by the larger toe pads and shorter digits.

*Description*. Rostral about as high as wide, its dorsal edge "M" shaped, with a short median vertical groove; two internasals, somewhat triangular in shape, their median edges not in contact but separated by three azygous scales (snout granules); internasals bordered posteriorly and medially by small granules and postnasal of each side; nostril surrounded by rostral, labial, internasal, and two postnasals; nostril area somewhat swollen by elevation of postnasals and internasal; first supralabial in broad contact with ventral edge of nostril; moderate depression between internasals, slight depression in frontal region; scales in posterior loreal region about twice the size of midorbital scales; eye large, its diameter contained in snout length about 1.5 times; eyelid with two rows of granules and one larger outer row of scales, the last three to six are pointed; diameter of ear contained in eye diameter about 2 times; ear opening denticulate on anterior and posterior margins, rear of head granular; usually 8 supralabials and 5 or 6 infralabials to point below center of eye; mental straight-edged, rounded posteriorly, about 2.5 times longer than wide; postmentals absent, mental bordered by small chin scales.

Dorsum without enlarged tubercular rows, scales subequal in size, somewhat flattened, about half size of midventral scales; latero-ventral scales smaller than dorsal and ventral scales; very large preanal plate (scaleless), surrounded by about 25 ventral scales; preanal plate about 20 to 30 times larger than adjoining ventral scales; enlarged postanal scales on each side, somewhat flattened.

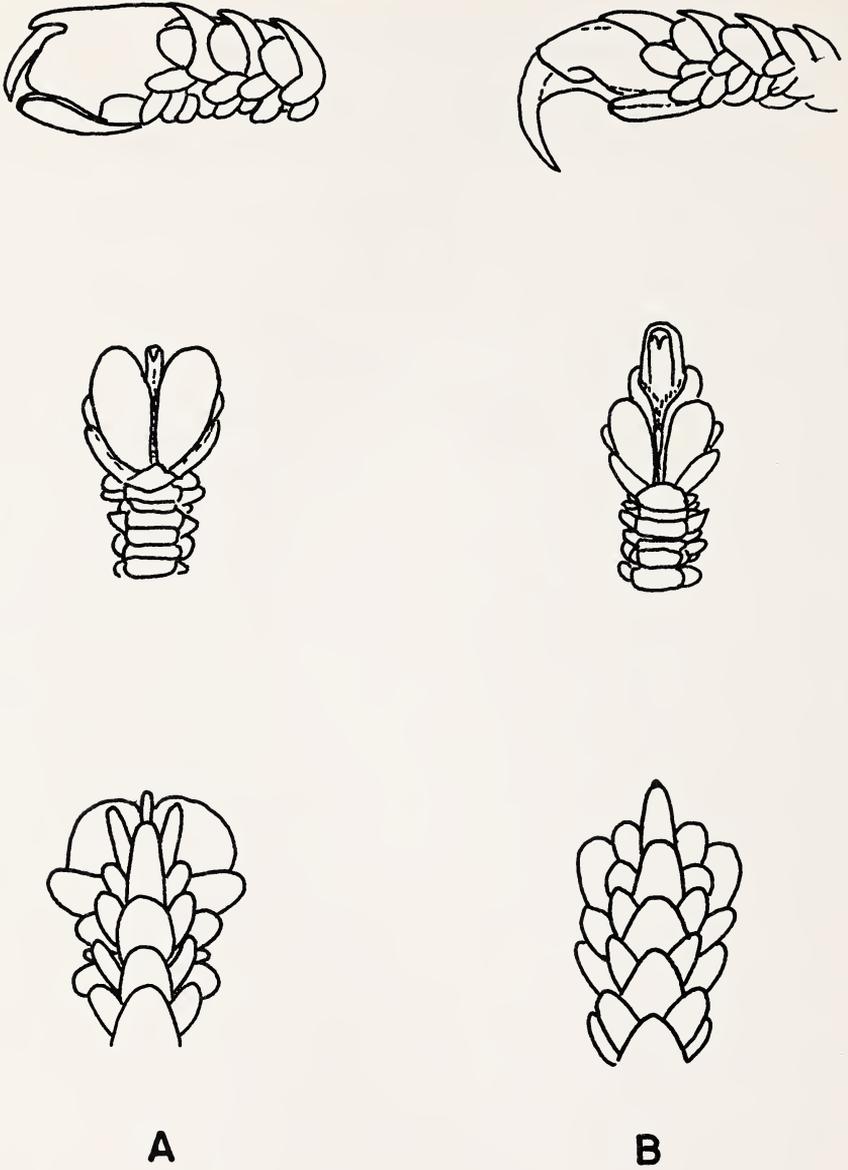


Figure 1. Lateral, ventral and dorsal view of the distal end of the fourth toe of (A) *P. gerrhopygus* and (B) *P. angustidigitus*.

Dorsal surface of upper arm with flattened scales, forearm with larger, slightly elevated scales; dorsal surface of thigh and lower leg with flattened, but slightly elevated scales; claw moderately exposed when viewed from below; terminal lamellae twice as long as wide, somewhat reduced in size with claw extending beyond tip of terminal lamellae; tail with all scales of ventral surface of equal size, scales of dorsal surface smaller than those of ventral surface.

Color in alcohol: ground color tan, with light orange tint; dorsum with four broad light brown bands with undulating edges bands composed of suffusion of brown and tan scales intermixed (freckled), with tan interspaces slightly wider than dark bands; upper and lower arms and legs with faint brownish bands; tail with nine bands similar in color to dorsal bands, with yellowish tan interspaces; posterior part of head and nape with reticulating brown lines on ground color; top of head spotted with brown; brownish stripe from nostril to eye; brownish reticulating lines between eye and ear; labials faintly flecked with dark brown; ventral surfaces of head, body, and tail immaculate white.

*Variation.* Snout-vent length of young adult and adult males varies from 32 to 56 mm (43.9), females from 32 to 55 mm (42.8), juveniles from 25 to 31 mm (28.9), and males and females together average 42.7 mm; postmentals absent in 96.4 percent of sample; three of 98 specimens have two postmentals, one specimen had one postmental on one side, none on the other side; mental much longer than wide, extending posteriorly beyond the tips of adjoining labials; number of transverse chin scales immediately following and touching mental vary from 3 to 8 (4.6); scales across midorbital region vary from 13 to 20 (15.9), across the snout at level of third labial from 12 to 18 (14.7); number of scales bordering internasals vary from 6 to 10 (7.7), internasals always separated along median line by 1 to 3 granules; transverse row of scales across venter vary from 20 to 30 (24.7), longitudinally 64 to 76 (69.1); preanal shield large, without scales, generally 20 to 30 times larger than adjoining scales; scales between eye and nostril vary from 8 to 12 (10.4); number of lamellae beneath fourth toe vary from 12 to 15 (13.1); all scales of dorsum, limbs, and tail subequal in size, relatively smooth, and slightly elevated to some extent; supralabials vary from 7 to 9 to a point below center of eye, 8 being most common; dorsal bands (if present) number 4 to 6, tail bands 6 to 9.

Color pattern consists of body bands or blotches that tend to appear freckled with tan and brown scales intermixed, but occasionally some specimens are uniform tan or light brown; tail usually banded; belly usually immaculate white; parietal region and lateral area of head behind ear usually with reticulated brown lines on ground color; limbs usually faintly banded with brown.

*Habitat and natural history.* Of 98 individuals examined, only five were collected by one of us. One of these was collected during the day from beneath

a piece of tin in an open sand dune area where some vegetative cover was present. Four individuals were found active after dark along the base of sand dunes approximately 150 m from a sand and rock rubble beach, and approximately 50 m from a ravine where some plant cover was present. The dunes were approximately 50 to 75 m in height and without vegetation. Silverfish, beetles, and spiders appear to be the only food items available in the area where the five specimens were taken.

The absence of individuals along the beach might be explained by the presence of hundreds of ghost crabs occupying the intertidal zone.

One specimen in the University of California Museum of Vertebrate Zoology with field data was taken from beneath a stone in a sandy wash. Garman (1875) mentions that his specimens were found beneath stones in a sandy plain near Arequipa, Peru.

Through the courtesy of Stanley W. Taft, a Peace Corps Volunteer from New Mexico State University, we were able to obtain some habitat data on *P. gerrhopygus* from the San Juan de Marcona area of Peru. The San Juan Marcona area is approximately 157 airline km SSE of Ica, at an elevation of 0 to 150 m. The general terrain is rolling sand hills with sandy beaches and large outcroppings of a red limestone-like formation. Taft (*personal communication*) indicated that large hematite deposits were present in the area which probably give the red color to the sandy areas. The only vegetation of the immediate area consisted of a few scattered *Capparis* sp. shrubs.

A series of *P. gerrhopygus* collected by Taft were taken from rock walled terraces, outside walls of houses, and from sidewalks. Taft indicated that the geckos were occupying small holes made by the absence of plaster or mortar between the rocks and cement blocks of terrace walls and houses. All of his specimens were collected at night, and two were taken from a terrace wall near a sodium vapor light. Taft stated that several were seen along the sandy beaches at night but were not collected.

From an examination of living and preserved females, there appears to be only one egg laid per clutch. Nests of this species have not been found under natural conditions.

*Distribution.* This gecko apparently occupies a variety of habitats along the desert coast, foothills, and mountains from central Peru to northern Chile between the elevations of sea level and 2,750 m (fig. 2). We have examined 98 specimens from the following localities: CHILE. *Tarapaca*: Arica UMMZ 11576; 3 mi S Arica AMNH 65343-59. 50 km from Iquique MCZ 56247. Pica FMNH 6327-29, 9984. Pintados FMNH 6326. Putre FMNH 6330, 6331(3), 6332-41. PERU. *Arequipa*: Arequipa AMNH 22238, 36525-26, FMNH 3577(4), 43769. 12 mi SE Camana CAS 84769. Chucarapi FMNH 34236-37. 16 km S. La Joya MVZ 84636. Mollendo CAS 84760-68, FMNH 34248(4). Tambo FMNH 4005-06. Vitor FMNH 34179. Yura FMNH 34047(9), 34205(5), 34182-83, 34190. *Ica*: 1 km NNW Jaguay LACM 48465-66, TCWC 28064-65; Marcona TCWC 27874-78. 6.3 km ESE Pozo

Santo TCWC 28063. San Juan Port (Salamanquejo) SDSNH 31091-92.  
 Lima: Isla San Lorenzo USNM 17542 (probably in error).

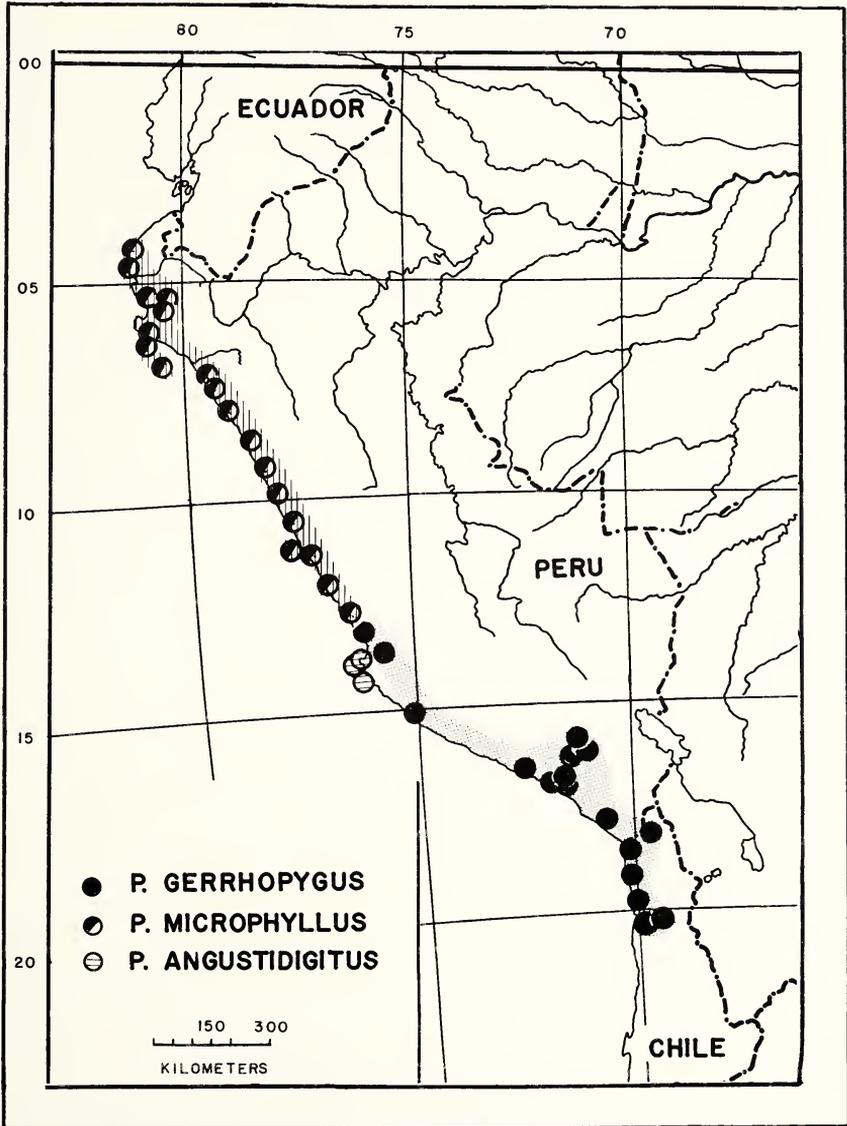


Figure 2. Distribution of *P. gerrhopygus*, *P. microphyllus* and *P. angustidigitus* in western South America.

***Phyllodactylus angustidigitus* sp. nov.**

*Phyllodactylus gerrhopygus*, (part) Burt and Burt 1930; Proc. U. S. Nat. Mus., 78(2849):4.

*Holotype*. Adult male, TCWC 27915, collected by James R. Dixon and John W. Wright, 11 November 1968. Type locality. One km S new port of Pisco, northeast side of Paracas Peninsula, 19 km by road south and west of Paracas, Department of Ica, Peru, sea level.

*Definition*. A moderate-sized gecko, maximum known snout-vent length of 57 mm; large preanal plate present; scales of head, body, tail, and limbs uniform in size; tubercles absent; no enlarged scales beneath tail; tail 48 to 52 percent of total length; mental much longer than wide, without enlarged postmentals; terminal lamellae very small, claw greatly extended beyond tip of terminal lamellae; fourth toe lamellae numerous (15 to 20) (fig. 8a, 8b).

*Diagnosis*. *Phyllodactylus angustidigitus* differs from all other species of *Phyllodactylus* except *gerrhopygus* and *heterurus*, by having an enlarged preanal plate; from *heterurus* by absence of tail tubercles and small terminal lamellae; from *gerrhopygus* by small terminal lamellae and high number of fourth toe lamellae, 15 to 20, rather than 12 to 15.

*Description of holotype*. Rostral about twice as wide as high, its dorsal edge with a broad "M" shape, with dorsal vertical groove one-half depth of rostral; two internasals, somewhat rounded, their median edges separated by two granules, bordered posteriorly by two granules and postnasal of each side; nostril surrounded by rostral, labial, internasal, and two postnasals; first labial in narrow contact with ventral edge of nostril; shallow depression between internasals, no depression in frontal region; 10 scales on line between nostril and eye; scales in posterior loreal region about twice size of midorbital scales; 15 scales across snout at level of third labial, 14 scales at anterior edge of orbits, 18 midorbital scales; eye large, its diameter contained in snout length 1.7 times; eyelid (brille) with one row of granules and one larger outer row of scales, last three to four are pointed; diameter of ear contained in diameter of eye 2.3 times; ear opening denticulate on posterior margin; all dorsal scales small, smooth, slightly convex; seven supralabials and six infralabials to point below center of eye; mental with parallel sides, about 2.5 times longer than wide, bordered posteriorly by six chin scales; enlarged postmentals absent; dorsum with 75 granules and scales around body; venter with 29 scales across belly, from throat to vent 79; postanal tubercles number four on one side, three on opposite side; dorsal surfaces of limbs similar to dorsum; lamellae formula for hand 7-11-12-13-11, foot 7-12-16-18-16; claw completely visible when viewed from below; terminal lamellae very small, not much wider than width of fifth lamella counted from base of digit.

Measurements in mm; snout-vent length 53.5, axilla-groin length 25.8, length of leg 24.0, length of arm 18.0, length of tail 55.0, length of head 13.3, depth of head 6.2, width of head 10.5, length of snout 5.0, diameter of eye 2.9, diameter of ear 1.2, distance from eye to ear 3.8.

Color in life: ground color yellowish tan; dorsum with fine network of thin, dark brown, reticulating lines, broken at midbody by median stripe of ground color, bordered on each side by dark brown line; paravertebral lines begin at shoulder and terminate at level of groin; arm with four light brown bands with interspaces of ground color; lower part of leg with three indistinct light brown bands; upper part of thigh with faint indication of bands with irregular edges; tail with 11 broad, brownish black bands that contain light brown diffuse spots within their borders, interspaces ground color, about one-third width of dark bands; head with fine network of light brown, reticulating lines; diffuse brownish black stripe from nostril to eye; iris of eye blue gray with black and silver flecks; ventral surfaces dirty white, with grayish wash across chest and throat.

*Variation.* Snout-vent lengths of young adult and adult males vary from 41 to 57 mm (50.3), females from 37 to 54 mm (47.8), juveniles from 30 to 36 mm (32.8), and males plus females average 48.7 mm; postmentals absent in 99.3 per cent of sample, two of 254 individuals had three enlarged postmentals; number of chin scales immediately following and touching mental vary from 3 to 8 (5.8); scales across snout at level of third labial vary from 13 to 17 (15.1), across midorbital region 16 to 20 (18.2); internasals separated by small granules in 99.5 per cent of sample; scales bordering internasals vary from 7 to 10 (8.7); scales across venter vary from 23 to 28 (25.6), from throat to vent 64 to 70 (67.5); enlarged preanal shield without scale covering, 20 to 25 times larger than surrounded scales; scales between eye and nostril vary from 10 to 12 (11.0); number of fourth toe lamellae vary from 15 to 20 (16.8).

Ventral color generally uniform dirty white with some grayish wash on chest and throat; dorsal coloration highly variable, from almost uniform wash of yellowish tan to broad, dark brown bands; majority of individuals with some form of dark dorsal reticulations or bands, usually heavily suffused with ground color; tail generally banded, but width of dark bands and light interspaces highly variable; regenerated tails either near black with light areas or ground color with dark flecks; ground color variable, from light tan to very dark grayish brown.

*Comment.* Since populations of *angustidigitus* appear to be closely related to *gerrhopygus*, the following statement of our ideas on the evolutionary trends in this population emphasizes its rate of speciation. The Paracas Peninsula was apparently an island, probably as late as the Pleistocene, and within recent times has become connected to the mainland. The attributes of *angustidigitus* populations on Islas Sangallan and Viejas are identical with those of the Paracas Peninsula, lending some support to this idea. The original invasion of the islands by prototypes of a *angustidigitus*-like population may have occurred by rafting, or by land invasion while the land masses were connected early in the formation of the continental shelf.

The islands and peninsula populations are presently restricted in distribu-

tion to the narrow shell and rubble beaches probably due to cover and food availability. The adaptations for living in the shell and rubble resulted in the reduction of the size of the terminal lamellae and increase in the exposure of the claw as a means of walking and digging in this environment. The longer toe length affords better traction on a shell and rubble substratum. The large terminal lamellae adapted to sand or a scansorial habit are unsuited for life on a shell or rubble beach.

The presence of a few *angustidigitus* living along a mud beach towards the southeast part of the peninsula where it connects with the mainland and also two individuals found in beach dunes on the mainland a few kilometers away may indicate a recent invasion of the mainland by this species. This may be due, in part, to the great density of the population now occupying the shell and rubble beaches. Density dependent factors related to population pressure may be forcing individuals farther away from their preferred habitat. Hence, a few hardy individuals are surviving in a marginal habitat which is generally unfit for the population as a whole.

An individual of *P. gerrhopygus* was found 25 kilometers from the easternmost record of *P. angustidigitus*, with no indication of intergradation or hybridization between the two species. Thus some period of genetic isolation of the peninsular population has allowed *angustidigitus* to evolve through natural selection.

*Habitat and natural history.* This species is apparently restricted to the narrow shell and rubble beaches of the Paracas Peninsula and its associated islands. Of 241 specimens taken from the east side of the peninsula only three were found more than 10 m from the storm tide zone. One was found beneath a stone at the edge of a bluff approximately 20 m from the ocean and two were found about the same distance away on a small granite hill covered with a thin layer of sand. There are no macroscopic plants on the peninsula and no surface water. Away from the beach the only physical cover consists of a few outcrops of granite and small amounts of condensed salt forming a hard surface crust. The only food items available appear to be silverfish, amphipods, and spiders that live in beach debris of the storm and intertidal zones. The paucity of food and cover elsewhere on the peninsula may account for the concentration of individuals along the storm and intertidal zones. A total of 157 individuals were taken along a 100 m stretch of shell beach in one evening between the hours of 8:00 and 9:30 p.m.

Individuals of this species emerge from cover soon after dark, but they seem to be most abundant two to three hours following darkness. Several individuals were observed emerging from beneath dried seaweed and shell debris about 9 p.m. During the day individuals were found beneath the carcasses of dead birds, dried seaweed, and assorted trash cover. Seven specimens were found along a narrow mud beach where the only retreat consisted of cracks in a vertical mudstone cliff. All specimens were found in cracks one

to two meters above the mud beach. The only food items observed were a few amphipods under damp seaweed on the beach and pseudoscorpions in cracks along the mudstone cliff.

Wherever the beach was composed principally of sand, only a few individuals of this species could be found. These were taken along the base of cliffs bordering the beach even though there was considerable storm debris near the beach. The near absence of geckos along these stretches of beach may be due to the great abundance of ghost crabs occupying the storm and intertidal zones of these areas. Crabs were not observed feeding on geckos but their nocturnal activity corresponded with that of the geckos, and the crabs may have been possible predators.

When disturbed, the majority of geckos attempted to escape by running towards the cliffs above the beach or hiding beneath shell debris. However, on two occasions individuals ran into the ocean. One immediately turned and made its way back to shore while the other swam a few meters out to sea. The latter individual, apparently tired, spread its limbs horizontal to the body and allowed wave action to return it to shore.

A few individuals were observed climbing boulders and cliffs during their nocturnal activities. Their actions were slow and deliberate and when disturbed, frequently fell off the surface in an attempt to escape. They seem to have difficulty in clinging to vertical surfaces and any rapid movement on their part dislodges their hold on the surface. The absence of large terminal lamellae normally found in scansorial species is a probable factor in their inability to move rapidly on vertical surfaces.

Body temperatures were taken from several individuals during their nocturnal activities and found to be closely associated with the substratum temperature, varying approximately  $0.5^{\circ}\text{C}$  above or below the latter temperature.

This species appears to lay only one egg at a time. All gravid females examined contained one large developing egg and those confined in captivity laid only one egg.

*Distribution.* This species is apparently confined to the narrow shell and rubble beaches of the Paracas Peninsula and associated islands of Peru although a few individuals may be found on the periphery of the former area (fig. 2).

Specimens (246) have been examined from: *Ica*: Islas Sangallan USNM 38570; Islas Viejas SDSNH 31093-94; Lagunillas (Gallinazo) Bay FMNH 34337-40; Paracas Peninsula AMNH 36505-07, 36510-12; 7.2 km SW Paracas LACM 48705, TCWC 27983; 1 km S Puerto Pisco (new) LACM 48593-627, TCWC 27915, 27944-79; 3 km S Puerto Pisco (new) LACM 48632-704, 48706, TCWC 27984-8062; 7 km S Puerto Pisco (new) LACM 48628-31, TCWC 27980-82.

**Phyllodactylus inaequalis** Cope

*Phyllodactylus inaequalis* Cope 1876. Jour. Acad. Nat. Sci., Phila., ser. 2, 8:174.

*Holotype*. Adult female, ANSP 11365, collected by James Orton in 1867-1868. Type-locality, from Pacasmayo, Department of Lambayeque, Peru.

*Definition*. A small gecko with a maximum known snout-vent length of 42 mm; tibia and femur tubercles absent; ear denticulation absent; tubercles on rear of head absent; median row of scales below tail equal in size to adjoining scales (occasionally widened in some specimens); enlarged preanal plate absent; enlarged dorsal rows of flattened tubercles usually absent at midbody (occasionally two rows present); tail about 45 per cent of total length; tail tubercles absent; terminal lamellae of digits distinctly widened and truncate; ground color light gray with dark gray bands usually present; tail usually banded with dark gray on light ground color; belly brilliant white to light yellow (fig. 12b).

*Diagnosis*. *Phyllodactylus inaequalis* may be distinguished from *gerhopygus*, *angustidigitus*, and *heterurus* by the absence of an enlarged preanal plate; from *clinatus*, *dixonii*, *internadinus*, *pumilus*, *johnwrighti*, *kofordi*, *lepidopygus*, *sentosus*, *reissi*, and *ventralis* by having less than 10 dorsal rows of enlarged, flattened tubercles at midbody; from *microphyllus* by its smaller maximum snout-vent length (42 mm rather than 56 mm), and by having the terminal lamellae of the digits distinctly enlarged and truncate with claw mostly hidden rather than very small terminal lamellae with claw mostly exposed.

*Description*. Rostral twice as wide as high, its dorsal edge almost straight with a short median vertical groove; internasals somewhat rounded, their median edges in narrow contact, bordered posteriorly by small granules and postnasal of each side; nostril surrounded by rostral, labial, internasal and two postnasals; first supralabial in narrow contact with ventral edge of nostril; shallow depression between internasals, slight depression in frontal region; scales in posterior loreal region about two to three times larger than scales in midorbital region; eye large, its diameter contained in snout length about 1.4 times; eyelid with two rows of granules and one large outer row of scales, last three to five are pointed; diameter of ear contained in eye diameter four times; ear opening small, scales on anterior edge rounded, subequal, those on posterior margin rounded but with elevated scales lying within the ear opening; rear of head granular, without larger intermixed tubercles; six to seven supralabials and five to six infralabials to a point below center of eye; mental bell-shaped, longer than wide, bordered posteriorly by two postmentals; postmentals wider than long, their median edges in narrow contact, followed by transverse row of granular scales.

Distal one-third of dorsum with none to 10 indistinct rows of slightly

enlarged, flattened tubercles, paravertebral row of each side reach to shoulder in some individuals; paravertebral rows usually separated from each other by four rows of granules; each tubercle of enlarged dorsal series separated from preceding tubercle by two to four granules; postanal tubercles number four on each side, distinct and elevated.

Dorsal surface of upper arm with flattened, rounded scales, forearm with slightly smaller scales that are rounded and slightly elevated; dorsal surface of thigh and lower leg with rounded, slightly elevated scales; claw short but visible when viewed from below; terminal pad large, longer than wide with somewhat rounded edges; about every other median scale on ventral surface of tail slightly widened; cloacal sacs with external plicate lips.

Color in alcohol: ground color light gray; dorsum with dark gray transverse bands, somewhat broken along midline of back; width of bands equal to ground color interspaces; dorsal bands somewhat diffuse with white granules intermixed with few black granules; lateral area of body with suffusion of intermixed white, gray, and black granules; arms and legs with suffuse spotting of gray, brownish gray, and black granules and scales, without definite pattern; tail with five dark gray bands, twice as wide as whitish interspaces; top of head with suffusion of dark gray and ground color, no definite pattern; dark gray stripe from nostril through eye, over ear, to just posterior of arm insertion, bordered above and below by pale whitish line from internasal to just posterior of ear; belly brilliant white.

*Variation.* Snout-vent length of subadult and adult males varies from 33 to 40 mm (37.0), females from 30 to 42 mm (36.8), juveniles from 19 to 28 mm (23.0), males and females together average 36.9 mm; two postmentals in all specimens examined; postmentals contacting first labial in only 54.6 per cent of the sample, first and second labials in 22.7 per cent, and no labials contact in 22.7 per cent; number of transverse scales immediately following the postmentals vary from 7 to 10 (8.3); scales across the midorbital region range from 20 to 22 (20.8), across the snout at level of third labial 20 to 24 (21.3); number of scales bordering internasals vary from 7 to 8 (7.3) with an azygous scale separating the internasals in 3 to 59 specimens; transverse row of scales across belly vary from 26 to 32 (29.4), longitudinally 55 to 62 (58.4); scales on a line between nostril and eye vary from 11 to 12 (11.6); lamellae beneath fourth toe vary from 10 to 12 (10.7); enlarged rows of dorsal tubercles scarcely evident at midbody, none present in seven specimens, two rows present in four specimens; dorsal tubercular rows more evident across rump and base of tail; rows of tubercles across base of tail vary from four to eight, six being most common.

Color pattern fairly consistent, with shades of gray ground color and dark gray bands somewhat variable; bands may be straight or slightly undulating; all have dark grayish brown spot in center of parietal area; dark head stripe from nostril to arm in seven specimens, to anterior third of body in

three, to ear in one; body bands (if present) number 4 to 6, five being most common; tail bands (if present) number 6 to 7 in about equal numbers; tail bands generally fade towards distal fourth of tail.

*Comments.* (See comments under *Phyllodactylus microphyllus*.)

*Habitat and natural history.* *Phyllodactylus inaequalis* principally inhabits the desert foothills of northwestern Peru. Specimens have been taken in a variety of foothill localities where the vegetation may be classified as very sparse to dense.

The Cerro Amotape area rises out of the northern end of the Sechura Desert and is contiguous to the northeast foothills of the western chain of the Andes. This area is moderately barren with exfoliating granite boulders and abundant cacti, but the vegetation is less dense than other foothill localities to the east. Three specimens were obtained in a dry wash on the south slope of the cerro where scattered small shrubs were present.

The Las Lomas area lies at the foot of the Andes and contrasts with the Cerro Amotape region in having more dense vegetation, principally thorn scrub with scattered larger trees. One lizard was found foraging on the ground beneath small leafless shrubs.

The Abra de Naupe area lies at the foot of the Andes south and east of the Las Lomas region. This region consists of low hills composed of weathering granite (nonexfoliating) with scattered cacti, mesquite, acacia, and small amounts of grass. One specimen was found during the day beneath a rotting cactus.

The Pacasmayo area (type locality) lies near the base of the Andes where the southern end of the Sechura Desert meets the Jequetepeque River. The vegetation is very sparse, consisting of mesquite groves along the river and a few cacti on the foothill slopes. A few individual plants of *Capparis* sp. occur in sandy flats at the base of the foothills. Seven individuals were taken at dusk from a flat area of hardpan soils at the base of the foothills on the north side of the Jequetepeque River. All seven specimens were found beneath such trash items as cardboard, cement sacks, and tarpaper.

The majority of specimens (47) collected by us were taken in the Cerro de la Vieja region. Although geographically a foothill locality, this cerro is separated from the main foothills lying several kilometers to the north and east. The cerro is approximately 150 m in height, with large exfoliating granite boulders and moderate plant cover. The larger plants of the area are mesquite, palo verde, cacti, and *Capparis* sp. (tree form). During the day *P. inaequalis* were found beneath a bridge under a stone and under small exfoliating flakes of granite on large boulders. Individuals were found actively foraging on the ground or on small boulders at night. Most individuals were found on the ground within one-half meter of the base of boulders. One lizard was taken on open soil approximately five meters from the nearest cover, and one individual was observed climbing a small shrub.

In all regions mentioned above except for the Pacasmayo area, *P. inae-*

*qualis* is sympatric with *reissi* and *kofordi*. There are however, some microhabitat preferences for daytime retreats unique to each species. Large exfoliating granite flakes were utilized by *P. reissi*, small flakes by *inaequalis*, and small burrows under boulders or cracks in the soil by *kofordi*. After dark, *P. reissi* generally preferred large vertical faces of boulders on which to forage, *P. inaequalis* generally on the ground at the base of boulders, and *P. kofordi* on boulders and on the ground.

The nocturnal body temperatures of *P. inaequalis* usually ranged between the substratum and air temperatures but generally closer to the substratum than to the air temperature. This was found to be true for other species as well.

This species lays only one egg at a time. Captive females laid only one egg and preserved gravid females contained a single egg, either in the right or left oviduct.

*Distribution.* This species occurs in widely scattered localities in northwestern Peru. It appears to be restricted to the desert foothills bordering the Sechura Desert (fig. 4). Specimens (59) have been examined from the following localities: *Lambayeque*: 7 km S Motupe LACM 48495, 48500-18, TCWC 28308-27, MVZ 82174, 85329-33, 7.2 km W Naupe TCWC 28328. *Libertad*: Pacasmayo ANSP 11365; 16.7 km ENE Pacasmayo LACM 48496-99, TCWC 28305-07. *Piura*: Cerro Amotape MVZ 82170, 82172, 82283; 5 km E Las Lomas MVZ 82171.

### ***Phyllodactylus microphyllus* Cope**

*Phyllodactylus microphyllus* Cope 1876. Jour. Acad. Nat. Sci. Phila., ser. 2, 8:175

*Phyllodactylus inaequalis*, (part) Noble 1924. Occ. Paps. Boston Soc. Nat. Hist., 5:111.

*Phyllodactylus gerrhopygus*, (part) Burt and Burt 1931; Bull. Amer. Mus. Nat. Hist., 61(7):250.

*Holotype.* Adult male, ANSP 11364, collected by James Orton in 1868-69. Type locality. Valley of Jequetepeque, Peru (Department of Lambayeque).

*Definition.* An average-sized gecko with a known maximum snout-vent length of 58 mm; very small terminal lamellae on all digits with fingers and toes short; dorsal tubercular rows indistinct, composed of small flat, oval tubercles that seldom form regular rows; enlarged tubercles absent from head, limbs, and tail; scales of ventral surface of tail uniform in size; scales surrounding nostril greatly swollen; ventral color of body, limbs, and tail brilliant white (fig. 9b).

*Diagnosis.* This species is readily distinguished from *P. gerrhopygus*, *heterurus*, and *angustidigitus* by the absence of an enlarged preanal plate; from *clinatus*, *dixonii*, *lepidopygus*, *interandinus*, *kofordi*, *sentosus*, *johnwrightii*, *reissi*, *ventralis* and *pumilus* by the absence of enlarged, regular rows of trihedral tubercles on dorsum; from *inaequalis* by the presence of a distinct swollen region about the nostril, larger size, and very small terminal lamellae.

*Description.* Rostral about twice as wide as high, its outer posterior edges elevated along inner edge of nostril; internasals small, rounded and swollen, their median edges separated in most specimens by three rows of granules; median and posterior borders of internasals contact small granules and postnasal of each side; nostril surrounded by rostral, internasal, and two postnasals, all greatly swollen about nostril; first supralabial not in contact with ventral edge of nostril; shallow depression between internasals and in frontal region; scales in posterior loreal region about twice size of midorbital scales; eye large, its diameter contained in snout length about 1.8 times; eyelid with 2 rows of granules and one larger outer row of scales, last 8 to 12 are pointed; diameter of ear contained in diameter of eye about 2.8 times; ear opening small, not denticulate, scales on anterior and posterior margins rounded; rear of head granular; usually six supralabials and five infralabials to point below center of eye; mental bell-shaped, slightly longer than wide, its distal tip extends beyond posterior border of first pair of labials; postmentals much longer than wide, their median edges usually in narrow contact, nearly separated by posterior projection of mental; postmentals bordered across chin by very small granules.

Dorsum with irregular rows of small, oval tubercles that tend to be flat, posterior dorsal edge with faint keel; dorsal tubercles not regular enough to count with accuracy; postanal tubercles usually number four on each side; limbs with somewhat small, flattened scales; main portion of claw visible when viewed from below; terminal lamellae very small.

Color pattern in life: ground color yellowish tan; dorsum with profusion of dark brown, brown, light tan, and white granules and larger scales (tubercles) that tend to give entire dorsal color a sandy appearance; arms and legs similar to dorsum; dorsal surface of tail faintly banded with light gray bands on yellowish tan ground color; dorsal surface of head similar to dorsum; loreal region with larger diffuse spots of brown and tan granules; ventral surfaces brilliant white.

*Variation.* Snout-vent lengths of subadult and adult males vary from 33 to 56 mm (46.7), females from 32 to 58 mm (46.5), juveniles 23 to 31 mm (27.1), males plus females average 46.6 mm; tail length varies from 42 to 53 per cent of total length; postmentals number from two to four, two occurring in 90.6 per cent three in 8.0 per cent and four in 1.4 per cent of sample; postmentals contacting adjacent labials vary from none to two on each side, none in 4 per cent, one on one side and none on opposite side in 4 per cent, one on each side in 89.2 per cent one on one side and two on opposite side in 1.4 per cent and two on each side in 1.4 per cent of sample; number of scales across chin immediately following postmentals varies from 6 to 9 (7.4); scales across midorbital region range from 18 to 25 (20.8), across snout at level of third labial 18 to 26 (21.8); median and posterior scales bordering internasals vary from 7 to 12 (8.7), with median edges of internasals separated by granules in 99.2 per cent of sample; scales from nostril to eye range

from 10 to 15 (12.4); scales across venter vary from 21 to 38 (27.3), mainland populations from 26 to 38 (31.0), island populations 21 to 33 (25.8); scales from throat to vent range from 62 to 72 (66.3) in all populations; dorsal tubercular rows range from 10 to 14 (11.9) when arranged in somewhat regular rows, but majority of individuals have irregular rows; lamellae beneath fourth toe vary from 12 to 15 (13.3); terminal lamellae generally very small, but variable in size dependent upon soil type from which specimens are obtained; tail generally shorter than snout-vent length and always devoid of tubercular rows, ventral surface with all scales of equal size.

Dorsal color pattern variable, from light brown, brown, and white freckled appearance on yellowish tan ground color to dark brown to black reticulating lines on gray, tan or light brown ground color; broad, but indistinct brown bands are occasionally present in adults, more frequently in young and juveniles; a brownish line usually present from nostril to eye, occasionally extends to ear; ventral surfaces brilliant white.

*Comments.* There has been considerable confusion in the application of the name *microphyllus* to the original population Cope described in 1876. Cope described *microphyllus* and *inaequalis* in the same paper, but failed to make clear the type of digital expansion found in *inaequalis* that would separate it from *microphyllus*. Noble (1924) used the name *inaequalis* (= *microphyllus*) for populations inhabiting the sandy deserts of the coast, apparently being unable to distinguish between Cope's two species. Cope (1877) later described another species, *nigrofasciatus*, and in the same paper explained the differences in digital expansion between *microphyllus* and *inaequalis*, apparently overlooked by Noble and later workers.

Burt and Burt (1930), apparently confused by Noble's use of the name *inaequalis* for the sandy desert form, listed *microphyllus*, *inaequalis*, and *gerrhopygus* from Peru, but had misidentified a specimen of *gerrhopygus* as being *inaequalis*. They later (1931) perpetuated this mistake by listing *inaequalis* (= *gerrhopygus*) from Arequipa, Peru, and in part, confused specimens of *microphyllus* with *inaequalis* in northwestern Peru. This mistake was repeated by Donoso-Barros (1966).

*Habitat and natural history.* *Phyllodactylus microphyllus* is a widespread species, but generally restricted to the western sandy areas of the Sechura Desert, sandy and sand rubble beaches of the Peruvian coast and offshore islands. The absence of vegetation does not seem to restrict its distribution in the drier parts of Peru. We have found specimens in areas where vegetation was absent, but these individuals were found within one kilometer of the beach. The storm and intertidal zones of the beach are probably the principal sources of food. The absence of food elsewhere is a possible factor limiting the distribution of this species. In northwestern Peru where vegetation is more abundant this species has been taken 60 kilometers (airline) from the nearest beach.

During the day individuals have been found under rocks, cow chips,

boards, bones, paper, tin, and other objects strewn on sandy surfaces. In one instance individuals were found in open Indian graves where remnants of burial cloth were exposed. Some of these daytime retreats are often fully exposed to sunlight and the body temperatures of individuals found under these conditions are about 10°C higher than their nocturnal temperatures. In the vicinity of Culebras, this species was observed emerging just prior to complete darkness and actively foraging for about four hours. In the Cerro Illescas area of northwestern Peru this species was found foraging in leaf litter and on the branches and trunks of shrubs, mainly *Capparis avicennifolia*, during winter months. We observed this species foraging on guano mounds on Cerro Azul and it was reported from guano mounds on Isla Lobos de Afuera by Burt and Myers (1942).

The behavior of this species is similar to that of members of the genus *Coleonyx*. When disturbed, the tail is raised, back is arched, and it feigns an attack accompanied by noise and walks diagonally away with full side view of body exposed to a potential predator. The movements of this lizard are deliberate, somewhat slow, and when disturbed, it does not seem able to run rapidly. One individual was observed utilizing a small rock to scrape shedding skin from its body.

This species apparently lays a single egg per clutch. Preserved females contained a single egg in either the right or left oviduct.

One specimen was removed from the stomach of a snake, *Liophis* sp., but actual predation was not observed. Potential predators consist of ghost crabs, snakes, and foxes.

As in other species of *Phyllodactylus*, the nocturnal body temperatures of this species closely approximates that of the substratum.

*Distribution.* This species is known only from Peru. It ranges from the northwestern coastal village of Los Organos, southward to the coastal village of Cerro Azul, an airline distance of 1,150 km. The western part of the Sechura Desert of northwestern Peru is the only area where its range extends inland from the coast (fig. 2).

Specimens (277) have been examined from the following localities: *Ancash*: 2 km N Culebras LACM 48589-92, TCWC 28151-55. 12 km N, 1 km W Pativilca LACM 48570-72, TCWC 28148-50. 24.7 km N Pativilca MVZ 82145, 82231. *Lambayeque*: 11 km S Chiclayo MVZ 82181. Eten MCZ 18138, 17692-94, AMNH 28517-18. 10 km S Mocupe TCWC 28162. 3 km SE Morrope MVZ 82146. *Libertad*: Jequetepeque Valley ANSP 11364. 4 km N Pacanguilla LACM 48574, TCWC 28156-57. *Lima*: Ancon AMNH 36513-19. Cerro Azul LACM 48567-69, TCWC 28145-47. 7 km SSE Chilca MVZ 85430-34, 85436-38, 85440-41. Chorillos MJP 3 (no numbers). Cruz de Hueso USNM 75390. Isla San Lorenzo USNM 17541. Lima MJP 5 (no numbers), 3 km N San Antonio TCWC 28174. 5.5 km NE San Bartolo MVZ 85421-29. *Piura*: 1 km S Bayovar, Cerro Illescas MVZ 85353-61. 5 km SSE Bayovar MVZ 85342-52. 12 km S, 8 km E Bayovar MVZ 82157-61,

82270. 20 km SE Bayovar MVZ 85362-63. Isla Lobos de Afuera SDSNH 31123-53, USNM 38571-74. Isla Lobos de Tierra FMNH 34226(7), 34234 (5), 40113-14, AMNH 38753-55, UMMZ 83099 (2). 3.7 km ENE Los Organos LACM 48588, TCWC 28173. Negritos FMNH 5726-27, 8363, 8453-54. Paita AMNH 28461, HM 1499 (2). mouth of Parinas Valley FMNH 41543-45. 13 mi N Piura CAS 85163. 10 km E Piura MVZ 82162. Punta Aguja MVZ 82148-52, 82228, 82248. Reventazon MVZ 82153-56. 30 km SSE Sechura MVZ 82147. Talara FMNH 53891, 53894, 57457. 2 km E Talara LACM 48575-78, TCWC 28158-61. 2 km N Talara TCWC 28163. 3 km S Talara LACM 48579-86, TCWC 28164-71. 5 km S Talara LACM 48587, TCWC 28172. Tric Trac MVZ 82163-68, 85334-41.

***Phyllodactylus clinatus* sp. nov.**

*Holotype.* Adult female, MVZ 82227, collected by Raymond B. Huey, 19 July 1967. Type locality. Punta Aguja, 37 km SW Sechura, Department of Piura, Peru.

*Definition:* A small gecko with a known snout-vent length of 46 mm; dorsum with 10 to 12 rows of enlarged, trihedral tubercles; tubercles absent on tail, thigh, tibia, and forearm; granules absent between internasals; ear very large, 56.7 per cent of diameter of eye; ear strongly denticulated on anterior and posterior margins; terminal lamellae of digits large, truncate; all scales of median row beneath tail widened, rectangular (fig. 11b).

*Diagnosis.* This species may be distinguished from *P. heterurus*, *angustidigitus*, and *gerrhopygus* by the absence of an enlarged preanal plate; from *inaequalis* and *microphyllus* by much larger ear, dorsal rows of enlarged, trihedral tubercles arranged in regular series, and by a widened row of scales beneath tail; from *dixonii*, *pumilus*, *kofordi*, *sentosus*, *johnwrightii*, *reissi*, and *ventralis* by the absence of tubercles on tibia and much larger ear; from *lepidopygus* and *interandinus* by presence of a row of widened, rectangular scales beneath tail, larger ear, and small, flattened granular scales on tibia.

*Description of holotype.* Rostral twice as wide as high with short median groove about one-third depth of rostral; two internasals, somewhat rectangular, their median edges in broad contact, and bordered posteriorly by three granules and postnasal of each side; nostril surrounded by rostral, labial, internasal, and two postnasals; first labial in broad contact with ventral edge of nostril; deep depression between internasals, moderate depression in frontal region; scales in posterior loreal region about 2.5 times larger than midorbital scales; 22 scales across snout at level of third labial, 14 scales across anterior edge of orbits, 20 midorbital scales; eye large, its diameter contained in snout length 1.5 times; eyelid with two rows of granules and one larger outer row of scales, last 4 to 5 are pointed; ear diameter contained in eye diameter 1.8 times; ear opening large, denticulate; rear of head granular with larger intermixed tubercles; six supralabials and five infralabials to point below center of eye; mental bell-shaped, as wide as long; bordered posteriorly by two post-

mentals; postmental as wide as long, their median edges in broad contact, immediately followed by transverse row of 9 scales, followed by second row of 13 smaller scales; postmentals contact first labial only of each side.

Dorsum with 10 rows of enlarged, trihedral tubercles that are somewhat flattened; paravertebral row with 45 tubercles from head to base of tail, 24 between axilla and groin; paravertebral rows separated from each other by 4 to 6 rows of granules; 4 rows of dorsal tubercles reach to nape, 6 to base of tail; each tubercle of enlarged dorsal series separated from preceding tubercle by 1 to 3 granules; postanal tubercles number two on each side, indistinct; 26 scales across venter; 60 from throat to vent; dorsal surfaces of arm with granules and larger flattened scales; dorsal surface of thigh with granules and larger flattened scales, tibia with small flat granules; lamellae formula for hand 6-8-10-13-9, foot 7-9-11-14-10; claw hidden when viewed from below; terminal lamellae large, longer than wide, truncate; digits slender.

Measurements in mm: snout-vent length 46.0, axilla-groin length 19.0, length of leg 16.5, length of arm 14.4, length of tail 46.0, length of head 14.0, depth of head 4.9, width of head 8.7, length of snout 4.9, diameter of eye 2.3, diameter of ear 1.8, distance from eye to ear 3.6.

Color in life: ground color sand brown; dorsum with six narrow, chocolate brown bars interrupted along median line, ground color interspaces four to five times width of dark bars; sides of body with light tan spots between dark bars, tending to form ocellated pattern with network of fine brown lines intermixed; arms with chocolate brown reticulating lines, tending to form bands on upper arm; hind limb with five chocolate brown bands, one-third as wide as ground color interspaces; tail with 11 dark brown bands, ground color interspaces twice width of dark bands; head with dark brown parietal spot, rear of head with thin, dark brown reticulating lines: dashed and partly wavy line from rear of eye to hind limb, connecting with lower edge of dark body bars; supralabials with upper half heavily pigmented with dark brown, lower half and all of infralabials with suffusion of minute black dots; dark brown stripe from nostril to eye, tending to be black from eye to side of body; ventral surfaces with faint brownish dots scattered along sides, more dense on tail; general ventral color pale yellow.

*Variation.* Snout-vent length of juvenile male 28 mm, females vary from 34 to 46 mm (40.3); tail length about 45 to 50 per cent of total length; postmentals number 2 in all, contacting first labial only in all; number of scales across chin immediately following postmentals range from 6 to 9 (7.3); scales across snout at level of third labial range from 21 to 23 (21.8), midorbital scales from 19 to 22 (19.5); scales bordering posterior edge of internasals number 5 in all; scales from nostril to eye range from 13 to 15 (13.8); scales across venter vary from 26 to 32 (28.8), from throat to vent 60 to 64 (61.8); dorsal tubercular rows range from 10 to 12 (10.5); paravertebral tubercles from head to base of tail range from 42 to 46 (44.5), from axilla to groin 24 to 29 (27.5); lamellae beneath fourth toe range from 13 to 15 (14.0);

terminal lamellae of digits large and truncate in all; ratio of ear diameter to that of eye ranges from .500 to .653 (.567); ratio of ear diameter to distance between eye and ear ranges from .419 to .487 (.444).

Dorsal color pattern varies from distinct bands, broken along median line, to series of dorsolateral spots connected longitudinally by thin dark brown line; bands or spots (one side) vary from 6 to 8 (6.5); tail bands number 11 in only specimens with complete tail; limbs usually banded but bands may be obscured by dark ground color; ventral surfaces pale yellow in all specimens.

*Habitat and natural history.* Having taken only four individuals of this species, very little natural history information of the species could be obtained. All four specimens were taken from the vicinity of Cerro Illescas where *Caparis avicennifolia*, *C. scabrada* and mesquite are the dominant plants.

Three specimens were obtained in July and August of 1967. One was taken from a snap trap at the base of a small boulder near the edge of a cliff. The substratum was sandy, although it was only one-third meter from a fragmented shale area. One was captured on the trunk of a mesquite about one m above the ground. The third specimen was taken one afternoon under a small rock on sandy substratum, near rock outcrops and mesquite.

In spite of intensive collecting in this general area in 1968, only one additional specimen was obtained. It was found 2.5 m above the ground on a mesquite branch.

*Distribution.* This species is known only from the Cerro Illescas area of northwestern Peru (fig. 4).

Four specimens have been examined: *Piura*: 4 km SSE Bayovar MVZ 82271; 5 km SSE Bayovar TCWC 28332; 10 km SE Bayovar MVZ 82269; Punta Aguja MVZ 82227.

### ***Phyllodactylus lepidopygus* (Tschudi)**

*Diplodactylus lepidopygus* Tschudi 1844-46, Untersuchungen über die Fauna Peruana. Herp.: 38.

*Discodactylus phacophorus* Tschudi 1844-46, Untersuchungen über die Fauna Peruana. Herp.: 38-39.

*Phyllodactylus nigrofasciatus* Cope 1877. Proc. Amer. Philos. Soc. Phila., 17:36.

*Phyllodactylus variegatus* Werner 1901. Abh. Mus. Dresden, 9(2): 2.

*Holotype.* NM 43, adult male, obtained by Tschudi prior to 1844. Type locality, Chorillos, Peru.

*Definition.* A moderate-sized gecko with known maximum snout-vent length of 55 mm; tibia and femur tubercles absent; ear denticulate on anterior margin; slightly enlarged tubercles among granules on rear of head; median row of scales on ventral surface of tail not enlarged; enlarged preanal scale absent; 10 to 16 (13.1) rows of enlarged trihedral tubercles on dorsum; tail length about 45 to 55 percent of total length, tail without enlarged tubercles;

terminal lamellae of digits moderately enlarged; body bands (may be broken on midline) 6 to 9 (7.2), tail bands 9 to 13 (11.0) (fig. 13a).

*Diagnosis.* This species is easily distinguished from *P. heterurus*, *angustidigitus*, and *gerrhopygus* by the absence of an enlarged preanal scale; from *kofordi*, *reissi*, *clinatus*, *dixoni*, *johnwrighti*, *pumilus*, *ventralis*, and *interandinus* by having all scales beneath the tail of equal size, rather than median row distinctly widened or enlarged; from *inaequalis* and *microphyllus* by having distinct dorsal rows of enlarged trihedral tubercles, rather than indistinct dorsal rows of small flattened tubercles or rows occasionally absent; from *sentosus* by the absence of tail, tibia, and thigh tubercles, rather than very large tubercles present.

*Description.* Rostral more than twice as wide as high; two internasals and two postnasals; nostril bordered by rostral, internasal, labial, and two postnasals; second supralabial separated from nostril by two granules and postnasal; postero-dorsal loreal scales about four times larger than interorbital scales; internasals slightly wider than long, bordered posteriorly by small scales; auricular opening very small, slightly denticulate, contained in snout length about eight times; eye large, contained in snout length about one and one-third times; rear of head granular with few larger, rounded tubercles; 7 to 9 supralabials and 5 to 6 infralabials to point below center of eye; mental slightly longer than wide, bordered posteriorly by two to three well defined postmentals; postmentals followed by irregular row of granular scales; eyelid with two rows of granules and larger palebral row of scales; last 2 to 5 scales in larger supercilliary series bearing long spines; regular rows of longitudinal, enlarged keeled tubercles on dorsum, 8 rows reach to rear of head and 8 to base of tail; all rows equally spaced apart, no wide granular area separating paravertebral rows; four well defined postnasal tubercles on either side of anus in males; venter scales moderately differentiated from lateral body scales; no enlarged preanal shield; arm covered with flat imbricated scales, no enlarged tubercles intermixed with flattened scales; femur with flat, imbricated scales on dorsal and ventral surfaces, posterior-ventral surface with granular scales; lower leg similar to femur; terminal pads slightly longer than wide; claw short, hidden between terminal pads.

*Variation.* Specimens of this species with a minimum snout-vent length of 32 mm are considered young adults. In a sample of 36 specimens, 8 are less than 32 mm snout-vent length, 13 are males with snout-vent from 32 to 50 mm (40.8), 15 are females with snout-vent from 36 to 55 mm (46.8). The average snout-vent length for males and females is 44.0 mm.

The number of postmentals varies from two to four, two occurring 58.4 per cent of the time, three 38.9 per cent and four 2.7 per cent; number of scales bordering the postmentals range from 5 to 8 (6.9); number of scales across the midorbital region 15 to 21 (18.2); number of scales across the snout at the level of the third supralabial 17 to 22 (20.1); scales bordering the internasal shields posteriorly number 5 to 11 (6.7), with one or two small

azygous scales separating the internasals in 7 of 36 specimens; transverse venter scales number 26 to 34 (29.4), longitudinally 65 to 74 (69.6); scales from posterior edge of nostril to eye number 10 to 14 (11.4); fourth toe lamellae number 10 to 14 (11.5); dorsal tubercular rows number 10 to 16 (13.1); tubercles in paravertebral row from rear of head to base of tail number 42 to 53 (47.8), axilla to groin 24 to 34 (28.9); body bands or blotches number 6 to 9 (7.2), tail bands 9 to 13 (11.0).

The general ground color in life varies from a greenish brown to a deep blackish brown; dorsal body markings vary from black spots to brown cross-bands or light tan blotches; general appearance consists of light ground color with darker spots irregularly arranged; head with blackish line from nostril through eye to above arm, occasionally continuing along side of body to hind limb; top of head from prefrontal area to posterior tip of parietal region consistently darker than remainder of body in all specimens but one; one specimen has reversal pattern of dark ground color with light blotches; tail generally banded with alternating black or brown bands with light tan to whitish interspaces; interspaces usually about half the width of dark bands but occasionally as wide or wider than dark bands; regenerated tails usually reticulated with dark lines on tan ground color; juvenile pattern similar to that of adults; venter yellowish tan to yellowish brown with dark brown spotting along lateral edges or occasionally to center of venter; chin and throat creamy yellow in young and subadults, becoming progressively darker with suffusion of brownish dots in old adults; ventral surface of tail generally darker than venter.

*Comments.* We have examined the holotype of *P. lepidopygus*, three syntypes of *P. phacophorus*, holotype of *P. nigrofasciatus* and find that they are identical in general shape, size of head and body. Their scale characters are within the range of variation of a relatively large sample of *P. lepidopygus* from a single locality and we therefore consider *P. phacophorus* and *P. nigrofasciatus* as subjective synonyms of *P. lepidopygus*. The nine syntypes of *P. variegatus* were destroyed during the fire bombing of Dresden, Germany, during World War II and Werner's (1901) original description is the only evidence we have for a comparison of *P. lepidopygus* and *P. variegatus*. Werner's description agrees with the characters attributed to *P. lepidopygus*. His description agrees to some extent with the salient features of *P. reissi*, a species found further to the north. The major exception is the presence of tibia tubercles in *P. reissi*, absent in *variegatus*, and to a minor degree, the short outer row of dorsal tubercles in *P. reissi*, not so in *variegatus*. Werner gave the type locality as Lima (9 specimens) and Chanchamayo (1 specimen), both areas some 1,500 km south of the nearest locality where *P. reissi* has been taken. However, *P. lepidopygus* occurs in the vicinity of Lima and *P. variegatus* is considered a synonym of *P. lepidopygus*.

*Habitat and natural history.* This species has been found associated with the lomas vegetation of the Lima region, the drier *Tillandsia* association of the desert coast, and the coastal foothills to an elevation of 1,400 m. The

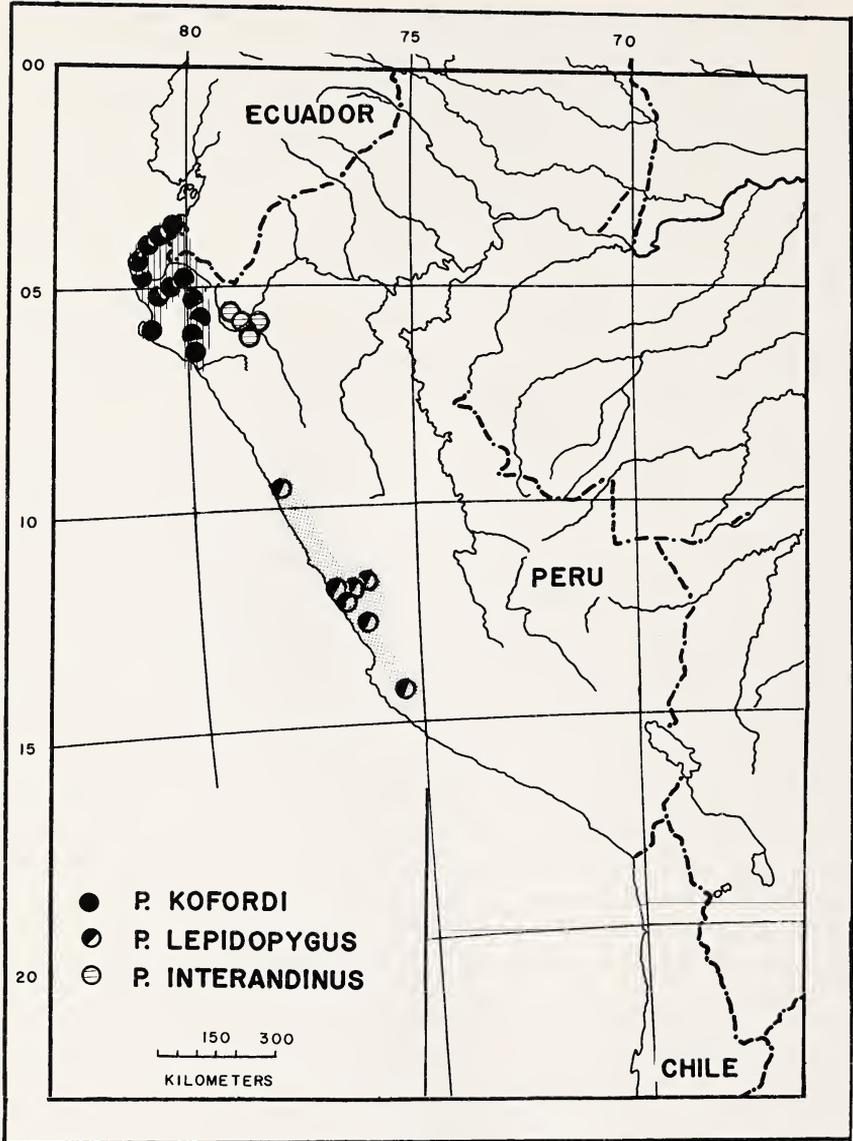


Figure 3. Distribution of *P. pumilus*, *P. kofordi*, *P. lepidopygus*, and *P. interandinus* in western South America.

microhabitat appears to be one of vertical surfaces of buildings, rock walls, large and small granite boulders, and crevices therein.

A series of 34 specimens taken by Huey, Dixon, and Wright from Lomas de Lachay were found exclusively on vertical surfaces of granite boulders, rock walls, or walls of buildings. No specimens were observed on rocks with abundant mossy growth, but lichen covered surfaces were utilized. Occasionally *P. lepidopygus* were seen in crevices or under smaller rocks resting on boulders during the day. This species became active as soon as it became dark, even on cold misty nights. The air temperature on 4 July 1967 was 13.2°C. approximately an hour and half after nightfall and seven geckos were taken subsequent to that time. Potential food items (e.g., *Porcellio*, spiders, moths) in the Lomas de Lachay region were plentiful on the rock surfaces at night. One specimen taken 24.7 km north of Pativilca was collected from a burro femur lying in a rolling sand hill region with few exposed surface rocks and *Tillandsia* as the only plant.

The only gecko observed in the Lomas de Lachay region was *P. lepidopygus*, but the rolling sand hill region 123 km north of Lima also contained *P. microphyllus*.

Of four specimens taken from the Asia area south of Lima, three were found actively foraging at night on a rock corral wall, and one was found on a small cerro on a rotting granite outcrop. All four were found on surfaces relatively free of heavy lichen growth.

Two individuals were found east of Chosica at an elevation of 1,700 m. Both specimens were taken from a wall of an abandoned adobe building that had been plastered. The coloration of both specimens was atypical, being almost translucent, without pattern, and inconspicuous against the light colored plaster. The two individuals had a more normal color pattern following a 24-hour period in a cloth sack.

An examination of the oviducts of preserved females reveals that this species lays a single egg per clutch. Natural nests were not observed but we suspect that eggs are deposited in cracks of large boulders in the Lomas de Lachay area. Several shells of *Phyllodactylus lepidopygus* eggs were found 40 km NNW Pativilca, 600 m, in dead cactus plants in a dry arroyo strewn with small boulders. No geckos were observed at this locality, but the location it within the known distribution of *lepidopygus*.

*Distribution.* The known range of this species is approximately 300 km north and 300 km south of Lima, and appears to be restricted to the rocky foothills from near sealevel to an elevation of 1,700 m (fig. 3).

Specimens (63) have been examined from the following localities: PERU. no specific locality BM 25440. *Ancash*: Chimbote Valley ANSP 11366. 24.7 km N Pativilca MVZ 82175. *Lima*: 2 km ESE Asia LACM 48473-74, TCWC 28142-43. 8 mi SE Chilca MVZ 85435. Chorillos NM 43. vicinity of Chorillos NM 41 (3). Chosica FMNH 34175. 26 km ENE Chosica LACM 48475, TCWC 28144. Lima MJP (3) unnumbered. Lomas de Lachay CAS

85143, LACM 48467-72, MVZ 82182-91, 82222-25, 82252-65, TCWC 28135-41. 20 km E Lurin MVZ 85411; Verrugas Canyon MCZ 26674. *Ica*: Ica FMNH 39367.

**Phyllodactylus interandinus** sp. nov.

*Phyllodactylus phacophorus*, (part) Noble 1924, Occ. Paps. Bost. Soc. Nat. Hist., 5: 111.

*Holotype*. Adult female, TCWC 27914, collected by John W. Wright and James R. Dixon, 26 November 1968. Type locality, 4.8 km S (by road) Belavista, 520 m, Department of Cajamarca, Peru.

*Definition*. A small gecko with a known snout-vent length of 47 mm; numerous rows of enlarged dorsal tubercles and tubercles in paravertebral row from head to tail and axilla to groin; terminal lamellae moderately large, digits short; distinctly banded, black, white, and yellowish green tail; tubercles absent on thigh, tibia, and forearm; distinct dorsal color pattern of three light and four dark longitudinal stripes (fig. 10a).

*Diagnosis*. This species is distinguished from *P. heterurus*, *angustidigitus* and *gerhopygus* by the absence of an enlarged preanal shield; from *inaequalis* and *microphyllus* by having some scales beneath tail enlarged, and by numerous rows of enlarged trihedral tubercles on dorsum; from *clinatus*, *dixoni*, *ventralis*, *lepidopygus*, *kofordi*, *sentosus*, *johnwrighti*, *pumilus*, and *reissi* by presence of 65 or more tubercles in paravertebral row from head to base of tail, and distinct dorsal color pattern of light and dark stripes.

*Description of holotype*. Rostral twice as wide as high, its dorsal edge with vertical groove one-half depth of rostral; two internasals, somewhat rounded, their median edges in broad contact, bordered posteriorly by six granules and postnasal of each side; nostril surrounded by rostral, labial, internasal, and two postnasals; first supralabial in narrow contact with ventral edge of nostril; shallow depression between internasals and in frontal region; 12 scales on line between nostril and eye; scales of posterior loreal region about two times larger than midorbital scales; 22 scales across snout at level of third labial, 14 scales across anterior edge of orbits, 16 midorbital scales; eye large, its diameter contained in snout length 1.6 times; eyelid with two rows of granules and one larger outer row of scales, last three are pointed; ear contained in eye diameter 2.6 times; ear opening denticulate, but denticulate scales low and somewhat rounded; rear of head with subequal scales; five supralabials and four infralabials to point below center of eye; mental bell-shaped, slightly longer than wide, bordered posteriorly by three postmentals; postmentals rounded, their median edges in broad contact, immediately followed by transverse row of 8 scales, followed by second row of 12 smaller scales; postmentals contact first labial only on each side.

Dorsum with 20 longitudinal rows of enlarged trihedral tubercles, somewhat flattened, paravertebral row with 71 tubercles from head to base of tail, 44 between axilla and groin; paravertebral rows separated from each other by

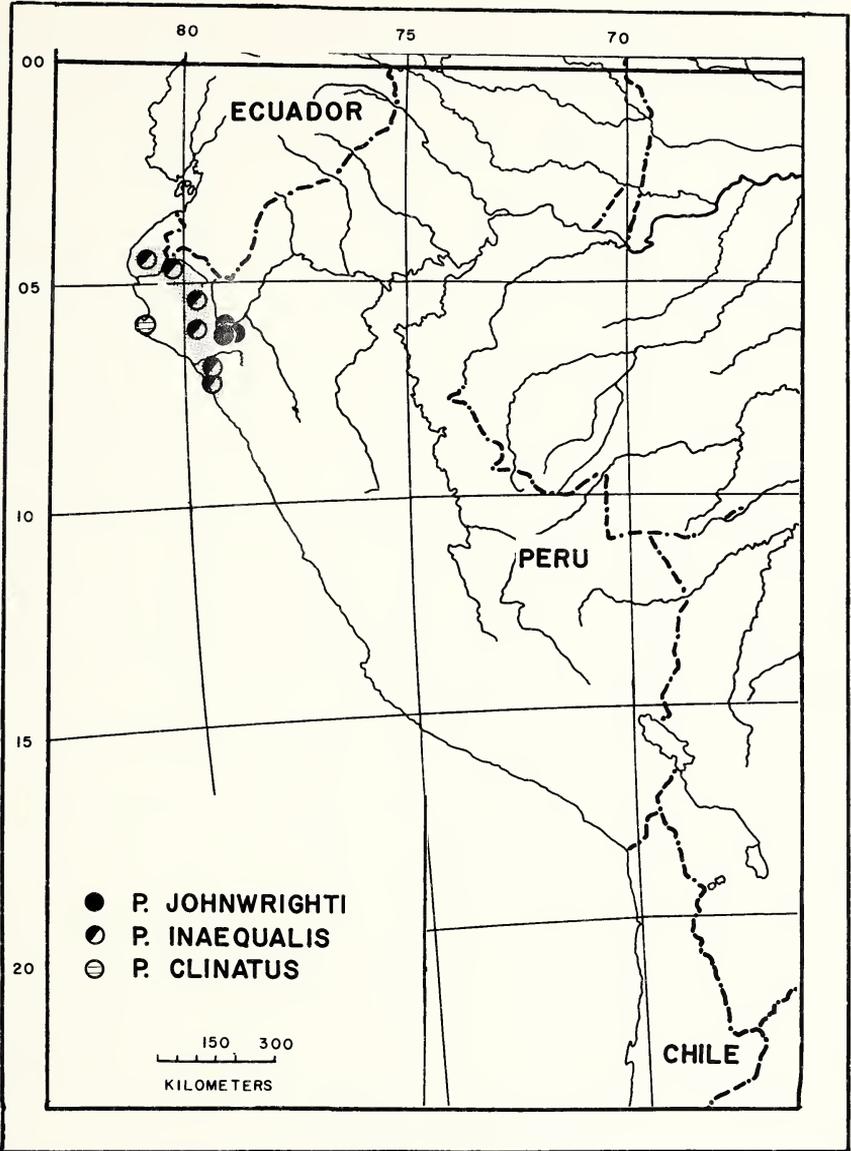


Figure 4. Distribution of *P. johnwrighti*, *P. inaequalis* and *P. clinatus* in western South America.

5 rows of granules, each tubercle of paravertebral row separated from preceding tubercle by 0 to 1 granule; 14 rows of tubercles extend across nape, 8 at base of tail; postanal tubercles number three on each side; 34 scales across venter, 58 from throat to vent; dorsal surface of arm with small flattened scales; dorsal surface of thigh without tubercles; tibia with subequal rounded, somewhat elevated scales; lamellae formula for hand 6-7-8-9-7, foot 6-9-10-11-10; claw barely visible when viewed from below; terminal lamellae moderately large, slightly longer than wide, rounded.

Measurements in mm: snout-vent length 41.0, axilla-groin length 18.6, length of leg 15.2, length of arm 12.1, length of tail 43.0, length of head 11.3, depth of head 5.2, width of head 8.1, length of snout 4.2, diameter of eye 2.6, diameter of ear 1.0, distance from eye to ear 3.3.

Color in life: ground color dark gray; dorsum with one median and two dorsolateral grayish white stripes, two dorsal and two lateral dark brown stripes; median light stripe from rear of head to base of tail, anterior part of median stripe bifurcates and extends anteriorly to above each eye; dorsal dark stripes tend to form series of loosely connected spots because of small clusters of grayish white spots scattered in dark fields; lateral dark stripe extends from snout to groin; limbs heavily mottled with grayish white and grayish black spots; tail with 11 black bands, posterior edge of each black band with white tipped scales; interspaces three times width of black bands, greenish yellow; dorsal surface of head with diffuse dark brown lines; ventral surfaces dusky, chin generally whitish, each scale with black dots.

*Variation.* Snout-vent lengths of subadult and adult males range from 32 to 45 mm (39.2), females 33 to 47 mm (41.1), young and juveniles 22 to 30 mm (29.0), males plus females average 40.1 mm; tail lengths vary from 48 to 55 per cent of total length; postmentals range from two to four, two occurring in 58.4 per cent, three in 38.9 per cent, and four in 2.7 per cent of sample; chin scales bordering postmentals range from 5 to 8 (6.9); postmentals contact first labial only of each side in 99.6 per cent, first labial on one side, none on opposite side in 0.4 per cent of sample; scales bordering internasals number 5 to 7 (6.2); scales from nostril to eye vary from 9 to 12 (10.8); scales across snout at level of third labial range from 22 to 27 (24.3), mid-orbital scales 18 to 22 (20.3); scales across venter vary from 26 to 33 (29.6), from throat to vent 56 to 65 (60.8); fourth toe lamellae range from 10 to 12 (11.6); longitudinal rows of dorsal tubercles vary from 14 to 22 (17.4); tubercles in paravertebral row from head to base of tail range from 65 to 85 (70.1), between axilla and groin 35 to 60 (40.7).

Color pattern consists of one median and two dorsolateral grayish white to yellowish tan stripes, separated by two dorsal and two lateral grayish brown to grayish black stripes; dark stripes usually bifurcates on nape, each arm extending anteriorly to posterior edge of eye or to tip of snout; broad, dark brown stripe usually present from snout to rear of head, lying between dorsolateral light stripes; ventral surfaces usually dusky with black dots on each

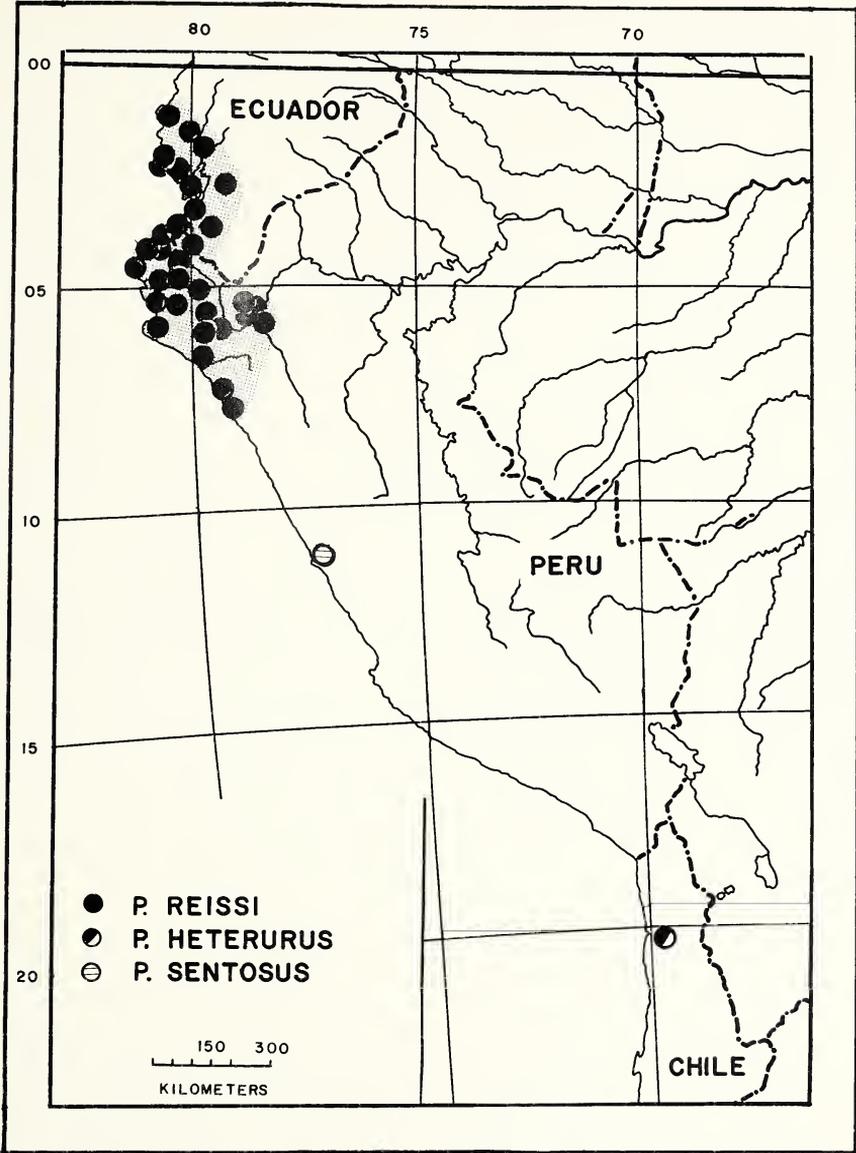


Figure 5. Distribution of *P. reissi*, *P. heterurus* and *P. sentosus* in western South America.

scale, chin and throat generally lighter in color than remainder of body; dorsal surface of tail with 11 to 16 narrow black bands edged with white posteriorly; broad interspaces bright reddish orange in juveniles, yellowish orange in subadults, yellowish green in adults.

*Comments.* Noble (1924) labeled a relatively large series of specimens from northwestern Peru as *P. phacophorus*, but the majority of the specimens are referable to *P. interandinus*. A critical examination of the entire series reveals four species were present in the collection, *interandinus*, *johnwrighti*, *kofordi*, and *reissi*.

*Habitat and natural history.* Noble (1924) recorded taking *phacophorus* (= *interandinus*) and *magister* (= *reissi*) from houses and deserted huts in Bellavista. We were unable to obtain *interandinus* in Bellavista but found *reissi* on the walls of houses. *Phyllodactylus interandinus* was abundant on a thorn scrub hillside a few kilometers south of Bellavista. Standing, dead *Cereus* sp. are the principal daytime retreats of this species with as many as seven individuals occupying one plant. Some individuals were taken as high as two meters above the ground, but the majority of specimens were found within one meter of the ground, usually beneath the bark, in the hollow trunks or branches. *Phyllodactylus reissi* and *interandinus* were taken from the same cactus plant, but the former species was not abundant. The distribution of *interandinus* is spotty, for similar areas of vegetation on other hillsides yielded only *reissi*. Hillsides and valleys were examined in the Department of Amazonas, east of the Rio Marañon, but only *reissi* were found in abundance. Only six individuals of *interandinus* were found east of the river, taken beneath rotting agave stumps and dead cactus litter. A total of 79 *reissi* were taken east of the river in a wide variety of habitats, including agave.

There seems to be potential competition between these two species for space but not for food. *Phyllodactylus reissi* is primarily scansorial while *interandinus* forages on the ground. Eggs of both species were found in a variety of rotting debris, but *reissi* eggs were far more numerous than those of *interandinus*.

An examination of preserved females of both species indicates that *P. interandinus* lays one egg per clutch and *reissi* two eggs per clutch.

There are distinct behavioral differences between *P. interandinus* and *reissi* when suddenly exposed to sunlight while in their daytime retreats. *Phyllodactylus interandinus* remains motionless for a few seconds, then seeks cover under debris within a few centimeters of where it was uncovered. *Phyllodactylus reissi* immediately runs up or down the plant upon which it was exposed, or jumps to the ground and runs to the nearest cover to hide.

The uneven distribution of *P. interandinus* in the Marañon Valley suggests that its niche requisites are more restricted than those of *reissi*.

*Distribution.* This species is an inhabitant of the Chinchipe, Marañon, and Utcubamba river valleys of the departments of Amazonas and Cajamarca, Peru. The locality of a series of specimens in the Museum of Zoology, Uni-

versity of Michigan, is given as Sullana, Peru. This locality is approximately 70 km west of the Andes, and lies at the north end of the Sechura Desert. The specimens are in a similar state of color and preservation as those collected by Noble in 1916. We believe this locality to be in error, and represent some of the specimens taken by Noble from the Chinchipe or Marañon river valley (fig. 3).

Specimens (149) have been examined from the following localities: PERU: *Amazonas*: 17 km S Bagua Chica LACM 48538, TCWC 28087. 10 km WSW Bagua Grande MVZ 82178-80, 82251. *Cajamarca*: Bellavista AMNH 39338, 39341-42, MCZ 18139, 18140(80), SMFM 8295, TCWC 24924-27. 4.8 km S Bellavista LACM 48519-37, 48539, TCWC 27914, 28066-68, 28070-86. Perico AMNH 28428-36. *Piura*: Sullana UMMZ 59034(4) (in error).

### ***Phyllodactylus kofordi* sp. nov.**

*Holotype*. Adult male, TCWC 27912, collected by James R. Dixon and John W. Wright, 19-20 Nov. 1968. Type locality. 7 km S Motupe, Cerro de la Vieja, Department of Lambayeque, Peru, 150 m elev.

*Definition*. A small gecko with a maximum known snout-vent length of 46 mm; tibia and femur tubercles present; ear denticulate on anterior and posterior margins; moderately enlarged tubercles on rear of head intermixed among granules; median row of scales below tail distinctly widened; enlarged preanal scale absent; 12 to 14 (12.1) rows of enlarged trihedral tubercles on dorsum; tail 50 to 55 per cent of total length; tail with an 8-6-4-2 or 6-6-4-2 reduction of enlarged tubercles per whorl from base to distal half of tail; terminal lamellae of digits moderately enlarged, truncate; body markings of three types, with spots, dots, or uniform coloration; tail markings of two types, uniform or banded; trihedral tubercles of tibia greatly enlarged (fig. 11a).

*Diagnosis*. This species may be distinguished from *P. heterurus*, *angustidigitus* and *gerrhopygus* by the absence of an enlarged preanal plate; from *johnwrighti*, *pumilus*, *interandinus*, *clinatus*, *inaequalis*, *lepidopygus*, and *microphyllus* by the presence of greatly enlarged trihedral tubercles on the dorsum, thigh, tibia, and forearm and by whorls of tubercles on the entire length of dorsal surface of the tail; from *sentosus* by having much larger terminal lamellae, smaller dorsal tubercles, and smaller snout-vent length; from *reissi* by the presence of tail tubercles, tubercles on the thigh, smaller body size (maximum 46 mm rather than 75 mm), fewer paravertebral tubercles from rear of head to base of tail (31 to 36 rather than 46 to 60), and fewer paravertebral tubercles between axilla and groin (16 to 21 rather than 28 to 38); from *dixonii* and *ventralis* by the latter two characters and smaller maximum snout-vent length.

*Description of holotype*. Rostral twice as wide as high; depression between internasals continues posteriorly through frontal and interorbital regions; internasals bordered posteriorly by 5 granular scales; 18 scales across

snout between third labials, 13 across snout between second labials; 14 between middle of orbits; 11 scales between eye and nostril; posterodorsal loreals slightly more than three times larger than interorbital scales; two postnasals; auricular opening strongly denticulate, two or three auricular scales bearing long spines, projecting posteriorly from anterior margin; eye diameter slightly less than two times the snout length; ear diameter contained in eye diameter three times, in snout length 5 times; second supralabial separated from nostril by two loreal scales and postnasal; antero-dorsal border of first supralabial forms projecting edge bordering nostril below; 6 supralabial and 5 infralabial scales to center of eye; mental slightly longer than wide, bordered posteriorly by two postmentals which contact only the first labial on one side and none on the opposite side; postmentals followed by irregular transverse row of 6 scales, followed by second row of 10 smaller scales;

Dorsum with 12 longitudinal rows of enlarged, keeled tubercles, 8 reach to rear of head, 6 reach base of tail; 28 scales across venter; 56 from gular region to vent; venter scales abruptly differentiated from lateral and dorsal scales, about 5 to 6 times larger; 6 rows of enlarged tubercles on anterior six whorls of tail, separated longitudinally by two annular rows of flat scales; distal half of tail with rapid reduction of tubercular rows, 6-4-2-0; ventral surface of tail with longitudinal row of 43 widened scales, about twice to three times larger than adjoining scales; three postanal tubercles on either side of vent; dorsal surface of femur and tibia with large trihedral tubercles intermixed with granular scales; postero-ventral surface of femur granular; upper arm with large, flat scales; forearm with enlarged tubercles intermixed with smaller flattened scales; terminal pads slightly longer than wide; claw not extending beyond pad tips nor visible from below; lamellae formula for hand 7-8-9-11-8, foot 7-9-10-12-11.

Measurements in mm: Snout-vent length 44.0; head width 9.0; head length 13.1; head depth 6.4; axilla-groin length 21.2; tail length 47.0; leg 18.6; arm 12.5; snout length 5.0; eye diameter 2.7; ear diameter 1.2; distance from eye to ear 4.1.

Color in alcohol: Narrow broken, diagonal and transverse black lines across dorsum, 13 complete bands on tail; dark brownish stripe from nostril through eye to arm insertion; each enlarged dorsal tubercle flecked with black; venter immaculate, pale white; labials stippled with brown; limbs faintly spotted with brown.

*Variation.* Snout-vent length of subadult and adult males ranges from 30 to 45 mm (38.0), females from 30 to 46 mm (38.6), juveniles from 18 to 29 mm (25.4), males and females together average 38.3 mm; postmentals vary from two to four, two occurring 104 times, three 5 times, and 4 one time; postmentals contact the first labial only in 89.8 per cent of the sample, first and second labial in 11.2 per cent; number of scales immediately following postmentals across the chin vary from 5 to 8 (6.7); scales across the midorbital region range from 13 to 19 (15.8), across the snout at the level

of the third labial 16 to 20 (17.3); number of scales bordering the internasals vary from 4 to 8 (5.8) with an azygous scale separating the internasals in 14 of 110 specimens; transverse rows of scales across the venter number 22 to 30 (25.0), longitudinally 47 to 56 (50.6); dorsal tubercular rows number 12 to 14 (12.1); paravertebral tubercles from head to tail number 31 to 36 (34.0), from axilla to groin 16 to 21 (18.0); scales on a line between nostril and eye number 10 to 13 (11.5); lamellae beneath fourth toe number 11 to 13 (11.5); body markings (if present) number 5 to 8 (7.1); tail bands (if present) 8 to 11 (9.9).

Tubercles on the dorsum, tibia, and thigh usually much enlarged, strongly keeled and trihedral; tail tubercles large, somewhat flattened, keeled and elevated posteriorly.

Color pattern consists of three distinct types; (1) presence of distinct black spots, lines or blotches, (2) distinct but very small black dots, (3) uniform coloration; ground color generally pale brown in all specimens; in those with dorsal markings, the head is usually spotted with profusion of dark brown on ground color; dark brown to black stripe present from nostril through eye to above arm or slightly beyond; tail generally banded with dark brown to black on proximal three-fourths of tail, black and white on distal one-fourth; those with uniform pale brown dorsal color occasionally have dark lateral head stripe and faint tail bands; venter of all specimens pale white to white; chin, throat, and chest with suffusion of light brown flecks on each scale; ventral surface of tail usually heavily suffused with dark brown to black flecks, much darker than venter color.

*Comment.* This species is named in honor of Carl Koford, who has added much to our knowledge of the mammalian and reptilian fauna of Peru in the past twenty years.

*Habitat and natural history.* This small gecko is widespread and abundant in northwestern Peru. It has been found in every type of plant community from sea level to 650 m, except for the main dune areas of the Sechura Desert. This species is primarily a ground forager although it has been taken occasionally on boulders and plants. The daytime retreats of this lizard are usually holes beneath rocks, cracks in the ground, holes in sand banks, leaf litter at the base of plants, under or in hollow limbs of cacti, under bark of shrubs or stumps of rotting trees, in beach debris or trash dumped along the roadside. Occasionally a few individuals were found beneath exfoliating flakes of granite.

Eggs of this species were found under rotting cacti (mainly *Cereus*) in the Piura and Tumbes areas. One dead *Cereus* sp. plant contained 15 eggs of *P. kofordi* and 4 eggs of *reissi*. Eggs were not found in other types of cactus litter, nor in debris of acacia and mesquite. It appears that dead *Cereus* sp. affords the necessary protection for the survival of the eggs and this plant is sought out by females for egg deposition. This species lays one egg per clutch. Captive females laid a single egg and preserved females contained only one egg.

Gravid females and small juveniles were found in July, August, Novem-

ber, and December, indicating at least summer and winter breeding periods. Diurnal body temperatures were 8°C above the lizard's nocturnal temperatures during foraging periods.

This species is sympatric with *P. reissi* throughout most of its range, with *reissi* and *inaequalis* along the desert foothills, and with *reissi*, *clinatus*, and *microphyllus* in the Cerro Illescas area near the coast. Somewhere between Los Organos and Cancas (on the northwest coastline) the northern distribution of *microphyllus* terminates, and the habitat (beach dunes community) left vacant is effectively taken over by *kofordi* from Cancas to the Ecuadorian border. Both were found in the same general microhabitat near Talara (beach dunes) but *microphyllus* was much more abundant than *kofordi*.

*Distribution.* *Phyllodactylus kofordi* is a Peruvian species, found on the periphery of the Sechura Desert, western foothills of the Andes, and along the coast from Eten north to the Ecuadorian border. It probably occurs in the southwestern part of Lojas and the southern part of El Oro Departments, Ecuador (fig. 3).

Specimens (167) have been examined from the following localities: *Lambayeque*: Chiclayo MVZ 82221. Eten BMNH 1900.2.26.1. 5 km SSW Motupe MVZ 82209. 7 km S Motupe MVZ 82249-50, LACM 48540, 48559-66, TCWC 27912, 28107-14. 7.2 km W Naupe LACM 48543-46, TCWC 28117-20. 22 km E Olmos LACM 48541-42, TCWC 28115-16. *Piura*: Bayovar FMNH 9803. 1 km S Bayovar, Cerro Illescas MVZ 85268, 85290-91, 85293-304. 4 km SSE Bayovar MVZ 82203-05, 82230. 5 km SSE Bayovar MVZ 85287-89. 12 km S, 8 km E Bayovar MVZ 82176. Cerro Amotape MVZ 82193-94, 82210-16, 82233-37, 82239-40, 82242, 82281, 82284. Chongollapi AMNH 28465. 8 km S, 8.4 km SSE Chulucanas LACM 48547, TCWC 28121. Fondo MVZ 82274. 2 km NE Las Lomas MVZ 85259, 85278-84. 3 km ENE Las Lomas LACM 48556-58, TCWC 28131-34. 5 km E Las Lomas MVZ 82243-47, 82296. 30 mi S Lobitos BMNH 1932.9.5.1-2. 2 mi S Lobitos BMNH 1926.3.24.5. Negritos FMNH 8362. Paita AMNH 28460, 28462-64. Punta Aguja MVZ 82192, 82226, 82266-69. Reventazon MVZ 82229. 40 km WNW Sullana LACM 48548, TCWC 28122. Talara FMNH 57455. 2 km N Talara TCWC 28123. Tric Trac MVZ 82206, 85252-58, 85260-67, 85269-77, 85285, 85292, 85305-06. *Tumbes*: 1.2 km S Cancas LACM 48549-50, TCWC 28125-27. 1.2 km S, 1 km E Puerto Pizarro LACM 48551-55, TCWC 28128-30. Quebrada Seca FMNH 9810, TCWC 28124.

#### ***Phyllodactylus ventralis* O'Shaughnessy**

*Phyllodactylus ventralis* O'Shaughnessy 1875. Ann. & Mag. Nat. Hist., (4) 16:263.

*Phyllodactylus mulleri* Parker 1935. Ann. & Mag. Nat. Hist., (10) 15:483.

*Phyllodactylus underwoodi* Dixon 1962. Southwest. Nat., 7:218.

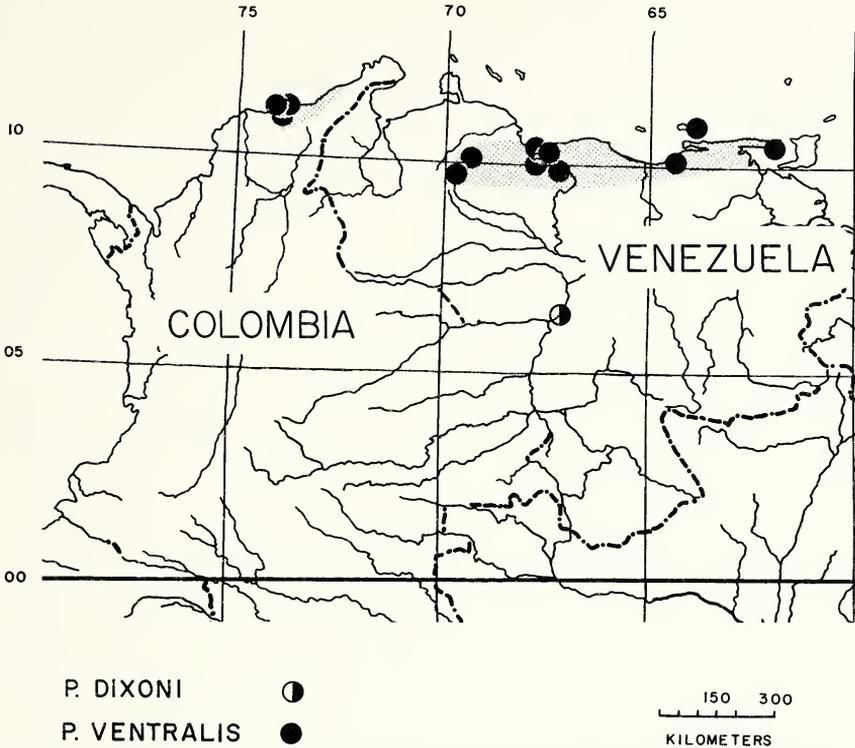


Figure 6. Distribution of *P. dixonii* and *P. ventralis* in northeastern South America.

*Holotype.* Adult male, BMNH 53.6.1.33, collector unknown, date of collection unknown. Type locality, Island of Jamaica (in error).

*Definition.* A large gecko with a maximum known snout-vent length of 75 mm; tibia and thigh tubercles present; ear denticulation usually present; enlarged preanal scale absent; terminal lamellae of digits distinctly widened and usually truncate at tips; median row of scales beneath tail distinctly widened; dorsal rows of enlarged tubercles close together, trihedral, and strongly carinate; six to eight rows of tubercles across base of tail; rear of head with rounded tubercles dispersed among granular scales (fig. 14a).

*Diagnosis.* *Phyllodactylus ventralis* is distinguished from *heterurus*, *gerhopygus*, and *angustidigitus* by the absence of an enlarged preanal scale; from *inaequalis* and *microphyllus* by the presence of regular rows of large trihedral, strongly keeled dorsal tubercles; from *clinatus*, *lepidopygus*, and *interandinus* by the presence of large tibia tubercles; from *johnwrighti*, *pumilus* and *reissi* by the presence of large tubercles on forearm; from *sentosus* by having terminal digital lamellae distinctly widened and enlarged; from

*kofordi* by greater maximum snout-vent length of 75 mm, rather than 46 mm; and 19 or more paravertebral tubercles between axilla and groin; from *dixoni* by having 24 or less scales across venter, rather than 26 or more, and dorsal tubercles four or more times the size of those in *dixoni*.

*Description.* Rostral about one and one half times higher than wide; two internasals, bordered posteriorly by small granular scales and postnasal of each side; nostril surrounded by rostral, labial, two postnasals and internasal; ventral edge of nostril scale in broad contact with first labial; deep depression between internasals and in frontal region; scales of posterior loreal region six to seven times larger than midorbital scales; eye large, contained in snout length about two times; eye brille with one to two rows of granules and one larger outer row of scales, posterior half are pointed; ear diameter contained in eye diameter about three times; ear opening slightly denticulate anteriorly, none posteriorly; rear of head with very large tubercles dispersed among granular scales; supralabials usually six to seven and infralabials five to six to a point below center of eye; mental slightly longer than wide, somewhat triangular in shape.

Dorsum with regular longitudinal rows of very large, trihedral tubercles, 10 to 14 rows reach nape, 6 to 8 rows reach base of tail; paravertebral rows of tubercles separated along median line by four to five rows of granules; postanal tubercles usually number three to four and very distinct in adult males.

Forearm with large trihedral tubercles dispersed among granular scales; upper arm with large flat scales; dorsal surface of thigh and tibia with 10 to 20 very large tubercles dispersed among granular scales; terminal digital lamellae large, either rounded or truncate; claw short, hidden when viewed from below.

*Variation.* Snout-vent lengths of adult males from 50 to 74 mm (62.4), adult females from 52 to 75 mm (62.3), subadults 40 to 45 (42.2), juveniles 24 and 29 mm; postmentals normally two, three occurring once in 22 specimens; postmentals contact first labial only in 25 per cent; first and second labials in 75 per cent of sample; scales bordering internasals vary from 4 to 6 (5.1); scales from nostril to eye vary from 9 to 12 (10.3); scales across snout at level of third labials vary from 17 to 23 (19.4); midorbital scales 12 to 17 (14.4); dorsum with 14 to 19 (16.4) longitudinal rows of enlarged trihedral tubercles; paravertebral tubercles from head to base of tail vary from 34 to 49 (41.2), axilla to groin 19 to 25 (22.1); venter scales from gular region to vent vary from 46 to 54 (52.0), across venter from 18 to 24 (20.6); fourth toe lamellae vary from 12 to 14 (13.6).

Color pattern varies from seven to 10 narrow, undulating, dark brown cross bands on a light brown to tan ground color, to a linear series of 10 to 20 dark brown spots on a yellowish brown ground color; dorsal surface of head generally brown with or without dark brown spots or reticulating lines;

side of head usually with a dark brown line from nostril through eye to arm insertion, bordered above and below by whitish lines or ground color; labials usually spotted or mottled with brown and dirty white; venter dirty white to yellowish brown.

*Comments.* In 1962 one of us (Dixon) described a new species, *Phyllodactylus underwoodi*, from the island of Grenada, Windward Islands. The holotype is the only available specimen and is unique in several features of scalation. Miss Alice G. C. Grandison (*personal communication*) informed us that there was an error in the labeling of this specimen, and it should have been labeled as Colombia. This specimen was a part of a relatively small collection made by F. A. Simons, purchased from a Mr. Janson by the British Museum of Natural History, and bore the locality New Grenada.

Dixon (1962) noted the similarity of *P. underwoodi* to *ventralis*, but it differed in three major scale characters. It is now apparent that *P. underwoodi* is likely an aberrant *ventralis*, having three postmentals, 14 rows of enlarged dorsal tubercles, and six rows of tubercles across the base of the tail. No specimens of *ventralis* from Colombia or Venezuela have this combination of scale counts. However, only 22 specimens of *P. ventralis* have been examined, and additional material may reveal a wider range of variation.

*Habitat and natural history.* This species has not been collected by either of us, therefore we rely upon information from the literature and from personal observations of others. Ruthven (1922) records *P. ventralis* from houses, buildings, under stones and bark of trees. Two specimens were found in a dry thorn forest and one in a thorny scrub and cacti association under a stone. Mechler (1968) found three specimens in debris of an abandoned house in Bonda, Colombia. Janis A. Roze (*personal communication*) states that *P. ventralis* occurs in dry, semixerophytic areas, but occasionally penetrates more moist habitats where cactus and thorny vegetation is replaced by a rich variety of shrubs and trees. Roze (1964) states that *P. ventralis* is often found in occupied houses, in abandoned buildings, and trees near buildings. Roze indicated that competition between *Thecadactylus rapicauda* and *P. ventralis* for human dwellings is being won by *T. rapicauda*.

*Distribution.* This species is found in the dry thorn forests and savannahs of northern Venezuela and Colombia (fig. 6).

Specimens (22) have been examined from the following localities: COLOMBIA. *Magdalena*: Bolivar UMMZ 54737. "Grenada" BMNH 1880.2.26.6. Santa Marta UMMZ 48177. Santa Marta Mountains MCZ 24881, UMMZ 45462-63. VENEZUELA. *Anzoátegui*: Barcelona MBUCV 3144. *Aragua*: Maracay MCZ 39980. *Carabobo*: Caizuire MBUCV 3151. Isla de Burro MBUCV 3143. *Falcón*: Coro MBUCV 3148. *Guárico*: San Juan de los Morros MBUCV 3149. Sosa MBUCV 3145. *Portuguesa*: Acarigua MCZ (unnumbered). Aparicion MBUCV 3146. *Sucre*: Isla Patos BMNH 1935.10.1. 10-11, 1940.2.15.1, 1945.11.1.41-42. Puerto de Hierro MCZ 50744-45.

**Phyllodactylus dixonii** Rivero-Blanco and Lancini

*Phyllodactylus dixonii* Rivero-Blanco and Lancini 1968. Mem. Soc. Cienc. Nat. La Salle, 27: 168.

*Holotype*. Adult female, MBUCV III-8.450, collected by Juhani Ojasti in a cave on 5 October 1964. Type locality, Desembocadura del Rio Parguaza, afluyente del Orinoco Medio en el Estado Bolivar, Venezuela.

*Definition*. A large gecko with a maximum known snout-vent length of 76 mm; tibia, thigh, and forearm tubercles present; ear with little or no denticulation; enlarged preanal scale absent; terminal lamellae of digits distinctly widened and truncate; median row of scales beneath tail distinctly widened; dorsal rows of enlarged tubercles somewhat small, low and slightly trihedral; each dorsal row of tubercles separated from the other by three to five rows of granules; six to eight rows of dorsal tubercles across base of tail; rear of head with rounded tubercles dispersed among granular scales, almost subequal in size (fig. 14b).

*Diagnosis*. *Phyllodactylus dixonii* may be distinguished from all other mainland species except *ventralis*, by having no enlarged preanal scale; regular dorsal rows of keeled tubercles; presence of tubercles on forearm, thigh and tibia; distinctly enlarged and widened terminal digital lamellae; large maximum snout-vent length of 76 mm; 23 or more paravertebral tubercles between axilla and groin; from *ventralis* by having dorsal tubercles about one fourth the size of those of *ventralis*; 26 or more scales across the venter rather than 24 or less.

*Description*. Rostral twice as wide as high, its dorsal edge with median vertical groove about one half depth of rostral; two internasals, bordered posteriorly by small granules and postnasal of each side; nostril surrounded by rostral, labial, internasal and two postnasals; first labial in broad contact with ventral edge of nostril scale; shallow depression between internasals, moderate depression in frontal region; scales in posterior area of loreal region about three to four times larger than scales in midorbital region; eye large, its diameter contained in snout length about 1.5 times; eye brille with two rows of granules and one larger outer row of scales, last five to eight pointed; ear diameter contained in eye diameter about two times; ear opening without denticulation, scales on posterior and anterior borders rounded; rear of head with granular scales with slightly larger rounded and elevated scales intermixed; supralabials six to seven and infralabials five to six to a point below center of eye; mental bell shaped, about as wide as long; two postmentals, slightly longer than wide and in contact on median line; postmentals contact only first labial.

Dorsum with regular rows of enlarged, keeled tubercles that are somewhat oval in outline; paravertebral rows separated from each other by four to five rows of granules; 10 rows of dorsal tubercles reach nape, 6 to 8 reach

base of tail; postanal tubercles number three to four on each side in males; venter scales abruptly differentiated from lateral body granules.

Dorsal surface of upper arm with flattened scales; posterodorsal surface of forearm with tubercles interspersed among small scales; dorsal surface of thigh with 15 to 25 tubercles dispersed among smaller flattened scales; tibia with large tubercles dispersed among granular scales; terminal lamellae large, somewhat truncate, about twice as long as wide; claw long, visible when viewed from below.

*Variation.* The known snout-vent lengths of adults range from 56 to 76 mm (67.8), subadults 39 and 46 mm, juvenile lengths unknown; scales bordering postmentals vary from 5 to 8 (6.1); scales from nostril to eye vary from 11 to 12 (11.3); scales across snout at level of third labials vary from 17 to 20 (18.6), midorbital scales 15 to 19 (17.5); scales bordering internasals vary from 5 to 6 (5.1); longitudinal rows of enlarged dorsal tubercles vary from 13 to 16 (14.9); number of paravertebral tubercles from head to base of tail vary from 41 to 50 (46.7), axilla to groin 23 to 26 (24.7); venter scales from gular region to vent vary from 59 to 66 (61.7), across venter 26 to 28 (27.1); fourth toe lamellae vary from 11 to 13 (11.3).

Dorsal color pattern usually consists of five to eight undulating, dark brown cross bands on a brownish gray ground color from occiput to base of tail; tail banded with dark brown and light gray in juveniles, sometimes irregular bands or spots in adults; head usually brownish gray with a suffusion of dark brown spots; labials spotted with dark brown; venter usually brownish cream; lower sides of body brownish yellow; ventral surfaces of toes dark brown.

*Habitat and natural history.* Dr. Janis Roze (*personal communication*) states that the type series of *P. dixonii* was taken from beneath flakes of black basaltic rocks. The flakes were associated with immense, grayish black rock bluffs some 500 meters from the mouth of the Rio Parguaza. The immediate vicinity was essentially void of vegetation except for a few scattered shrubs and bromeliads. During the day, the temperature of the rocks reached 60°C and the lizards took refuge beneath flakes or within cracks of boulders.

The majority of lizards were taken by breaking off the rock flakes or by beating upon the flakes until the lizards ran out. Some lizards were observed running about in the late afternoon in the shade of scant vegetation or in the shade of rock boulders (Roze, *personal communication*).

*Distribution.* *Phyllodactylus dixonii* is known only from the type locality. The type locality is approximately 35 km NE of Puerto Carreno, Colombia, and 385 km (airline) south of San Juan de los Morros, Venezuela, the nearest locality of *P. ventralis* (fig. 6).

Seven specimens have been examined from the following locality:

VENEZUELA. *Bolivar*: mouth of Rio Parguaza, on the Rio Orinoco MCNC 5479-80, MBUCV III 8451-54, TCWC 23827.

***Phyllodactylus sentosus* sp. nov.**

*Phyllodactylus phacophorus*, (part) Boulenger 1885, Cat. Lizards in the British Museum (Natural History) 2:84.

*Holotype*. Adult female, TCWC 27913. Collected by Fortunato Blancas, November 1949; Type locality, Lima, Department of Lima, Peru.

*Definition*. An average-sized gecko with maximum snout-vent length of 56 mm; large preanal plate absent; very large trihedral tubercles present on dorsum, forearm, thigh, tibia, and tail; ear denticulate on anterior and posterior margins; median row of scales beneath tail with few scales slightly enlarged, rounded; tail 45 to 50 per cent of total length; terminal lamellae of digits separated along median line, small, claw visible between and beyond tip of terminal lamellae when viewed from below (fig. 12a).

*Diagnosis*. This species may be distinguished from all other western South American species except *P. kofordi*, by the presence of very large tubercles on dorsum, thigh, tibia, forearm, and tail. *Phyllodactylus sentosus* differs from *kofordi* by having very small terminal lamellae on the digits and generally uniform sized scales beneath ventral surface of tail, rather than terminal lamellae large and all scales of median row beneath tail enlarged, rectangular.

*Description of holotype*. Rostral completely divided by vertical groove, twice as wide as high, its dorsal and lateral edges straight; two internasals, somewhat rounded, their median edges in narrow contact, bordered posteriorly by four granules and supranasal of each side; nostril surrounded by rostral, labial, supranasal, and one postnasal; first supralabial in narrow contact with ventral edge of nostril; no depression between internasals, slight depression in frontal region; 9 scales between eye and nostril, scales in posterior loreal region about three to four times larger than scales in midorbital region; 18 scales across snout at level of third labials, 12 scales across head between anterior edge of eyes, 14 midorbital scales; eye large, its diameter contained in snout length 1.7 times; eyelid with one to two rows of granules and one larger outer row of scales, last four to five are pointed; ear diameter contained in eye diameter 2.3 times; ear opening denticulate, scales on anterior and posterior margins pointed; rear of head granular with many larger intermixed tubercles; six supralabials and five infralabials to a point below center of eye; mental bell-shaped, slightly longer than wide, bordered posteriorly by three postmentals; postmentals rounded, slightly longer than wide, their median edges in broad contact, followed by transverse row of eight small scales, followed by second row of 11 smaller scales; postmentals contact first labial.

Dorsum with 16 longitudinal rows of enlarged, trihedral tubercles, paravertebral row with 26 tubercles from rear of head to base of tail, 13 between axilla and groin; paravertebral rows separated from each other by three rows of granules; 10 rows of tubercles reach to rear of head, 8 to base of tail; each tubercle of enlarged dorsal series separated from preceding tubercle by one to two granules; postanal tubercles number three on each side;

venter with 18 longitudinal and 48 transverse rows of scales; tail with 8 rows of tubercles in proximal eight whorls, distal one-third of tail regenerated.

Dorsal surface of upper arm with flattened scales, forearm with larger tubercles interspersed among smaller flattened scales; dorsal surface of thigh with 8 to 9 tubercles interspersed among granular scales, tibia with 13 to 15 tubercles; lamellae formula for hand 6-8-12-11-8, foot 7-10-11-12-10; claw largely visible between and beyond tip of terminal lamellae when viewed from below; terminal lamellae small, about three times as long as wide.

Measurements in mm: Snout-vent length 50.0; axilla-groin length 25.0; leg length 19.3; arm length 16.0; tail length 46.3; head length 9.6; head height 7.8; head width 9.6; snout length 5.1; distance from eye to ear 4.6; eye diameter 3.0; ear diameter 1.3.

Color in alcohol: ground color fawn; dorsum with nine undulating crossbands of reddish brown, first two crossbands complete, remainder broken along midline of dorsum by cream middorsal stripe that begins about level of shoulder; each dorsal tubercle generally flecked with dark brown; limbs with brownish spots, forming faint reticulations on ground color; tail with six brown crossbands, about one-half width of ground color interspaces; distal one-third of tail regenerated; head brownish with wash of light brown; dark brown stripe from nostril to posterior edge of ear, bordered above by cream line on snout, above and below by cream line between eye and ear; ventral surfaces pale white, scales below tail with flecks of brown.

*Variation.* Snout-vent length of two males 49 and 56 mm (52.5); two females 39 and 50 mm (44.5); postmentals number two in three specimens, three in one; postmentals contact first labial only in all; number of scales across chin immediately following postmentals varies from 6 to 8 (7.3); number of scales bordering posterior edge of internasals vary from 5 to 7 (6.3), with internasals completely separated by an azygous scale in two of four specimens; scales across snout at level of third labial varies from 16 to 18 (16.5) midorbital scales vary from 13 to 14 (13.3); scales across venter vary from 18 to 21 (19.3); longitudinally 47 to 55 (50.3); number of enlarged rows of dorsal tubercles vary from 14 to 16 (15.0); number of paravertebral tubercles from rear of head to base of tail vary from 26 to 31 (28.8); from axilla to groin 13 to 16 (15.0); scales along line from nostril to eye vary from 9 to 10 (9.3); number of fourth toe lamellae vary from 12 to 13 (12.5); terminal lamellae of all digits very small, twice as long as wide; claw visible beyond tip of pad when viewed from below; number of enlarged rows of tubercles at base of tail number 8 in three specimens, 6 in one; 8 tubercles occur in each of 8 to 11 whorls on proximal two-thirds of tail, reducing rapidly in sequence to 6-4-2-0 on distal third of tail; median row of scales beneath tail generally uniform in size to other scales but occasionally a larger, rounded scale may be present.

Number of dorsal body bands varies from 8 to 10 (9.0), with majority of bands broken along midline of body in three specimens, bands loosely con-

nect and form reticulated pattern in one; tail bands number 13 and 14 in two specimens with complete tails; venter pale white to dirty cream; dark lateral face stripe continues to shoulder region as dashed line in two specimens, reaches to ear in two.

*Comments.* *Phyllodactylus sentosus* closely resembles *kofordi* (NW Peru), *darwini* (Galapagos Islands), *wirshingi* (Puerto Rico), and *martini* (Dutch Leeward Islands) in general appearance. The latter four species have enlarged trihedral tubercles on the dorsum, tail, thigh, tibia, and forearm. However, the four species have the median row of scales beneath the tail much enlarged and widened, and have moderately large, well defined terminal lamellae on all digits. In addition, *martini* and *wirshingi* have higher numbers of enlarged rows of dorsal tubercles (18 to 20) and higher numbers of paravertebral tubercles from head to base of tail (32 to 40). The number of enlarged dorsal rows of tubercles in *darwini* are identical with those of *sentosus*, but *darwini* has higher numbers of paravertebral tubercles from head to base of tail (33 to 38) and differs in several other features of squamation.

*Natural history.* The only known habitat of this species is the grounds surrounding the University of San Marcos in Lima. Dr. Gambini (*personal communication*) indicated that she found one specimen running across a sidewalk on the campus just after dark.

*Distribution.* Known from the University of San Marcos campus, Lima, Peru, and from the vicinity of the city (fig. 5). Six specimens have been examined: Lima: Lima BMNH 63.2.3.18-19, TCWC 27913, 28329-31.

### **Phyllodactylus reissi** Peters

*Phyllodactylus reissi* Peters, W. 1862. Monatsb. Konigl. Akad. Wiss. Berlin, Nov., 1862, pp. 626-27.

*Phyllodactylus baessleri* Werner 1901. Abh. u. Ber. d.k. Zool. u. Anthr.-Ethn. Mus. zu. Dresden, 9(2):2.

*Phyllodactylus guayaquilensis* Werner 1910. Mitt. Naturh. Mus. Hamburg, 27(2):4.

*Phyllodactylus abrupteseriatus* Werner 1912. Mitt. Naturh. Mus. Hamburg, 30:4.

*Phyllodactylus magister* Noble 1924. Occ. Pap. Boston Soc. Nat. Hist., 5:110.

*Syntypes.* Berlin Mus. 3734 (4), 4567 (2); BM 4567, ad. female, snout-vent 64 mm, herein selected as the Lectotype; Carl Reiss, collector; date of collection unknown. Type locality: Guayaquil, Ecuador.

*Definition.* A large gecko, maximum snout-vent length of 75 mm; femur tubercles absent, tibia tubercles present; ear strongly denticulate on anterior and posterior margins; enlarged tubercles on rear of head present; median row of scales beneath tail distinctly widened; enlarged preanal plate absent; 12 to 18 rows of enlarged trihedral tubercles on dorsum; tail about 48 to 58

per cent of total length, without whorls of enlarged tubercles; terminal lamellae of digits moderately enlarged, truncate; dorsal color pattern variable, uniform in color to bold bands; venter usually yellowish (fig. 13b).

*Diagnosis.* This species may be distinguished from *P. heterurus*, *angustidigitus*, and *gerrhopygus* by the absence of enlarged preanal plate; from *lepidopygus*, *microphyllus*, *clinatus*, and *inaequalis* by the presence of tibia tubercles and larger size; from *interandinus* by its larger size (average s-v of 58.3 mm rather than 40.1 mm), fewer number of head to tail tubercles in paravertebral row, 47 to 60 rather than 64 to 81; from *kofordi* by its larger size (as above) rather than average of 44.0 mm, and by having more head to tail tubercles in paravertebral row (as above) rather than 31 to 36; from *johnwrighti* and *pumilus* by larger size, a maximum snout-vent length of 75 mm rather than 51 mm; thigh tubercles absent, rather than present; from *sentosus* by absence of tail and forearm tubercles, larger scales in median row beneath tail, larger terminal lamellae, and color pattern.

*Description.* Rostral about twice as wide as high; internasals rounded, their median edges in broad contact, bordered posteriorly by small granules and postnasal of each side; nostril surrounded by rostral, labial, internasal, and two postnasals; first labial in broad contact with ventral edge of nostril; shallow depression between internasals, deep depression in frontal region; scales in posterior loreal region about 3 to 4 times larger than midorbital scales; eye large, its diameter contained in snout length about 1.8 times; eyelid with 2 rows of granules and 1 larger outer row of scales, last 3 to 6 of which are pointed; diameter of ear contained in eye diameter about 2.1 times; ear opening strongly denticulate with pointed scales on the anterior and posterior margins; rear of head granular with larger intermixed tubercles; 6 to 7 supralabials and 5 to 6 infralabials to a point below center of eye; mental bell shaped, as wide as long, bordered posteriorly by two to four postmentals; postmentals slightly longer than wide, their median edges in broad contact.

Dorsum with longitudinal rows of enlarged trihedral tubercles that are somewhat elevated; paravertebral rows separated from each other by 4 to 5 rows of granules; 6 rows of tubercles reach to nape, 6 to base of tail; each tubercle of enlarged dorsal series separated from preceding tubercle by 0 to 2 granules; postanal tubercles number 4 on each side, distinct and slightly elevated posteriorly in males; dorsal surface of upperarm with flattened scales, forearm with slightly larger flattened scales; dorsal surface of thigh without tubercles intermixed among smaller flattened scales; tibia with large tubercles scattered among granular scales; claw slightly visible when viewed from below; terminal pad large, slightly longer than wide, somewhat truncate at tip.

*Variation.* Snout-vent length of subadult and adult males range from 42 to 75 mm (59.4), females from 37 to 73 mm (57.5), juveniles from 22 to 35 mm (28.9), and males plus females average 58.3 mm; 48 per cent of total sample (753 specimens) were 60 mm or more in snout-vent length; postmentals vary from two to four, two occurring 97.4 per cent of the time, three

1.9 per cent and four 0.7 per cent; postmentals contact the first labial only in 96.8 per cent of sample, first and second labials 3.2 per cent; number of scales immediately following postmentals across chin vary from 5 to 8 (6.3); scales across midorbital region vary from 16 to 24 (20.2); scales across snout at level of third labial vary from 18 to 27 (23.7); scales bordering internasals posteriorly vary from 5 to 9 (6.7) with an azygous scale separating the internasals in 23.1 per cent of sample; transverse rows of scales across venter vary from 24 to 37 (29.7), longitudinally 54 to 77 (60.0); dorsal tubercular rows vary from 12 to 18 (13.2); paravertebral tubercles from head to tail vary from 47 to 60 (53.0); between axilla and groin 25 to 38 (31.3); scales along a line between nostril and eye vary from 10 to 16 (12.5); lamellae beneath fourth toe vary from 11 to 17 (13.5).

Dorsal color pattern highly variable, ranging from uniform yellowish tan without darker markings to light gray ground color with bold black undulating crossbands half the width of ground color interspaces; those with dark dorsal markings on ground color may have spots, crossbands, blotches, or lines that are either bold black, dark brown, brown, to indistinct grayish brown; in a few specimens the lines coalesce, forming a variegated pattern; when body markings are distinct enough to be counted, they generally vary from 5 to 7 pairs or single bands.

Coloration of dorsal surface of tail somewhat similar to that of dorsum; when bands are present they vary from 8 to 11 with 9 and 10 being most common; interspaces usually lighter than those of dorsum, tending to be more in contrast with darker bands; dorsal surface of head is either uniform in color, spotted or reticulated with dark brown to black lines or spots on ground color; side of head with or without distinct dark line from nostril through eye to arm; limbs similar to dorsum in color and pattern, with forearm and lower leg generally banded with dark on ground color in most specimens.

Ventral surfaces generally grayish white in alcohol (uniform pale yellow to tan with yellowish cast in life), with dark color of sides encroaching on venter in large individuals; ventral surface of tail usually darker than venter.

An examination of three populations of *P. reissi* from the coastal and coastal foothills of Ecuador, desert foothills surrounding the Sechura Desert of Peru, and the Marañon-Chinchipe Valley of northern Peru reveal very little variation in the majority of characters. The Ecuadoran population has an azygous scale separating the internasals in 43.1 per cent of the sample, 32.3 per cent in the Sechura Desert sample, and 14.3 per cent in the Marañon-Chinchipe sample. The number of enlarged dorsal tubercular rows vary from 12 to 16 (14 the common number), 12 to 16 (12 common), and 14 to 18 (16 common) respectively, in the three samples indicated above.

*Comments.* The types of *P. baessleri*, *abrupteseriatus*, and *quayaquilensis* were destroyed during World War II, but the characters mentioned in the

original descriptions of the latter two species fall within the variation present in *reissi*. An analysis of the characters of a large sample of *magister* from the *Marañon* and *Chinchipe* Valleys of Peru indicates only minor differences between it and populations of *reissi* from Ecuador and northern Peru. We, therefore, consider *abrupteseriatus*, *guayaquilensis*, and *magister* as subjective synonyms of *reissi*.

Werner's (1901) original description of *P. baessleri* is the only evidence we have for comparison of his species with those known to occur in Peru. His description does not correspond in its entirety to any population of *Phyllodactylus* we currently recognize in Peru. A translation of Werner's (1901, p. 2) original description follows:

"Closely related to *P. tuberculosus*, snout one and a half times as long as eye, somewhat longer than distance between eye and ear; frontal region with slight concave; ear opening diagonal, small diameter of ear one half that of eye; snout with large flattened, rounded scales, those of the rear of the head smaller, here they seem to differ by being mixed with small rounded tubercles; ear opening with three pointed scales on the anterior margin; rostral four-sided, the posterior margin with a short median notch; nostril surrounded by first labial and three nasals, of which the upper one contacts the upper nasal of the other side; 7-8 upper labials, 6th below eye; 7 infralabials; mental large, bell-shaped, followed by two small polygonal postmentals in contact with each other; followed by successfully smaller scales in size; upper side of rump with 12 rows of strongly keeled tubercles, tubercles of each row close together; the two outer rows near the venter do not reach the forelimb; venter scales flat, overlapping, cycloid-hexagonal; tibia with enlarged keeled tubercles on the upper side; finger and toe ending with strongly enlarged lamellae, similar to *P. tuberculosus*; 4th toe with 16 lamellae, of which the distal one and mostly proximal ones are divided.

Color above, light grayish brown with black spots on head, tail, base of tail and legs; four long, black, parallel lines, from rear of eye to base of foreleg, two from back of head to middle of back, between the limbs; underside whitish.

Total length 91 mm, most of tail regenerated (39 mm); The single example on hand (D 1780 M. Dr.) came from Chanchamayo. The species is named in honor of Prof. A. Baessler."

From Werner's description (1901), we may eliminate the Peruvian species without strongly keeled tubercles on the dorsum, i.e. *P. microphyllus*, *inaequalis*, *gerrhopygus*, *angustidigitus*, and *heterurus*. His description mentions the presence of tibial tubercles, therefore we may eliminate *clinatus*, *interandinus*, and *lepidopygus*. The remaining species, *reissi*, *johnwrighti*, *sentosus*, and *kofordi* agree in part with his original description.

The latter four species have denticulate scales on the anterior and posterior margins of the ear, tibia tubercles, and strongly keeled dorsal tubercles.

Of these four species, only *P. reissi* has a fourth toe lamellae count (12 to 17) that falls within the range given by Werner for *baessleri*. Occasionally, *P. interandinus* has a few small tubercles on the tibia.

The color description given by Werner (1901) does not agree with any species of *Phyllodactylus* in Peru, while all other features mentioned in his original description agree with most of the species.

Werner's type locality, Chanchamayo, is also questionable. Chanchamayo is a well known, tropical lowland locality at the headwaters of the Rio Perene on the east side of the Andes. There are no known species of *Phyllodactylus* inhabiting the selva of eastern Peru.

We provisionally place *P. baessleri* as a subjective synonym of *reissi*, based upon the destruction of the holotype, a possible error in the type locality, and discrepancies in the original description when compared with known species in Peru.

*Habitat and natural history.* *Phyllodactylus reissi* is the most abundant scansorial gecko of northern Peru. Daytime retreats consist of any object that affords protection from predators and adverse temperatures. Individuals were found beneath bark of living, dead, standing, or prone trees, fence posts, fallen banana plants, standing and prone cacti, cracks in adobe walls, crevices in boulders, knot holes in trees, beneath bridges, rotting tree stumps, beneath palm leaves, construction materials and fruit crates. Their nocturnal activities were essentially on vertical surfaces, i.e., trunks of trees, walls of buildings, boulders, cacti, and fence posts, but occasionally were found actively foraging on the ground. Several were found foraging on open ground two to three meters from large boulders and in leaf litter in cacao groves.

This species is always found in association with some type of plant cover.

When exposed to daylight, *P. reissi* actively seeks a dark place to hide. When exposed in its daytime retreat, it hesitates only a few seconds before rapidly moving to another dark retreat. Its movements are usually vertical, but on horizontal limbs or tree trunks *reissi* usually runs to the ventral surfaces.

Two eggs are laid and usually deposited in rotting debris at the base of trees, beneath leaf litter in forests, in rotting agave stumps, hollow branches of dead cacti filled with debris, or in any rotting debris associated with its general habitat.

*Phyllodactylus reissi* has been found occupying the same cactus plant with *interandinus* in the upper Amazon Basin, and with *kofordi* in northwestern Peru. It has been found on the same tree with *Pseudogonatodes barboursi* and *Gonatodes atricucullaris*, and in the same general habitat with *inaequalis*, *clinatus*, and *microphyllus*.

As in all of the species of *Phyllodactylus* found in Peru, the nocturnal body temperatures of *reissi* closely approximated that of the substratum upon which it was active.

*Distribution.* This species is found from sea level to about 2,000 m in southern Ecuador and northwestern Peru. Its principal habitat seems to be

arid tropical scrub west of the Andes, and cacti dominated areas of the northern interandean basins of Peru (fig. 5).

Specimens (772) have been examined from the following localities:

ECUADOR. *Azuay*: 4 km E San Francisco USNM 167183 (23). *El Oro*: Machacha USNM 167182. Santa Rosa AMNH 22068. *Guayas*: Ancon Camp BMNH 1931.10.21.1-2. 6 km SW Colonche USNM 167189. Daule River MCZ 4740 (2). Guayaquil AMNH 21845. ANSP 7526. BM 3734 (4), 4567 (2). CMF 16504, 16540-46, 16658-61, 16676, 16695, 16700, 16850-51, 16889-900. EPN 4618 (18). FMNH 61210. HM 3386. Playas MVZ 77217-20, 77268. USNM 167181. Poza Huancaulca CMF 16512, 16515. Puente Chimbo AMNH 24343. Puna CAS 84770. 1 km NW Punta Cornero USNM 167190 (6). 0.5 km N Punta Cornero USNM 167191 (10). Salinas CMF 16531. *Loja*: BMNH 1930.10.12.13. Rio Casanga AMNH 18304-05. *Manabi*: Manta CMF 16522; FMNH 53896-98. 1 km S Manta USNM 167186 (5). 6 km E Manta, 5 km W Montecristi USNM 167188 (8). No specific locality in Ecuador AMNH 64569 (4); ANSP 7530; USNM 14052-53.

PERU. *Amazonas*: 14 km S Bagua Chica TCWC 28259. 17 km S Bagua Chica LACM 48766-72, TCWC 28260-64. 19 km S Bagua Chica LACM 48739-58, 48786; TCWC 28228-49. 10 km WSW Bagua Grande MVZ 82301. 8 km WSW Bagua Grande MVZ 82208, 82302-06. 15.5 km WSW Bagua Grande LACM 48759-64. TCWC 28250-55. 3.5 km SE Bagua Grande LACM 48765. TCWC 28256-58. *Cajamarca*: Bellavista AMNH 28525-27, 39339-40. FMNH 73379. LACM 48734-38. MCZ 42233 (3), 18126-29, 18141-42 (+ 208 unnumbered). TCWC 24923, 28210-21. UIMNH 41515, 40747. UMMZ 59029 (4). 4.8 km S Bellavista LACM 48734-38. TCWC 28222-27. Perico FMNH 100182-83. MCZ 17974, 18145-50. *Lambayeque*: 11 km N Jayanca MVZ 82197-201. 5 km SSW Motupe MVZ 82299. 7 km S Motupe LACM 48707-21, 48811-29. MVZ 82300; TCWC 28175-208. 15 km S Naupe MVZ 82202. 7.2 km W Naupe LACM 48773-74. TCWC 28265. 22 km E Olmos TCWC 28209. *Libertad*: Chiclin FMNH 34266. Pacasmayo HM (3 unnumbered); SMFM 8285, 8289. USNM 167180. *Piura*: Bayovar FMNH 9798-802, 9804. 1 km S Bayovar (Cerro Illescas) MVZ 85308-09, 85316-28. 1.1 km E Bocana LACM 48810. TCWC 28278-79. 1 km N, 28 km E Cabo Blanco MVZ 82177, 82232, 82280. Capullana Point FMNH 41551. Catalinas FMNH 9816-17. Cerro Amotape MVZ 82169, 82173, 82195, 82217-18, 82238, 82241, 82282, 82285-95. 8 km S, 8.4 km ESE Chulucanas LACM 48775-81. TCWC 28266-71. 2.4 km SW Chulucanas LACM 48782, TCWC 28272-73. El Alto FMNH 41548, 41550. Fondo MVZ 82272-73. La Breita BMNH 1926.3.24.6. 5 km E Las Lomas MVZ 82219-20, 82297-98. 2 km NE Las Lomas MVZ 85310-15. 3 km ENE Las Lomas LACM 48802-09. TCWC 28297-304. 5 km E, 4.2 km NNE Lobitos LACM 48798-801. TCWC 28291-96. Monte Grande MVZ 82279. Negritos FMNH 8364-65, 8384. Parinas MVZ 82207, 82276-77. Punta Sal SMFM 41913. Sechura Desert CAS 92346. 40 km WNW Sullana LACM 48783-84; TCWC 28274-75. 4 mi W Suyo

TCWC 24072-91. Talara AMNH 66600-01; FMNH 41547, 41549, 53895, 53892-93, 57456. 1 km SW Talara MVZ 82275. 2 km E Talara LACM 48785; TCWC 28276-77. Tamboa AMNH 28426-27. Tric Trac MVZ 85307. between Verdun Alto and Negritos FMNH 41546. *Tumbes*: Las Vocas USNM 38569. 1.2 km S, 1 km E Puerto Pizzaro LACM 48792-97; TCWC 28285-90. Quebrada Seca FMNH 9809, 9811-12; LACM 48787-91; TCWC 28280-84. no specific locality in Peru ANSP 13121; FMNH 41552-53; SMFM 8290.

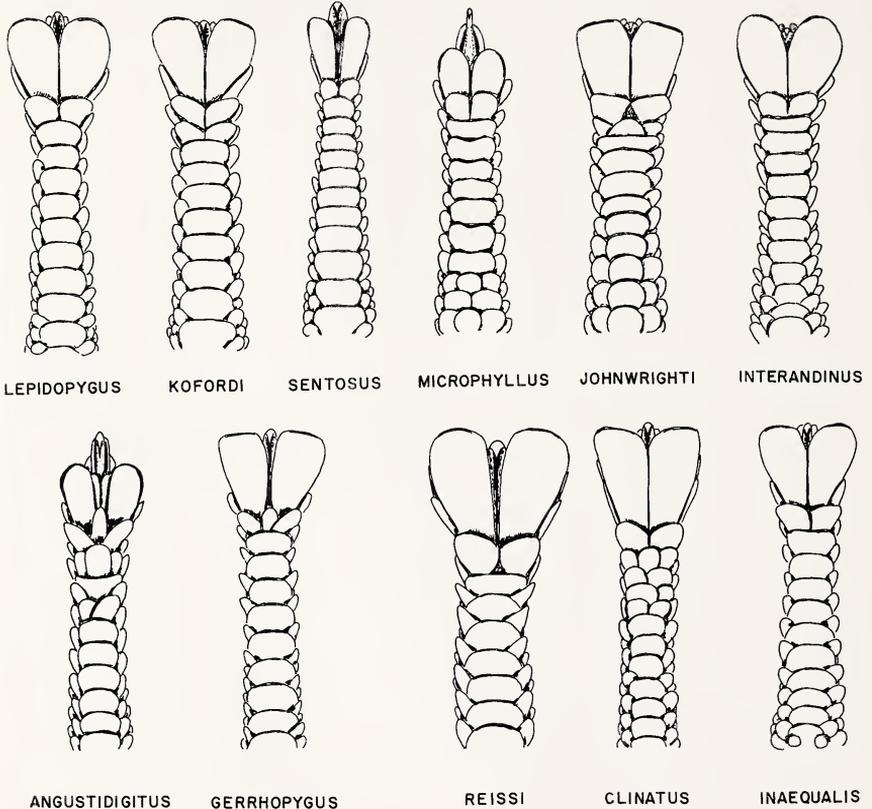


Figure 7. Ventral view of the fourth toe of all species of *Phyllodactylus* (except *heterurus* and *pumilis*) found on the mainland of western South America.

***Phyllodactylus johnwrighti* sp. nov.**

*Phyllodactylus phacophorus*, (part) Noble 1924, Occ. Paps. Boston Soc. Nat. Hist., 5:111.

*Holotype*. Adult male, TCWC 27916, collected by James R. Dixon and John W. Wright, 28 November 1968. Type locality. 13 km SSE (by road) Hacienda Molino Viejo, 1190 m, Department of Cajamarca, Peru.

*Definition.* A small gecko with a known maximum snout-vent length of 50 mm; enlarged preanal shield absent; dorsum and tibia with tubercles, absent from thigh, forearm, and tail; some scales of median row beneath tail widened and rounded; tail length about 49 per cent of total length; terminal lamellae moderately enlarged, rectangular; dark stripe from nostril to arm insertion always present (fig. 10b).

*Diagnosis.* This species differs from *P. angustidigitus*, *gerrhopygus* and *heterurus* by the absence of enlarged preanal shield; from *interandinus* by absence of dorsal stripes, presence of tubercles on tibia, and maximum number of 49 tubercles in paravertebral row from head to tail, rather than minimum of 65 in *interandinus*; from *kofordi* and *sentosus* by absence of forearm, tail, and thigh tubercles; from *reissi* by smaller maximum size, 50 mm rather than 75 mm, and absence of wide, rectangular row of scales beneath tail; from *microphyllus* and *inaequalis* by presence of regular longitudinal rows of enlarged trihedral tubercles on dorsum, from *lepidopygus* and *clinatus* by presence of tibia tubercles; from *pumilus* by absence of tail tubercles and smaller supraorbital scales.

*Description of holotype.* Rostral rectangular, twice as wide as high, its dorsal edge with vertical groove one-half depth of rostral; two internasals, subrectangular, their median groove edges separated by two granules; internasals bordered by rostral, nostril, six granules and postnasal of each side; nostril surrounded by rostral, labial, internasal, and two postnasals; first labial in broad contact with ventral edge of nostril; slight depression between internasals and in frontal region; 10 scales between eye and nostril; scales in posterior loreal region about 2.5 times larger than midorbital scales; 22 scales across snout at level of third labial, 14 scales across anterior edge of orbits, 20 midorbital scales; eye large, its diameter contained in snout length 1.6 times; eyelid with two rows of granules and one larger outer row of scales, last three to four are pointed; ear diameter contained in eye diameter 2.4 times; ear opening slightly denticulate, scales on anterior and posterior margins small, rounded and subequal; rear of head granular with intermixed tubercles; six supralabials and five infralabials to point below center of eye; mental bell-shaped, as wide as long, bordered posteriorly by two postmentals; postmentals rounded, slightly larger than other chin scales, their median edges in broad contact; postmentals immediately followed by transverse row of 7 scales, followed by second row of 10 smaller scales; postmentals contact first labial only of each side.

Dorsum with 14 longitudinal rows of enlarged trihedral tubercles; 10 rows reach to nape, 6 to base of tail; paravertebral row of 45 tubercles from head to tail, 26 between axilla and groin; paravertebral rows of tubercles separated from each other by five rows of granules, each tubercle separated from preceding tubercle by one to two granules; postanal tubercles three on each side; 26 scales across venter, 55 from throat to vent; tail without tubercles, median row of scales beneath tail with every other scale distinctly



Figure 8. (a) dorsolateral view of *P. angustidigitus*; (b) ventral view of preanal plate of *P. angustidigitus*.

widened; arms and thigh with small flattened scales; thigh with five to six tubercles intermixed among scales; tibia with 17 to 19 tubercles intermixed among granules; lamellae formula for hand 6-8-9-10-8, foot 7-9-11-12-11; claw slightly visible when viewed from below; terminal lamellae large, rectangular, longer than wide.

Measurements in mm: Snout-vent length 39.0, axilla-groin length 17.4, leg length 14.8, arm length 11.8, tail length 34.0, head length 11.1, head depth 4.5, head width 7.6, snout length 4.2, eye diameter 2.7, ear diameter 1.1, distance from eye to ear 3.3.

Color in life: Ground color grayish tan; dorsum without distinct bands; grayish brown spots on anterior half of body, fading posteriorly; grayish yellow median stripe from nape to base of tail; posterior edge of scales on limbs stippled with dark brown, rest of scale ground color; head with diffuse spotting of grayish brown; grayish brown line from nostril to above arm insertion, bordered above by dirty cream line from nostril to ear; tail with 2 brownish black bands with yellowish brown interspaces; ventral surfaces dirty gray, with three to five black dots on each scale, more dense on tail.

*Variation.* Snout-vent lengths of subadult and adult males range from 32 to 40 mm (37.9), females from 33 to 44 mm (39.0), juveniles 21 to 31 mm (26.4), males plus females average 38.4 mm; tail length ranges from 46 to 51 per cent (48.8%) of total length; postmentals vary from two to four, three occurring twice and four once in 40 specimens; postmentals always contact first labial; number of scales immediately following postmentals vary from 5 to 8 (6.2); midorbital scales vary from 17 to 21 (18.8), scales across snout at level of third labials 20 to 26 (21.7); scales bordering internasals vary from 6 to 9 (7.5), internasals separated along median line by granules in 97.7 per cent of sample; scales from nostril to eye vary from 10 to 12 (11.1); scales across venter range from 26 to 32 (27.4), from throat to vent 47 to 57 (51.8); dorsal tubercular rows vary from 12 to 15 (13.9); paravertebral tubercles from head to base of tail range from 40 to 49 (45.0), between axilla and groin 22 to 29 (26.4); lamellae beneath fourth toe range from 10 to 12 (11.4); tubercles absent from tail.

Dorsal pattern generally uniform tan to pinkish tan, few individuals with double row of 9 to 12 small, grayish brown spots or transverse lines; tail usually banded with 11 to 16 black bands, with ground color interspaces of equal width; tail bands of juveniles usually bright orange and black, subadults yellowish orange and black, and adults yellowish brown and black; iris of eye pinkish gold, ventral surfaces generally dirty white in all specimens.

*Comments.* A distinct population of this species occurs on the east slope of the Andes at an elevation of 2100 m. One specimen of this population was taken by Noble from near the headwaters of the Rio Huancabamba in 1916, and three individuals were taken by us from near the summit of the Andes on the Olmos to Bagua road in 1968. These four specimens are similar in squamation to our series from near Molino Viejo, but differ in color pattern and

have a more decidedly depressed head and body. One male measured 50 mm and a female 46 mm in snout-vent length. The dorsal pattern consists of a fine reticulation of dark lines on ground color with a light median stripe. The lateral dark stripe extends from the nostril to midbody. Until additional specimens of this population are available, we are not in a position to analyze this population further.

This species is named in honor of Dr. John W. Wright, who discovered the original population along the Rio Huancabamba near Molino Viejo, and who provided us with an immeasurable amount of help in the field.

*Habitat and natural history.* This species occupies two distinct vegetation communities, the high, barren eastern slopes of the Andes where only a few cacti and shrubs are present, and a more extensive community of cacti, shrubs, mesquite, and broad leafed trees along the Rio Huancabamba and associated hillsides. The specimens from 2100 m were taken beneath dead *Cereus sp.* and a cholla-like cactus. Those along the Rio Huancabamba, taken during the day, were found beneath the bark of mesquite or under fallen trees. After dark, individuals were found emerging from beneath fallen *Cereus sp.* and from their branches as high as two meters above the ground. Later in the evening about 20 individuals were found foraging around the bases of small rocks, *Opuntia sp.*, weeds, and on open gravel soil. When disturbed, most individuals sought cover in small patches of weeds or among small rocks. Their nocturnal body temperatures averaged 23°C and closely approximated that of the substratum. Eggs of this species were found in rotting stumps of dead trees. An examination of the oviducts of preserved females indicates that this species lays one egg per clutch.

*Distribution.* This species has been found only on the arid slopes of the Rio Huancabamba Valley and higher barren slopes of the east side of the Andes in northwestern Peru (fig. 4).

Specimens (41) have been examined from the following localities.

PERU. *Cajamarca*: El Arenal MVZ 82196. 4.5 km W El Tambo TCWC 28088. 23.5 km WNW El Tambo TCWC 28104-05. 25.2 km WSW El Tambo TCWC 28106. 13 km SSE Molino Viejo LACM 48476, 48479-94, TCWC 27916, 28089-90, 28092-103. 11 km WNW Las Juntas LACM 48477-78, TCWC 28091. *Piura*: Huancabamba AMNH 28466.

### ***Phyllodactylus pumilus* sp. nov.**

*Holotype.* Adult male, USNM 167227, collected by James A. Peters, October 1965. Type locality, 1 km S Manta, Department of Manabi, sea level, Ecuador.

*Definition.* A small gecko with a known maximum snout-vent length of 51 mm; enlarged preanal shield absent; dorsum, tibia, and part of tail with tubercles; scales of median row beneath tail widened and rounded posteriorly; tail about 50 per cent of total length; scales in supraocular region largest of interorbital series; dark brown to black stripe from nostril to arm insertion

always present; terminal digital lamellae moderately enlarged and somewhat rectangular in shape (fig. 14c).

*Diagnosis.* This species differs from *P. angustidigitus*, *gerrhopygus*, and *heterurus* by absence of enlarged preanal shield; from *interandinus* by absence of dorsal stripes and presence of tubercles on tail and tibia; from *kofordi* and *sentosus* by absence of forearm tubercles and tubercles on distal two-thirds of tail; from *microphyllus* and *inaequalis* by presence of regular rows of enlarged trihedral tubercles on dorsum; from *lepidopygus* and *clinatus* by presence of tibia tubercles; from *reissi* by smaller maximum snout-vent length of 51 mm rather than 75 mm, scales in supraocular region largest of interorbital series, and at least two rows of enlarged, flattened scales on proximal one-fourth of tail; from *johnwrighti* by presence of at least two rows of enlarged, flattened scales on proximal one-fourth of tail; more transverse

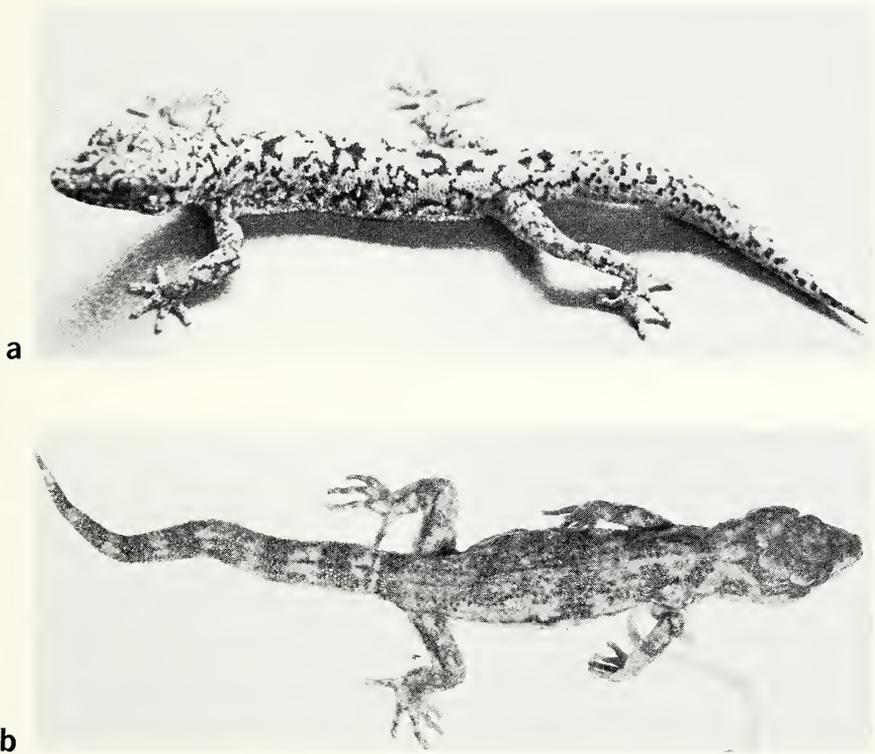


Figure 9. (a) dorsolateral view of *P. gerrhopygus*; (b) dorsal view of *P. microphyllus*.

ventral scales from throat to vent, 53 to 62 (57.6) rather than 47 to 57 (46.4); fewer paravertebral tubercles from head to base of tail, 37 to 43 (39.4) rather than 40 to 49 (45.0).

*Description of holotype.* Rostral twice as wide as high, its dorsal edge with short median, vertical groove; two internasals, somewhat rectangular and in contact along median edges; nostril surrounded by rostral, labial, internasal, and three postnasals; first supralabial in broad contact with ventral edge of nostril; shallow depression between internasals and in frontal region; 11 scales between nostril and eye; scales in posterior loreal region about three times larger than interorbital scales; 19 scales across snout at level of third labials, 17 interorbital scales, 18 at anterior edge of orbits; eye large, its diameter contained in snout length 1.7 times; eyelid (brille) with one to two rows of granules and one larger outer row of scales; diameter of ear contained in eye diameter about three times; ear opening strongly denticulate on anterior and posterior margins; rear of head granular with a few larger tubercles intermixed; six supralabials and five infralabials to point below center of eye; mental bell-shaped, as wide as long, bordered posteriorly by two postmentals; postmental about as long as wide, their median edges in broad contact; postmentals immediately followed by transverse row of six scales, followed by second row of 10 smaller scales; postmentals contact first labial only.

Dorsum with 14 longitudinal rows of enlarged trihedral tubercles that are somewhat flat; paravertebral row with 42 tubercles from rear of head to base of tail, 25 between axilla and groin; paravertebral rows separated from each other by four rows of granules; five rows of tubercles reach nape, six to base of tail; each tubercle of dorsal series separated from preceding tubercle by none to two granules; postanal tubercles number four to each side; venter with 27 longitudinal and 61 transverse rows of scales.

Dorsal surface of arm with large, flat scales; dorsal surface of thigh with three to five tubercles scattered among granular scales; lamellae formula for hand 7-8-9-9-7, foot 7-8-12-12-10; claw slightly visible when viewed from below; terminal lamellae slightly longer than wide, moderately enlarged; distal three-fourths of tail regenerated, proximal one-fourth with a 6-4-2 reduction in number of tubercles per whorl, decreasing in number towards distal portion of tail; median row of scales beneath tail widened, rounded posteriorly.

Measurements in mm: snout-vent length 49.0, axilla-groin length 22.0, leg length 17.5, arm length 12.5, tail length 44.5, head length 13.0, head width 9.3, head depth 5.7, snout length 5.2, eye diameter 3.0, ear diameter 1.1, eye to ear distance 3.7.

Color in alcohol: ground color grayish tan; dorsal surface of body with faint indication of six light brown bands, broken along median line of body by longitudinal stripe of ground color; limbs without pattern, ground color; top of head from occiput to snout uniform light brown; brownish stripe from nostril to arm insertion, passing over ear; supralabials spotted with dark brown,

less so on infralabials; venter grayish white with a few minute black dots on each scale; ventral surfaces of hands and feet slightly darker than venter; tail with faint indication of banding.

*Variation.* Snout-vent length of young adult and adult males range from 37 to 51 mm (44.0), females from 41 to 44 mm (42.0), juvenile 25 mm; males plus females average 43.2 mm; tail partly regenerated in all specimens except one and averages about 50 per cent of total length; two postmentals in all, contacting first labial only in 100 per cent of sample; number of scales immediately following postmentals vary from 4 to 8 (6.1); midorbital scales vary from 15 to 18 (16.9), scales across snout at level of third labial 19 to 22 (20.1); scales bordering internasals vary from 5 to 8 (6.0); internasals in contact along their median edges in 90.1 per cent of sample; scales between nostril and eye vary from 10 to 13 (11.6); scales across venter range from 27 to 30 (28.5), from throat to vent 53 to 62 (57.5); dorsal tubercular rows vary from 12 to 14 (13.3); paravertebral tubercles from head to base of tail range from 37 to 43 (39.4), between axilla and groin 23 to 27 (24.7); lamellae beneath fourth toe vary from 11 to 13 (12.0); at least two rows on enlarged, flat scales (may be elevated and tubercular-like) on proximal one-fourth of tail.

Dorsal color pattern highly variable, from an almost uniform light brown to definite paravertebral rows of dark brown spots or bands; head usually uniform light brown, but faintly mottled with light gray in some specimens; dark brown stripe from nostril to arm insertion in all but one specimen which has stripe continuing to groin region; median grayish stripe on dorsum in all specimens, but faintly interrupted by black reticulating lines in one; tail banded brown and gray in only specimen with complete, original tail; venter grayish white in all.

*Habitat and natural history.* Dr. James A. Peters (*personal communication*) states that the type locality is a vertical rocky cliff on the beach, just above the high tide zone, 1 km south of Manta. The cliff surface is somewhat rotten, crumbles easily, and contains numerous holes and crevices. Four specimens of *P. pumilus* were taken from beneath rocks or in crevices along the cliff face. Peters indicated that he had not seen other specimens of *Phyllodactylus* this close to the ocean at any other point on the Ecuadorian coast.

Peters indicated that all specimens of this species were taken during daylight hours. Other specimens were found beneath loose bark on trees and stumps in a semi-desert area with low scrubby vegetation, or in a transition, dry to subdry forest.

*Phyllodactylus reissi* were taken with *pumilus* from the stump of an old ceiba tree 6 km E of Manta, and at the type locality.

*Distribution.* This species has been taken west of the Cordillera de Balzar in the department of Manabi of Ecuador, from sea level to approximately 200 m (fig. 3).

Specimens (11) have been examined from the following localities: ECUADOR. *Manabi*: 8 km W Jipijapa USNM 167184. 1 km S Manta USNM

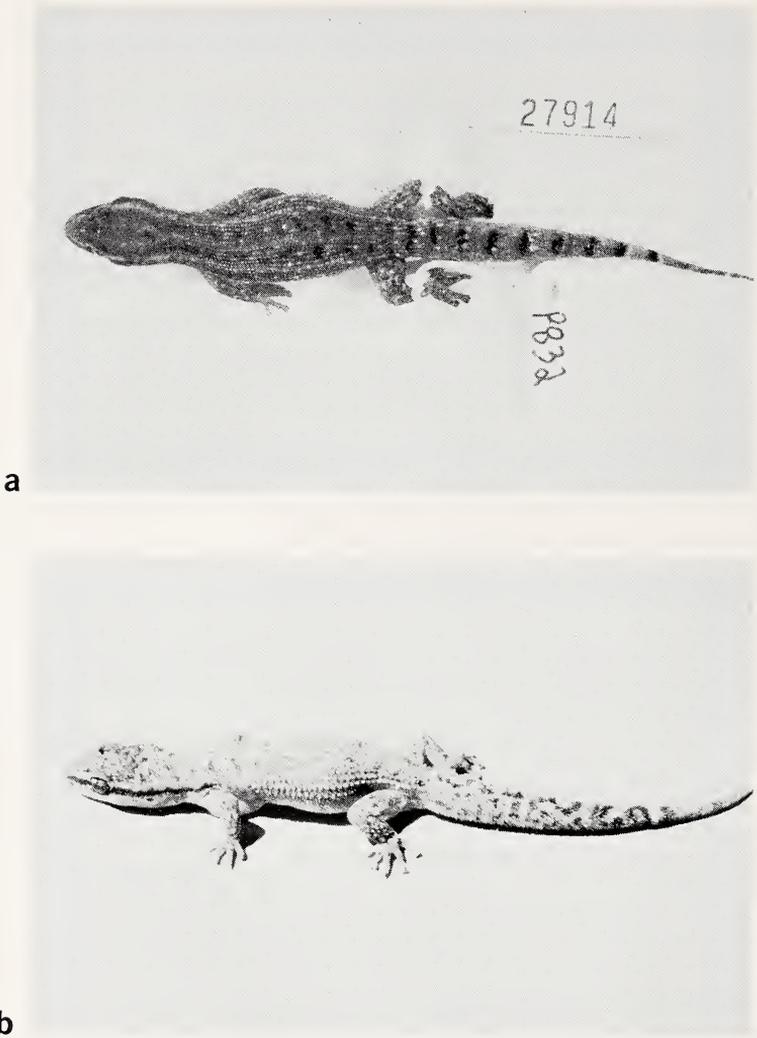


Figure 10. (a) dorsal view of *P. interandinus*; (b) dorsolateral view of *P. johnwrighti*.

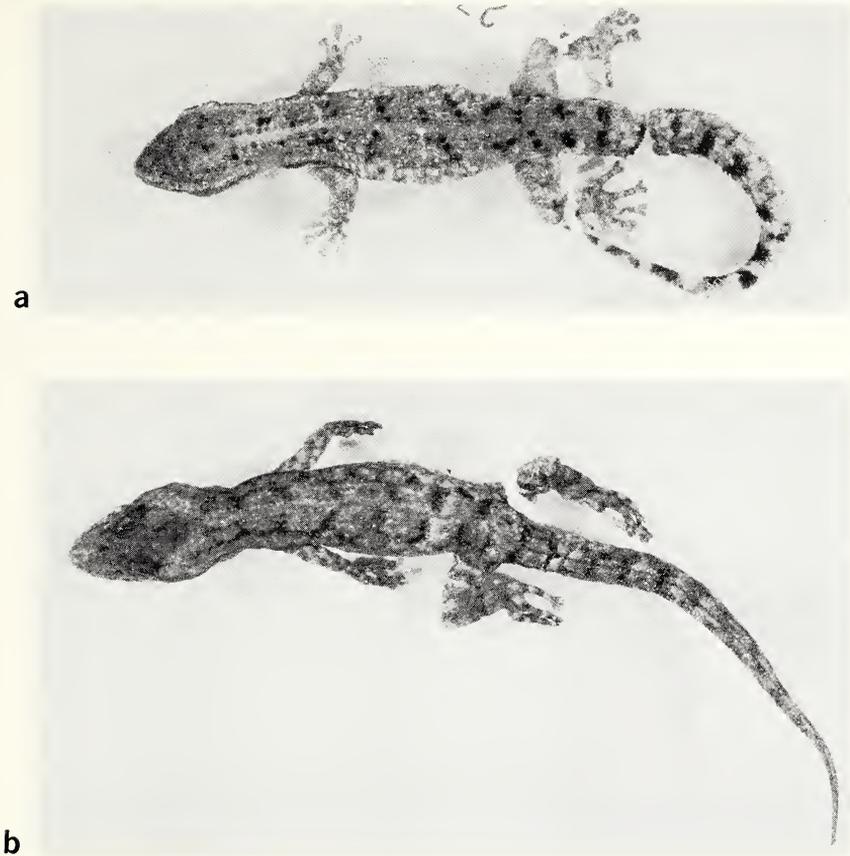


Figure 11. (a) dorsal view of *P. kofordi* (holotype); (b) dorsal view of *P. clinatus* (holotype).

167227-30. 6 km E Manta, 5 km W Montecristi USNM 167233. 11 km W Portoviejo USNM 167185, 167226. 9 km N San Vicente USNM 167187, 167231-32.

#### ADAPTATION TO HABITAT

Species of *Phyllodactylus* are, in the more restricted sense, geckos of arid and semiarid regions. Only on the mainland of British Honduras and some islands of the Caribbean are they found in a more tropical environment.

Adaptations of species of *Phyllodactylus* for living in arid deserts and

tropical deciduous forests are generally of two types, scansorial and terrestrial. Most of these lizards are found in areas where sufficient physical objects are available for scansorial habits, i.e. trees, rocks and cliffs. All species of Mexico, Central America, and eastern South America are scansorial. Most prefer a rock substratum, but are frequently found on trees and shrubs. Only on the mainland of western South America does one find a shift to the terrestrial habit, and even then the terrestrial species are occasionally scansorial.

Underwood (1954) indicates that the most primitive condition in geckos is one of terrestrial habits with simple, clawed digits. Adaptations to a scansorial habit involved the development of pilose, friction lamellae beneath the digits, and in some cases, beneath the tip of the tail. He also states that there has been a number of independent reversions to terrestrial habits with a loss or reduction in the size of the lamellae.

Of the 15 mainland species of western South America, four are terrestrial: *P. microphyllus*, *angustidigitus*, *gerrhopygus*, and *sentosus*. Of these four species, *microphyllus* has become well adapted to an open, deep sand habitat, through reduction in size of the terminal lamellae, shorter and more muscular limbs, and swollen scales about the nostril with the nasal opening a very small slit and lying in an anterior, dorsolateral position.

*Phyllodactylus angustidigitus* has become adapted to a shell and rubble beach habitat through reduction in the terminal lamellae, enlargement of the claw, elevated and swollen scales about the nostril, but unlike *microphyllus*, the limbs are very slender, long, and without much muscular development. Little is known about the habits of *sentosus*, but all known specimens were taken from the ground and they have relatively small terminal lamellae and well developed claws, but the region about the nostril is unswollen. We find it difficult to explain the presence of enlarged terminal lamellae in a terrestrial species, such as *gerrhopygus*. This species has very large, well developed terminal lamellae like those of scansorial species (fig. 7), but has the area about the nostril greatly swollen, and the limbs are intermediate in size and shape between *angustidigitus* and *microphyllus*.

There appears to be differential development for a terrestrial habit for each of the four species, with evolutionary trends variable within each population. For example, *P. microphyllus* taken from hard surface sands or conglomerate soils have slightly larger terminal lamellae than those from soft sands. However, in *gerrhopygus*, the size of the terminal lamellae varies slightly within each population and does not seem dependent upon soil type. The reduction in the size of the terminal lamellae coupled with an enlargement of the claw in *angustidigitus*, seems to be a special modification for living on shell and rubble beaches. Whether the reduction in the terminal lamellae and enlargement of claws are for walking on shell and rubble, or for turning over these objects in search of food is not known, but the claw is approximately four times the size of the claw of *gerrhopygus*, a species that is frequently found on sandy beaches.

The terminal lamellae of the scansorial species (*P. reissi*, *lepidopygus*, and probably *clinatus*) are generally greatly enlarged. *Phyllodactylus reissi* has exceptionally large toe pads, possibly influenced by its large body size. Several geckos are intermediate in their microhabitat preferences, *P. kofordi*, *inaequalis*, *johnwrighti*, and *interandinus*, usually spending the day under bark or exfoliations, and at night foraging about on the ground. As one might expect, the toe pads are intermediate in size, reflecting an adaptation to both terrestrial and scansorial habits. In addition, a toe pad of intermediate size may facilitate terrestrial locomotion over a broken substratum and surface debris typical of the habitats where these geckos are found. Seemingly, the more scansorial a species becomes, the more natural selection favors an enlargement of the terminal lamellae. However, this does not explain the enlarged terminal lamellae of *gerrhopygus*. This species has been taken from terrace walls and walls of houses indicating it is not completely terrestrial. There may have been a recent shift from a scansorial to a terrestrial habit, and natural selection for small terminal lamellae is presently acting upon the population. However, it is possible that *gerrhopygus* is adapted for running upon soft surface sand and foraging for surface food items. This would, in part, account for the small claws and enlarged terminal lamellae. Larger and more lengthened claws may be used for turning over surface litter or for digging under it in search of food (*microphyllus*, *sentosus*, *angustidigitus*). Large terminal lamellae would likely hinder the ability to dig or clasp objects in the search for food, whereas a surface feeder might retain the large lamellae, enabling it to move faster, farther, and with more ease, in search of surface food items.

The swollen area about the nostril seems to be an adaptation for living in regions where deep sand is constantly being moved about by wind action. The scales about the nostril are elevated, rounded (swollen), and the position of the nostril has been shifted to a more anterior, dorsolateral position. The nasal opening is narrow and partially protected by an anterior extension of the upper postnasal scale into the nasal aperture. In effect, the elevated and rounded scales surrounding the nostril form a tubular opening. This type of nostril provides adequate air passage and prevents sand from clogging the aperture while the individual rests in daytime retreats or forages about on the sand at night.

*Phyllodactylus sentosus* is the only representative of a terrestrial species that does not have a tubular condition about the nostril. The substratum where it lives is more of a conglomerate soil, and selection for a tubular nostril is not one of the critical adaptive features for survival. None of the scansorial species have tubular nostrils.

#### SYMPATRIC RELATIONS OF *PHYLLODACTYLUS* IN WESTERN SOUTH AMERICA

An awareness of sympatry is essential in overcoming the subjectivity of morphological taxonomy. This section will briefly document known cases of

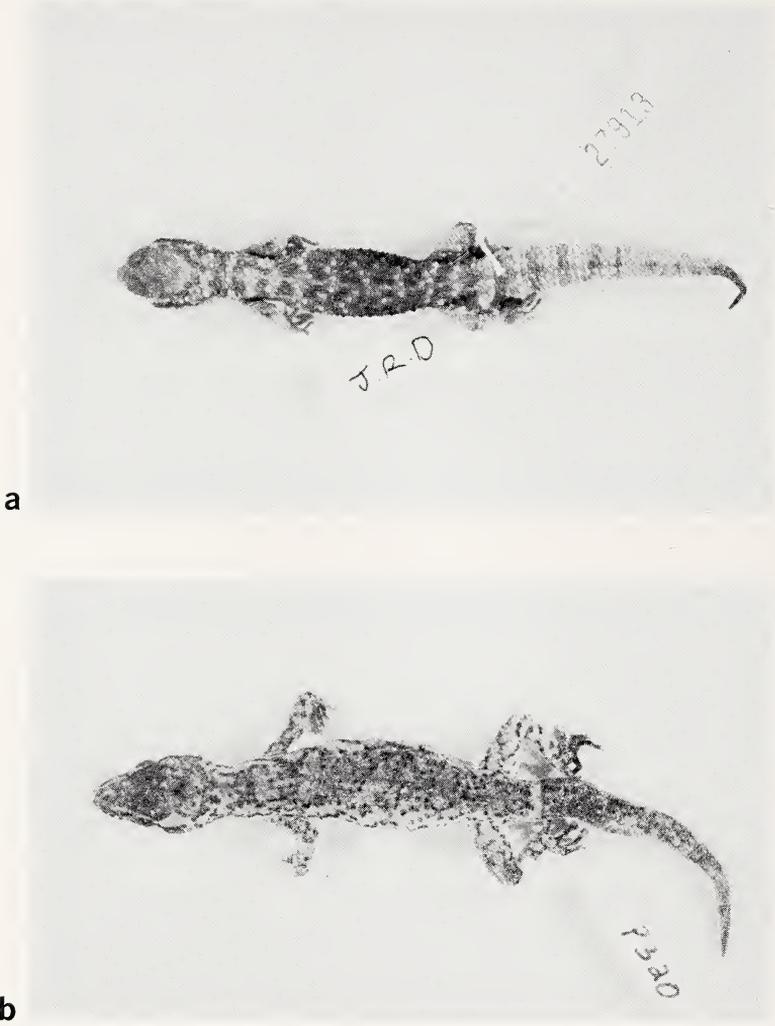


Figure 12. (a) dorsal view of *P. sentosus* (holotype); (b) dorsal view of *P. inaequalis*.

sympatry in western South America as well as describe certain aspects of ecological and evolutionary differences among the sympatric species.

The geographic distribution of species of *Phyllodactylus* is summarized in figs. 2-5. Known cases of sympatry are noted in Table 2.

When geckos occur sympatrically one consistently observes distinct differences in the degree of arboreality. For example, although both *P. reissi* and *interandinus* utilize arboreal perches for diurnal retreats, only *interandinus* moves to the ground for nocturnal foraging.

*Phyllodactylus reissi* and *kofordi* are commonly sympatric but have very little overlap in perch height. *Phyllodactylus reissi* is usually a scansorial forager, while *kofordi* is primarily a ground forager.

In some localities *P. inaequalis* is found with *kofordi* and *reissi* in sympatry. *Phyllodactylus inaequalis*, like *kofordi*, is a terrestrial forager. The relative abundance of these species seems to vary from locality to locality based on collecting records. It is not clear whether this is due to competition and/or to subtle environmental differences favoring one species at a given locality. There is some evidence of microhabitat separation between these two species at Cerro de la Vieja where *inaequalis* forages near the bases of boulders and *kofordi* forages more on open ground.

Another difference commonly found among sympatric geckos is in body size, presumably reflecting differences in prey size. In sympatric situations the only known exceptions to extreme body size differences are with *P. kofordi* and *inaequalis* as well as *kofordi* and *clinatus*. The fact that all of these geckos are small and appear to forage in different microhabitats probably accounts for their coexistence.

Some cases of sympatry are not clearly understood. The replacement of *P. microphyllus*, a sand gecko, by *kofordi*, normally a foothill gecko, along the sandy coast in extreme northwestern Peru is puzzling. Climatic, competitive, or physical environmental factors may be involved.

Selander and Giller (1963) observed that broad sympatry in woodpeckers of the genus *Centurus* occurs between distantly related species. Conversely, closely related species are allopatric or only narrowly sympatric. These workers concluded “. . . it is suggested that the evolution of reproductive isolating mechanisms tends to proceed more rapidly than does the evolution of ecologic isolation, with the result that competition and other interspecific interactions prevent extensive sympatry of closely related species . . .”

Pending completion of our osteological and karyological studies, the intrageneric relationships of the western South America *Phyllodactylus* are tentative. Strictly on the basis of external morphology, we suggest the following species are closely related and group them: *gerrhopygus*, *heterurus*, *angustidigitus*; *microphyllus*, *inaequalis*; *lepidopygus*, *clinatus*; *johnwrighti*, *pumilus*, *interandinus*; *sentosus*, *kofordi*; and *reissi*. Comparison of these groups with Table 2 shows only one known case of sympatry within a group, that of *gerrhopygus* and *heterurus*. However, the known extent of sympatry

TABLE 2

Sympatric relationships of 15 species of *Phyllodactylus* from the mainland of South America.

	<i>angustidigitus</i>	<i>clinatus</i>	<i>dixonii</i>	<i>gerrhopygus</i>	<i>heterurus</i>	<i>inaequalis</i>	<i>interandinus</i>	<i>johnwrighti</i>	<i>kofordi</i>	<i>lepidopygus</i>	<i>microphyllus</i>	<i>pumilus</i>	<i>reissi</i>	<i>sentosus</i>	<i>ventralis</i>	
<i>angustidigitus</i>																
<i>clinatus</i>						X			X		X		X			
<i>dixonii</i>																
<i>gerrhopygus</i>					X											
<i>heterurus</i>				X												
<i>inaequalis</i>		X							X					X		
<i>interandinus</i>														X		
<i>johnwrighti</i>																
<i>kofordi</i>		X				X					X		X			
<i>lepidopygus</i>											X					
<i>microphyllus</i>		X							X	X			X	X		
<i>pumilus</i>														X		
<i>reissi</i>		X				X	X		X		X	X				
<i>sentosus</i>											X					
<i>ventralis</i>																

(X = in sympatry)

of these species is based on one locality, and the status of *heterurus* is in doubt. Where broad sympatry does occur (e.g., among *inaequalis*, *kofordi*, and *reissi*), it is between or among very distinct species. Hence, Selander and Giller's (1963) conclusions might well be applicable to species of *Phyllodactylus* in South America.

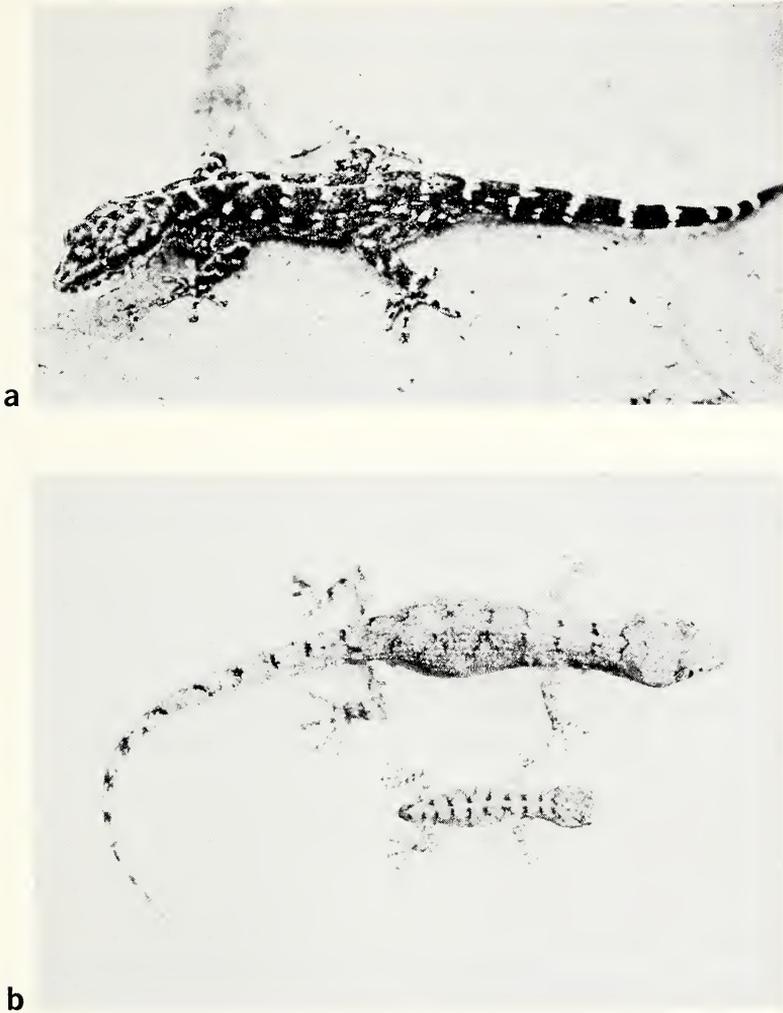


Figure 13. (a) dorsolateral view of *P. lepidopygus*; (b) dorsal view of an adult and young of *P. reissi*.

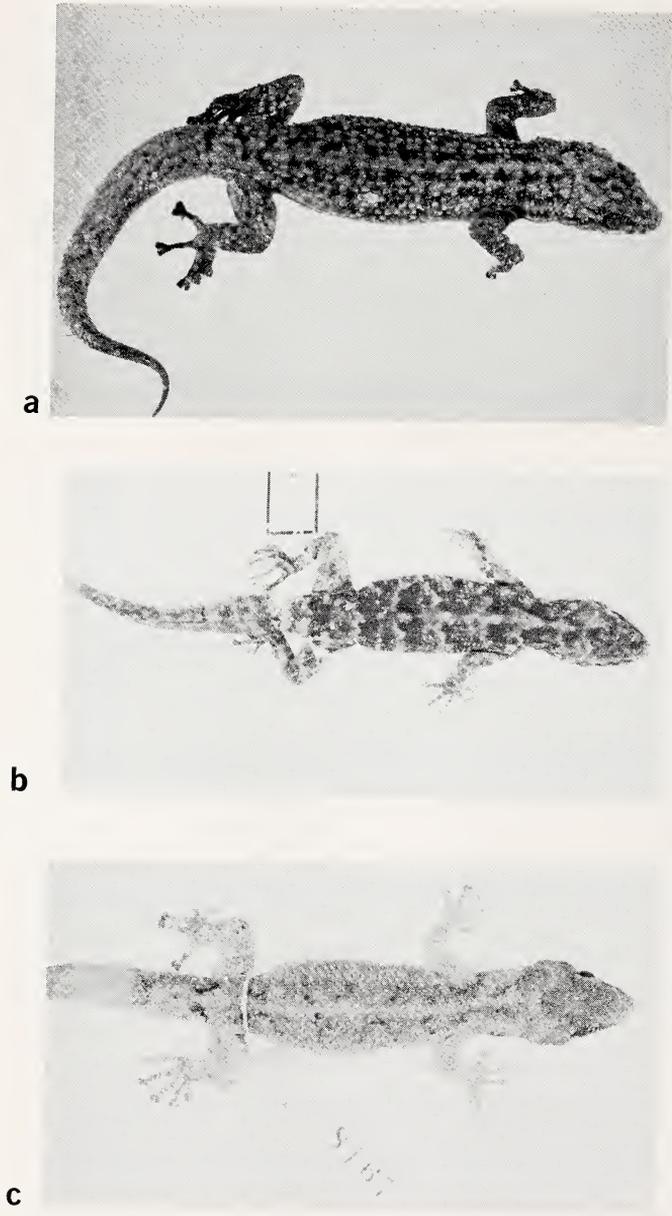


Figure 14. (a) dorsal view of *P. ventralis*; (b) dorsal view of *P. dixonii*; (c) dorsal view of *P. pumilus* (holotype).

## GAZETTEER

There are a large number of collecting localities in Ecuador, Peru, and Chile not shown in gazetteers, on maps, or generally unavailable to scientists working with material from western South America. We present the following list of localities with coordinates, arranged by country and political division.

## CHILE

*Tarapaca*

Arica	18°	29'S	70°	20'W
Iquique	20	13S	70	10W
Pica	20	30S	69	20W
Pintados	20	38S	69	38W
Pisagua	19	36S	70	13W
Putre	18	12S	69	35W

## ECUADOR

*Azuay*

San Francisco	3	37S	79	30W
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*El Oro*

Machacha	3	16S	79	57W
Santa Rosa	3	27S	79	58W

*Guayas*

Ancon Camp	2	20S	80	52W
Colonche	2	01S	80	40W
Daule River	1	53S	79	58W
Guayaquil	2	10S	79	52W
Playas	2	38S	80	23W

Puente de Chimbo	2	11S	79	07W
Puna	2	42S	79	55W

Punta Cornero	2	18S	80	55W
Salinas	2	13S	80	50W

*Loja*

Loja	4	00S	79	13W
Rio Casanga	4	08S	79	49W

*Manabi*

Jipijapa	1	20S	80	35W
Manta	0	57S	80	45W
Portoviejo	1	03S	80	27W
San Vicente	0	36S	80	24W

## PERU

*Amazonas*

Bagua Chica	5	38S	78	35W
Bagua Grande	5	47S	78	26W
Marañon Valley	4	30S	78	27W

*Ancash*

## Chimbote

Valley	9	07S	78	38W
Culebras	9	56S	78	14W
Pativilca	10	40S	77	48W

*Arequipa*

Arequipa	16	24S	71	32W
Camana	16	37S	72	42W
Chucarapi	17	04S	71	44W
La Joya	16	45S	71	52W
Mollendo	17	02S	72	01W
Tambo	17	06S	71	48W
Vitor	16	26S	71	49W
Yura	16	12S	71	42W

*Cajamarca*

Bellavista	5	37S	78	39W
Chinchipe Valley	5	28S	78	32W
El Arenal	5	56S	79	17W
El Tambo	5	46S	79	24W
Las Juntas	5	57S	79	14W
Molino Viejo	5	49S	79	23W
Perico	5	15S	78	45W

*Ica*

Ica	14	05S	75	44W
Isla Sangallan	13	50S	76	28W
Isla Viejas	14	17S	76	12W
Jaguay	13	23S	76	12W
Lagunillas				

Bay	13	54S	76	18W
Marcona	15	20S	75	10W
Paraca Bay	13	50S	76	16W
Paracas	13	48S	76	15W
Paracas				

Peninsula	13	48S	76	24W
Pozo Santo	13	54S	76	03W

## Puerto Pisco

(new)	13	47S	76	17W
San Juan Port	15	22S	75	12W

*Junin*

Chanchamayo	10	42S	75	08W
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*Lambayeque*

Chiclayo	6	46S	79	51W
Eten	6	54S	79	53W
Jayanca	6	24S	79	51W
Mocupe	7	00S	79	37W
Morrope	6	32S	80	02W
Motupe	6	09S	79	43W
Naupe	5	37S	79	54W
Olmos	6	00S	79	45W

*Libertad*

Chiclin	7	50S	79	10W
Jequetepeque				
Valley	7	21S	79	36W
Pacanguilla	7	10S	79	28W
Pacasmayo	7	24S	79	34W

*Lima*

Ancon	11	46S	77	10W
Asia	12	47S	76	35W
Cerro Azul	13	03S	76	30W
Chorillos	10	46S	77	46W
Chosica	11	54S	76	42W
Cruz de				
Hueso	12	23S	76	46W
Isla San				
Lorenzo	12	05S	77	15W
Lima	12	03S	77	03W
Lomas de				
Lechay	11	27S	77	18W
San Antonio	12	37S	76	37W
Verrugas				
Canyon	11	53S	76	32W

*Piura*

Bayovar	5	50S	81	03W
Bocana	4	41S	80	18W
Cabo Blanco	4	15S	81	14W

*Capullana*

Point	4	29S	81	17W
Catalinas	4	11S	80	58W
Cerro Amotape	4	40S	80	58W
Chongollapi	5	26S	79	37W
Chulucanas	5	06S	80	10W
El Alto	4	17S	81	12W
Fondo	4	28S	81	09W
Huancabamba	5	14S	79	27W
Isla Lobos de				
Afuera	6	57S	80	42W
Isla Lobos de				
Tierra	6	27S	80	52W
Las Lomas	4	40S	80	15W
Lobitos	4	26S	81	16W
Los Organos	4	09S	81	07W
Monte Grande	4	27S	81	02W
Negritos	4	38S	81	19W
Paita	5	06S	81	07W
Parinas Valley	4	30S	81	06W
Piura	5	11S	80	38W
Punta Aguja	5	47S	81	04W
Punta Sal	5	51S	80	56W
Reventazon	6	10S	81	00W
Sechura	5	34S	80	50W
Sechura Desert	5	50S	80	40W
Sullana	4	53S	80	41W
Talara	4	34S	81	17W
Tric Trac	5	51S	81	00W

*Tumbes*

Cancas	4	00S	81	00W
Las Vocas	3	25S	80	19W
Puerto Pizzaro	3	39S	80	24W
Quebrada Seca	4	23S	81	14W

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#### RESUMEN

Se hace una breve descripción del hábitat natural de las especies de *Phyllodactylus* encontradas en el continente de América del Sur. El micro-hábitat natural de cada especie se describe hasta donde ha sido posible. Poca a ninguna información se aporta sobre el micro-hábitat de *P. heterurus*, *setosus* y *clinatus*. Cuatro especies, *P. angustidigitus*, *gerrhopygus*, *microphyllus* y *setosus* son primariamente terrestres y alopátricas en distribución. Diez especies, *P. clinatus*, *dixonii*, *inaequalis*, *interandinus*, *johnwrighti*, *kofordi*, *lepidopygus*, *pumilus*, *reissi* y *ventralis* son aborícolas y únicamente *johnwrighti*, *ventralis* y *dixonii* no viven simpátricamente con una o más de las otras especies arborícolas. En donde tres o más especies viven simpátricamente, las áreas utilizadas para reposar durante el día y para la obtención de alimento se sobreponen escasamente.

Con la excepción de *P. reissi*, la cual produce dos huevos, todas las especies de *Phyllodactylus* encontradas en América del Sur continental depositan un sólo huevo por nidada. La deposición de huevos en forma comunal parece ocurrir con frecuencia entre el mayor número de especies, incluyendo aquellas que viven simpátricamente: *P. interandinus* y *reissi*, y *kofordi* y *reissi*.

Las especies del género *Phyllodactylus* parecen tener adaptaciones específicas a sus micro-hábitats naturales. Aquellas especies que habitan áreas rocosas se caracterizan por la presencia de laminillas digitales terminales ensanchadas, cabeza y cuerpo comprimidos dorsoventralmente y ventanas de la nariz localizadas lateralmente; en el caso de especies que habitan un micro-habitat arenoso las laminillas digitales terminales son pequeñas, la cabeza y el cuerpo redondeados y las ventanas de la nariz son valvulares y están localizadas dorsolateralmente; finalmente, las especies que viven en playas de concha tienen laminillas digitales con uñas alargadas, cabeza y cuerpo delgado y ventanas de la nariz con válvulas situadas dorsolateralmente. Dependiendo del grado en que el comportamiento es arborícola o terrestre algunas especies de *Phyllodactylus* poseen las adaptaciones descritas en forma intermedia.

Para cada especie, excepto *P. heterurus*, se incluye un mapa de distribución junto con fotografías; además, se presenta una lista de localidades importantes.

De los holotipos y sintipos de las especies descritas de América del Sur continental, existen diez (*dixonii*, *inaequalis*, *lepidopygus*, *magister*, *microphyllus*, *nigrofasciatus*, *phacophorus*, *pumilus*, *reissi*, y *ventralis*), ocho de los cuales han sido examinados.

Se describen siete nuevas especies (*angustidigitus*, *clinatus*, *interandinus*, *johnwrighti*, *kofordi*, *pumilus* y *setosus*); nueve nombres antiguos se relegan al sinonimio de otras especies (*abrupteseriatus*, *baessleri*, *guayaquilensis*, *lobensis*, *magister*, *nigrofasciatus*, *phacophorus*, *underwoodi*, *variegatus*).

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## HADROSAURIAN DINOSAUR BILLS—MORPHOLOGY AND FUNCTION

*By* WILLIAM J. MORRIS



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# HADROSAURIAN DINOSAUR BILLS—MORPHOLOGY AND FUNCTION

By WILLIAM J. MORRIS<sup>1</sup>

**ABSTRACT:** Reconsideration of the morphology and function of the bill of hadrosaurian dinosaurs is based upon an excellently preserved bill mold of a recently discovered specimen (LACM 23502) assigned to the genus *Anatosaurus*. Morphology suggests a filtering function for the bill and adaptation for discharge of fluid and small particles following intake and mastication of plant or invertebrate food.

## ACKNOWLEDGMENTS

The excellent specimen of *Anatosaurus cf. annectens* (LACM 23502) upon which this study is based was discovered and collected by H. Garbani and skillfully prepared by M. Odano, both of the Los Angeles County Museum of Natural History. The skeleton was found in the Hell Creek Formation south of Ft. Peck Reservoir, NE ¼, Sec. 36, T21N, R35E, Montana.

The project, leading to this discovery as well as other important dinosaur finds, was generously supported by Mr. and Mrs. William T. Sesnon, Jr., patrons of the Los Angeles County Museum of Natural History.

Constructive criticism of the manuscript by Dale Russell, Canadian National Museum, and Theodore Downs of the Los Angeles County Museum of Natural History is appreciated. Others on the staff of the Los Angeles County Museum whose help is acknowledged are: David Forstch and Alan Tabrum for their interest and discussion, and Joseph Cocke for his drawing of Figure 2. The remainder of the illustrations and photographs were done by the author.

## INTRODUCTION

Dinosaurs of the family Hadrosauridae are among the most familiar Late Cretaceous fossils. Indeed, the first dinosaurs described from North America, belonged to these so called duckbilled forms. Prior to a brief description by Cope (1883) the presence of a horny bill in hadrosaurs was conjectural. Cope, in preparing a specimen of *Anatosaurus annectens*, discovered portions of a mold of the bill. Later two other specimens in which most of the bill was preserved were described for *A. annectens* by Versluys (1923) and for *Corythosaurus excavatus* by Sternberg (1935). In all three cases we must rely upon the description of the bill as the original molds were either destroyed during preparation or subsequently lost. As a result, a recently discovered specimen of *Anatosaurus cf. annectens* (LACM 23502) from the Hell Creek beds of Montana containing a well preserved mold is most important in

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evaluating the morphology and function of the hadrosaurian bill. The letter designations are used to designate specimens in various museums: LACM, Los Angeles County Museum of Natural History; ROM, Royal Ontario Museum; NMC, National Museum of Natural Sciences, Ottawa.

BILL MORPHOLOGY OF ANATOSAURUS CF. *A. ANNECTENS* (LACM 23502)

The specimen is a mature individual approximately forty feet long. The skull is only slightly distorted mainly along a parasagittal section approximately midway between the orbits and narial openings. The mandibles, though offset to the right, are not distorted relative to the midline so that the bill mold is undistorted, (Fig. 1). Morphologically, the specimen is very similar to *A. annectens* but there are some differences between it and the holotype. Until the time when careful study has been made regarding individual variability of hadrosaurian dinosaurs, it is hazardous to make positive, specific references for specimens other than the type. This is especially true regarding the LACM specimen for it was found further north than the Lance Formation, Wyoming, localities from which the types of *A. annectens* were obtained.

The bill mold is composed of gray, lithic siltstone, the surface is accentuated by a thin veneer of iron oxide. In the figures, the mold appears dark due to the application of preservative although it has the same composition as the matrix. The entire anterior surface (attached dorsally to the premaxillary region) is preserved and only a small portion of the ventral edge is lacking. Only the left side is preserved.

Before discussing the form and function of the bill it is important to describe the geometry of the mold. Errors in interpretation by other authors seems largely to have resulted from misinterpretation of the geometry of the mold.

When the specimen was discovered, anterior and posterior sides of the mold were preserved with a very thin surface of weakness separating them. The surface, shown in Figures 1, A, B, C and D, is the posterior side of the mold, the one closest to the premaxillary region of the skull. It is important to note that matrix on both sides of the preserved surface was carefully prepared and other structures were not found within the matrix except the surface of the mold. Hence the entire bill, as preserved, is represented by two surfaces separated by less than 0.01 mm, one of which is shown in the figures.

The surface of the mold is vertically fluted, containing nine or possibly ten V-shaped channels. These are separated by dorsal-ventral pillars, rounded

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Figure 1. Partially prepared skull of *Anatosaurus* cf. *annectens*, LACM 23502.

(A) Complete skull, left side. The bill mold is not preserved on this side but the edge of the mold can be seen extending ventrally from the premaxillary below the prementary of the lower mandible. Note that the free margin of the mold extends below the prementary and is separated from the prementary by siltstone matrix.

(B) Anterior undulating surface of the bill mold showing the fluted channels preserved as an iron oxide veneer on the siltstone matrix. (C) Dorsal oblique aspect of the skull illustrating the very terminal position of the bill mold along the ventral margin of the premaxillary. (D) Ventral oblique view showing the bill mold and the matrix layer separating it from the prementary.



A



B



C



D

in cross section. Laterally, towards the maxillaries, the fluted surface is replaced by a smooth triangular plate.

The mold is approximately 110 mm long at the junction of the premaxillaries and it extends ventrally about 50 mm below the anterior margin of the prementary, decidedly overlapping the front of the lower jaw. Although the extreme ventral margin of the mold appears to be missing, the taper of the pillars and channels suggests that the entire bill was not much longer than shown in this specimen.

The premaxillary of the specimen, dorsal to the mold on the left side, is not well preserved and the surface separating bill and upper jaw cannot be seen. There is, however, little doubt that the bill was united with the upper mandible. A complimentary structure that would have been attached to the lower mandible was not found even though conditions for its preservation must have been similar to those for the upper bill mold.

#### INTERPRETIVE MORPHOLOGY

The surface of the mold forms an immediate extension of the premaxillary without break or offset. The actual horny bill must have been affixed anterior to the mold and, in order to be secure, must have extended up and onto the surface of the premaxillaries. Although there is no direct evidence indicating the posterior limit of the bill, it probably did not extend farther than the excavation surrounding the nares in the premaxillaries.

The geometry suggested by the anterior position of the mold suggests that the mold reflects the interior surface of the bill. Probably some compression of the bill occurred during compaction of the silt now forming the matrix, and

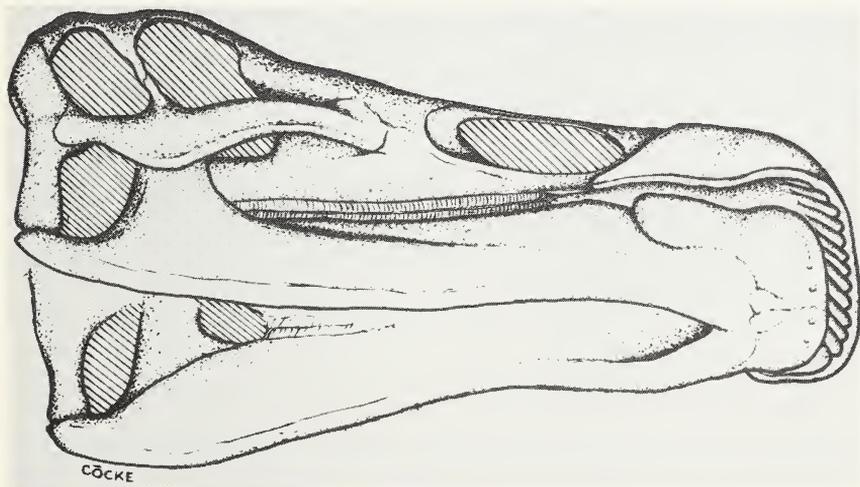


Figure 2. Restoration of the bill on the skull of *Anatosaurus* cf. *annectens*, LACM 23502. The undulating, fluted inner surface of the bill is shown. When the mandibles were closed and the prementary opposed to the bill, channels opening from the mouth were formed.

it is impossible to determine the original thickness of the specimen. The fluted surface was evidently confined to the interior of the bill as no comparable surface was found against the more dorsal surfaces of the premaxillary. Conceivably the original exterior fluting could have been destroyed during compaction but then why was it not also destroyed on the more ventral portion? It seems best to reconstruct a bill with the fluted surface only on the internal side.

The predentary is poorly preserved and furnishes no evidence for a bill on the lower jaw. Nor was evidence for the presence of a lower bill found in the matrix anterior to the predentary.

A restoration of the probable appearance of the upper bill is shown in Figure 5.

#### DISCUSSION OF PREVIOUSLY DESCRIBED BILL MOLDS

The specimen described by Cope was destroyed during preparation of the skull. Cope did not give a reason for destroying the mold, but one cannot help conjecturing that he thought his description vivid enough that future reference to the specimen would be unnecessary. The mold of the *Corythosaurus excavatus* specimen, except for a very small and unilluminating fragment, could not be located. In the third example Versluys apparently used the mold to cast what he took to be a plaster replica of the bill and, after obtaining the cast, the natural mold was not retained.

Cope appears to have misinterpreted a structure very similar to that of LACM 23502. The full text follows (1883:106): "Dermal or corneous structures have left distinct traces in the soft matrix about the end of the beak-like muzzle. Laminae of brown remnants of organic structures were exposed in removing the matrix. One of these extends as a broad vertical band round the sides, indicating a vertical rim to the lower jaw, like that which surrounds some tea trays, and which probably represents the tomia of the horny sheath of a bird's beak. At the front of the muzzle its face is sharply undulate, presenting the appearance of vertical columns with tooth-like apices. Corresponding tooth-like processes, of much smaller size, alternate with them from the upper jaw. These probably are the remains of a serration of the extremital part of the horny tomia, such as exists on the lateral portions in the lamellirostral birds."

Cope described an undulatory surface with tooth like terminations; however, he did not make it clear whether he considered the object examined a mold or the actual bill. He implies that the structure was attached to the lower jaw and that only small protuberances were present on the upper. Cope probably misinterpreted the area for attachment of the bill, judging from the LACM specimen. Versluys (1923) also believed that Cope's analysis was in error, but Lull and Wright (1942) and Ostrom (1961) both accepted Cope's (1883) description of a horny beak on the lower jaw. Probably the smaller, tooth like processes described by Cope were rugosities normally present distally on most hadrosaurian premaxillaries.

The morphology of the hadrosaurian bill was further confused by Lull and Wright who state (1942:43), "In the Senckenberg specimen [the one

described by Versluys] the impression shows a beak on the upper jaw which projected with a free lower border for about 8 cm over the ventral edge of the premaxillae. The beak stood vertically, with a regular, undulating surface which became smoother towards the sides. Cope described the same wavy appearance corresponding and alternating with the tooth-like processes in the jaw itself. . . . He [Cope] also described a similar horny beak on the lower jaw."

Cope of course had not described a wavy appearing structure occurring on both jaws, the upper being described as small tooth like processes. Ostrom (1961:152) apparently agreed with Lull and Wright stating, "Cope (1883), however, described beak impressions at the anterior extremities of both the upper and lower jaws in a specimen of *A. copei* (*Diclonius mirabilis*)." Yet neither LACM 23502 nor the equally well preserved Senckenberg specimen give any indication of a lower bill.

Sternberg figured a bill mold in describing a specimen of *C. excavatus* (NMC 8676), but in neither the plate explanation nor in the body of the paper did he state that the bill was attached to the lower mandible (Fig. 3). Ostrom, however, (1961:152) states, "Further evidence of a lower beak has been found in a third specimen (*Corythosaurus excavatus*), (NMC 8676), described by Charles M. Sternberg (1935), in the form of an impression of an incomplete horny beak in front of and along the left side of the prementary." As the plate from Sternberg's paper shows (Fig. 3) the mold is a fluted surface associated with the lower jaw but it is separated from the prementary by a considerable thickness of rock matrix. The presence of matrix between the surface and prementary is evidence that the mold is not the opposing surface of a prementary sheath. Upon examination of the plate and the small fragment in the collection of the Canadian National Museum, it appears as though the mold is that portion of the upper bill which originally projected over and in front of the prementary.

Although the fluted surface has been observed on three reported species, there is a problem regarding it. Does the fluted surface belong on the external surface or the internal surface of the bill?

Cope, (1883) having interpreted the mold as being attached to the lower jaw, apparently assigned the undulatory surface to the exterior of the lower bill. On the other hand, Versluys (1923) assigned the undulatory surface to the outer surface of the upper bill. Versluys presents excellent drawings showing that the bill was indeed attached to the upper mandible and that the feature is similar to the mold in LACM 23502. However, in reconstructing the bill he placed the undulatory surface on the exterior. Versluys removed the posterior portion of the bill mold and then poured a substance, probably plaster, against the anterior part of the mold, judging from the wording as translated from German. The resulting cast was retained but the rest of the mold was not. Versluys interpreted this cast as being the bill. He had apparently reproduced the posterior part of the original mold formerly occupied by matrix. Such a restoration would erroneously cause the undulatory surface to appear on the exterior rather than on the interior of the bill.

Sternberg (1935) did not state whether he believed the undulatory surface

of the beak to be on the exterior or the interior. Ostrom, however, in discussing the specimen of *Corythosaurus excavatus* described by Sternberg, states, (1961:152), "This specimen indicates the presence of small, tooth-like projections on the inner surface of the beak, which probably contributed to a firm union of this structure with the lower jaw." Sternberg's plate clearly shows a layer of matrix between the mold and predentary which is evidence against a firm union. In addition, the surface of the predentary, although rugose, is not appressed against the mold of the bill and the rugosities do not match the channels in the bill mold.

The various interpretations of the relationship of the undulatory surface to the mandibles is illustrated in Figure 4.

#### FUNCTION OF THE HADROSAURIAN BILL

Almost every conceivable mode of food gathering has been proposed at one time or another for the hadrosaurian dinosaurs. There are no existing



Figure 3. Lower jaw of *Corythosaurus excavatus*, NMC 8676, showing the bill mold (H.B.), predentary (P.D.), and dentary (D). This figure is reproduced from Plate II, Sternberg (3).

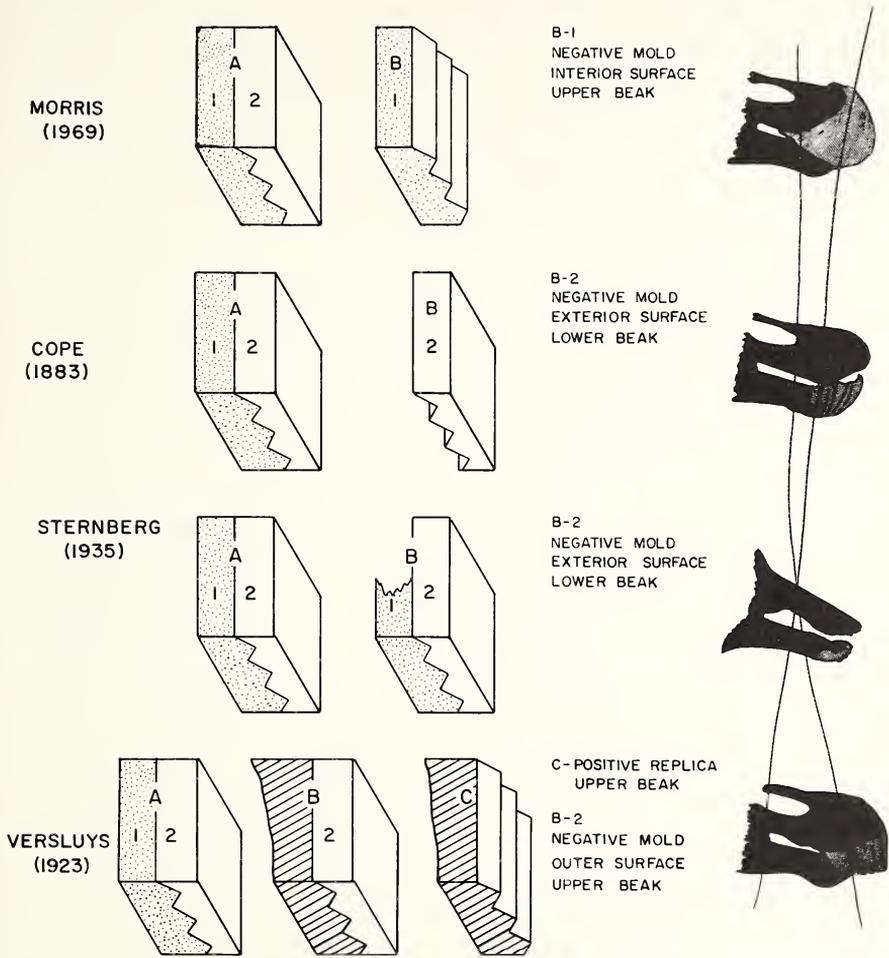


Figure 4. Diagram illustrating the interpretations of the four reported hadrosaurian bill molds. All interpretations are based upon molds preserved with specimens of *Anatosaurus annectens* except Sternberg (1935) which is based upon *Corythosaurus excavatus*. Blocks labeled represent the mold as discovered. Block 1 is the posterior part of the mold and 2 is the anterior. Blocks labeled B represent the parts of the mold preserved after preparation. Block C in the case of the interpretation by Versluys represents a plaster cast that was poured against B-2. Each group of blocks is followed by the interpretation placed upon them by the authors listed. Lastly, outline restorations are shown illustrating the interpretation by each other.

reptiles that have comparable feeding or masticating features. Cope suggested a diet of soft vegetable matter but this was based on the erroneous assumption that the teeth, in particular those of the dentary, were only loosely attached. Lull and Wright (1942:36) give the following picture, "The analogy now seems to be with the moose *Alces* whose diet is that of a browsing animal, that is the twigs and leaves of deciduous trees . . . and also certain conifers. In summer it turns to the tall, lush grass in swamps or near the margins of streams and lakes and, actually invading the water, feeds upon the leaves of the water lily or, with head entirely submerged, on the roots and stems of aquatic plants."

Versluys strongly rejected the idea of a ducklike feeding habit as reported by Abel (1912). Instead, he suggested that the structure was more beak than bill adapted for scraping bark and leaves from small scrubs and trees or even for the uprooting of plants.

There is only one report of stomach contents associated with a hadrosaurian skeleton. Unidentified plant debris and recognizable conifer needles were reported (Krausel, 1922) from the stomach cavity of *A. annectens*. As pointed out by Ostrom (1961), this might indicate merely that these creatures could feed on land plants, and it does not eliminate the possibility that they fed on aquatic vegetation as well. Indeed, the harsher fibers of land plants might be more readily preserved than the softer materials of aquatic plants.

In any analysis of their feeding habits, several morphological features must be taken into account and the assumption made that all of the features functioned together in an integrated well adapted system. The hadrosaurians were remarkably successful. Not only are their remains relatively common but genera have been recognized in North and South America and Eurasia. Despite considerable disparity, particularly in the shape of the skull, there are features related to feeding habits common to all genera. One is bulk. The probable weight of *Corythosaurus* and *Anatosaurus* was approximately 4 tons and yet the 30 to 40 foot hadrosaurians are not the largest recognized, being surpassed by *Edmontosaurus* and *Hypacrosaurus*. Small hadrosaurian remains have been collected but it is not known if these represent a truly small taxon or are immature individuals of the larger species. The few apparently undistorted skulls indicate that the hadrosaurians had a constricted buccal passage formed by the dentaries and maxillaries, and leading to the throat. In large anatosaurus, for example, it is doubtful that particles having a cross-sectional diameter larger than three or four inches could have passed along this narrow channel. Hadrosaurian dental batteries are very similar, consisting of dozens of teeth arranged in closely spaced rows. The occlusional surface is a pavement formed of the diamond-shaped crowns of the opposing dental batteries. In addition, in all genera three to six teeth are arranged in vertical rows and in each, only the most dorsal are in active use. The others serve for a highly effective replacement mechanism.

The bill as preserved in LACM 23502, seems to impose certain limiting parameters on hadrosaurian feeding habits. The structure seems best adapted for filtering. Although several workers have suggested that the bill closed

against the predentary of the lower jaw forming a cropping device, three characteristics of the bill seem to negate this function: 1) The bill was attached to the anterior and dorsal segment of the premaxillaries and its free edge extended well below the anterior dorsal margin of the predentary; 2) The very thin space between the anterior and posterior mold suggests that the bill itself was a relatively thin structure certainly not well adapted for foraging leaves and branches of trees and scrubs; 3) The last feature is the fluted, undulating inner surface of the bill which would have little or no function for foraging or browsing, and yet seems ideally suited as a filtering device.

Hadrosaurian dinosaurs, particularly such forms as *Corythosaurus* and *Hypacrosaurus*, are envisioned as mainly aquatic animals. A filtering device would be very important in assuring that these large animals could ingest large amounts of concentrated food relatively free of water in a manner similar to that of the dabbling ducks, such as *Dendrocygna*, *Anas* and *Aix*. These euryphagus forms have laminations on the inner surface of the dorsal bill which, when closed against the ventral bill, form an efficient filtering device. Such an interpretation certainly makes the name "duckbill" even more fitting for the hadrosaurian dinosaurs than previously supposed.

With their very efficient food gathering system, the hadrosaurs could take in all manner of food including mollusks and small crustaceans as well as plant material. In this sense they would, like many ducks, be relatively high protein as well as carbohydrate feeders. Plant material as well as more resistant invertebrates could be crushed between the broad occlusal surfaces of the impressive dental battery. By lowering the anterior part of the head, excess water as well as food particles smaller than approximately one cm would drain out of the mouth along the channels formed by the fluted bill and the opposing predentary. The resulting masticated material, highly concentrated, could then be made to flow down the very small passage between the dentaries to the stomach simply by raising the head.

The presence of the fluted bill, multiple grinding surfaces, mechanism for continuous replacement of teeth, and a constricted passage formed from the bones of the posterior mouth region makes such a feeding habit feasible.

Ostrom (1964) presents a very thorough compilation of prior hypotheses and information regarding the feeding habits of hadrosaurian dinosaurs. In his analysis of the paleoecology the conclusions reached vary only in detail from those expressed earlier (1961). In summary Ostrom states (1964:995), "Past interpretations of hadrosaurian ecology have pictured these animals as predominantly aquatic in their habits, living and feeding in swamps, lakes, or rivers and making only occasional and limited excursions out on surrounding lands. Anatomic evidence, however, contradicts this interpretation, indicating instead that the hadrosaurs as highly adept bipeds were primarily terrestrial animals. Other anatomic and botanical evidence shows them to have been active terrestrial foragers adapted for browsing on the harsher, fibrous, or even woody tissues of trees and shrubs."

The bill, as reconstructed from the mold of LACM 23502, is very thin relative to its lateral and vertical extent, and suggests a structurally weak

feature, too weak to be of use in browsing on fibrous or woody plants. Ostrom is in agreement with the conclusions presented here that hadrosaurian dental batteries together with a high degree of tooth wear must have been used to masticate food of substantial resistance; however, he suggests that this is evidence for foraging upon more resistant terrestrial vegetation. Such a dental battery could be used just as effectively for mastication of invertebrates. Ostrom (1964:987-989) suggests correctly that in the hadrosaurian localities of the Edmonton, Belly River, Judith River, Kirkland-Fruitland, Ojo Alamo and Lance marginal and aquatic vegetation are relatively rare in the paleoecosystems. This might, of course, be the result of fortuitous preservation, but even if truly representative it could be interpreted as evidence that aquatic and marginal vegetation was rare in the area where hadrosaurians were abundant, a position taken by Ostrom. On the other hand it could also be evidence for the needed addition of invertebrates in the hadrosaurian diet. One must keep in mind that the rarity of marginal and aquatic vegetation as computed by Ostrom is an absolute occurrence affected by all vagaries of preservation, but in the dynamics of the ecosystem it is the relative availability of the plants compared to the needs of the hadrosaurian that is significant.

Hadrosaurians were efficient bipeds and as Ostrom indicates (1964:990-993) the articular surfaces of the pes and hind limbs, the large fourth trochanter, ossified sacral tendons, and reduction of the carpus point strongly to this conclusion. These characteristics when treated by themselves may well suggest a terrestrial habitat but when the specialized nature of the bill is taken into consideration an alternative hypothesis seems more fitting. Therefore the conclusion that hadrosaurians were either aquatic or shallow water feeders seems appropriate. Under these circumstances the bipedalism as well as the specialized bill would be adaptively advantageous. In addition such a feeding habit would give credence to the more obvious adaptive significance of the laterally compressed tail and the probable presence of webbed hind feet, rather than to suggest that these characteristics were for protection allowing the otherwise defenseless hadrosaurian to retreat to the water when threatened (Ostrom, 1964:993-995).

#### RESTORATION OF HADROSAURIAN HEAD

Figures 5, A, B, and C are sketches illustrating the appearance of billed hadrosaurian dinosaurs. Evidence of bills have been found in *Anatosaurus annectens* and *Corythosaurus excavatus* but not in *C. intermedius* as restored in Figure 5C. In the skull of *C. intermedius*, however, the distal part of the dentary is greatly deflected while the maxillaries are not. The paratype skull of *C. intermedius* (ROM 4671) shows this deflection while, in the same skull, the tooth rows are occluded in normal position. If the specimen did not have a bill on the upper mandible, then there would have been a wide, opened gape at the anterior end of the mouth. The restoration of *C. intermedius* was made as this form has the most exaggerated gape of any hadrosaurian, a condition which suggests the presence of a bill, although the magnitude of the gape may be partly due to accidents of preservation.

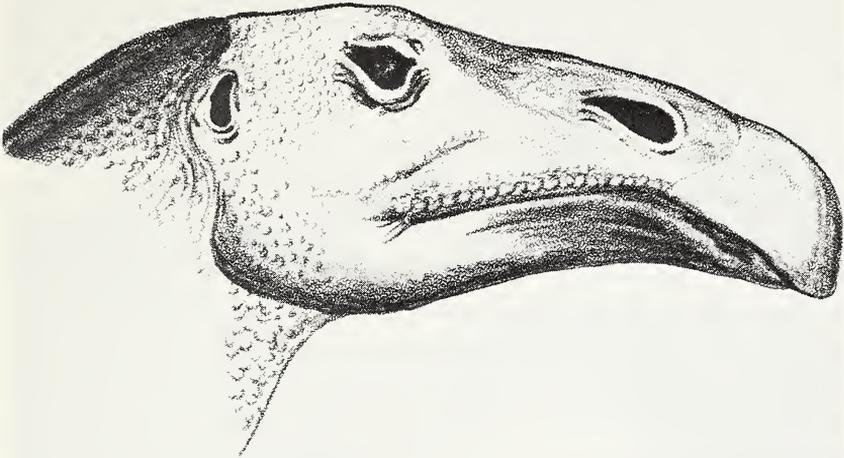


Figure 5. (A) Restoration of the skull of *Anatosaurus annectens*.

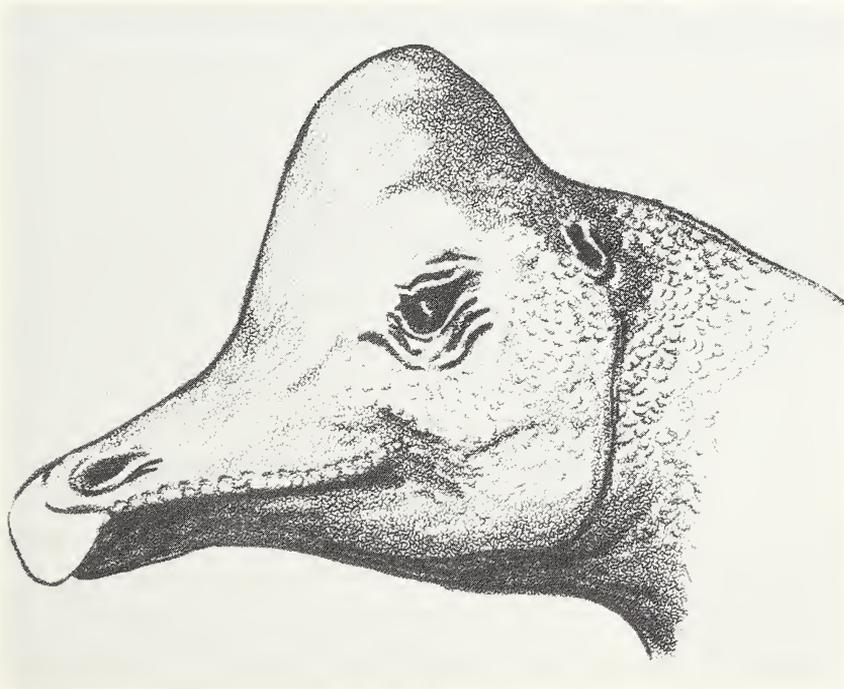


Figure 5. (B) Restoration of the skull of *Corythosaurus excavatus*.

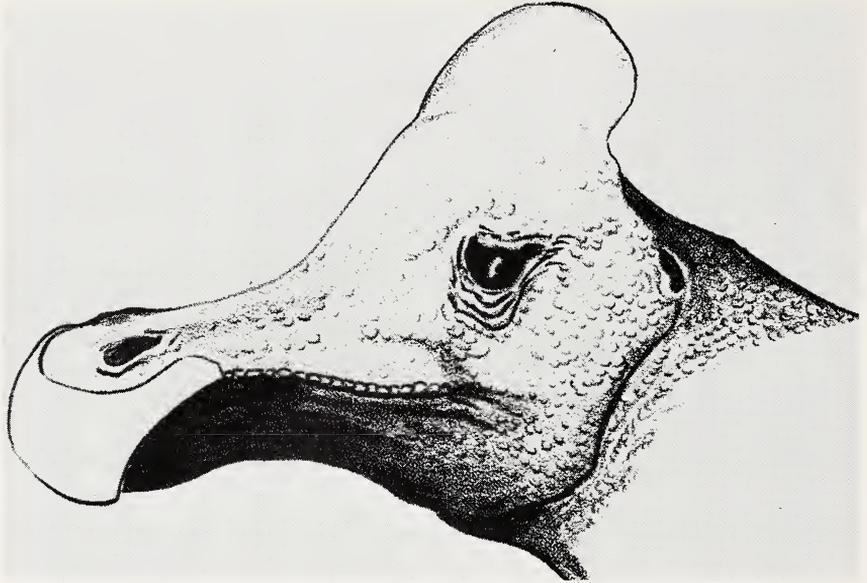


Figure 5. (C) Restoration of the skull of *Corythosaurus intermedius*.

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# CONTRIBUTIONS IN SCIENCE

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ANOTHER NEW NIGHT LIZARD (*XANTUSIA*) FROM  
DURANGO, MEXICO

By ROBERT G. WEBB



LOS ANGELES COUNTY MUSEUM OF NATURAL HISTORY • EXPOSITION PARK  
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VIRGINIA D. MILLER  
*Editor*

# ANOTHER NEW NIGHT LIZARD (*XANTUSIA*) FROM DURANGO, MEXICO

By ROBERT G. WEBB<sup>1</sup>

**ABSTRACT:** Ten specimens of *Xantusia* from a desert habitat in eastern Durango, Mexico are described as a new subspecies of the previously monotypic *X. henshawi*. The Durango population of *X. henshawi* is known only from the type locality; individuals occur in cracks and crevices of igneous (andesite) outcrops.

*Xantusia extorris* Webb is regarded as a subspecies of *X. vigilis*.

In May 1969, Dr. Charles C. Carpenter sent me one xantusiid lizard from the area in eastern Durango from which I had previously described *Xantusia extorris* (Webb, 1965). The specimen sent by Carpenter was not *X. extorris*, but resembled *X. henshawi*. Field work in August, 1969, yielded nine additional specimens from igneous outcrops and thereby revealed the presence of another disjunct population of *Xantusia* in eastern Durango. Its morphology suggests a subspecific relationship with *X. henshawi*.

I am grateful to Dr. Carpenter for sending me the specimen obtained by his field party in April, 1969; to Robert M. Kinniburgh for field assistance, and to the University of Texas at El Paso University Research Institute for defraying expenses in the field in August, 1969; to Dr. John W. Wright, Los Angeles County Museum of Natural History, and Drs. Alan E. Leviton and Steven C. Anderson, California Academy of Sciences, for the loan of comparative material; and to Dr. Jerry M. Hoffer, Department of Geology, University of Texas at El Paso, for analysis of rock samples.

Preserved specimens are in the collections of the following institutions, to which the abbreviations in parentheses refer in the text: The California Academy of Sciences (CAS), the Los Angeles County Museum of Natural History (LACM), and the University of Oklahoma (OU). The terminology for scales follows Savage (1963).

## ***Xantusia henshawi bolsonae*, new subspecies**

*Type material:* Holotype: LACM 55956 (Fig. 1), obtained 6-6.5 road miles NE Pedriceña on Mexican Highway 40, at an elevation of 4400 feet, Durango, México, by Robert G. Webb and Robert M. Kinniburgh (original field number, RGW 5365) on August 24-25, 1969. Paratypes: Eight specimens (LACM 55957-64) with same data as holotype. One specimen (OU 32848)

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from same locality as holotype, obtained by Jan Sassaman (member of field party headed by Charles C. Carpenter) on April 1, 1969.

*Diagnosis*: A subspecies of *X. henshawi* differing from *X. h. henshawi* in having fewer longitudinal rows of dorsal scales (averaging 50 rather than 63), seven (instead of six) supralabials, fewer femoral pores (averaging 7 rather than 11), in mostly lacking microscopic dark peppering laterally on the belly, in having a narrower head in relation to body length (head width/body length averaging 0.16 rather than 0.18), and probably in attaining a smaller (body length 57 rather than 68 mm) maximal size. For further detail, see comparisons and relationships.

#### DESCRIPTION OF HOLOTYPE

Female (on basis of relatively small size of femoral pores) with normal xantusiid body proportions; snout pointed, rounded at tip; nostrils partly visible in dorsal view; eye relatively large, slightly closer to nostril than to ear opening; ear opening ovoid and slightly diagonal; anterior preular fold indicated only by smaller scales that form two transverse rows medially; posterior preular fold, four scale rows anterior to gular fold, indicated only by short intercalary row of scales on either side; distinct gular fold with enlarged scales on edge abruptly differentiated from scales of fold immediately posterior; limbs relatively short, fingers and toes overlapping when limbs adpressed to body.

*Measurements* (in mm from dial calipers): Snout-vent or body length, 56.8; tail (seemingly regenerated), 61.9; head length, from tip of snout to upper anterior margin of ear opening, 12.0; maximal width of head, 8.7; depth of head, 4.4; length of large-scaled part of head, 11.5; diameter of eye, 2.4; distance from eye to tip of snout, 4.2; distance from tip of snout to gular fold, 9.1; length of leg, about 22.0; length of fourth toe, about 6.4; axilla-groin length, 28.3.

*Squamation*: Rostral broader than high, followed in order by two nasals, a frontonasal, two prefrontals, a median, two frontals, a hexagonal interparietal that separates two parietals, and two large postparietals; interparietal with obscure parietal eyespot; postparietals separated posteriorly by small, wedge-shaped interpostparietal that touches nuchals; nasals, prefrontals, frontals, and postparietals in contact; labials, loreal region and dorsal head scales minutely pustulose (pustules confined to edges of posterior head scales); nostril pierced in suture between rostral, nasal, postnasal, and first supralabial; nostril followed on side of head by postnasal, anterior loreal, large posterior loreal, two loreolabials, uppermost smallest, and small preocular scales of ocular ring; postnasal touching nasal and frontonasal above and first supralabial below; anterior loreal touching frontonasal and prefrontal above and first and second supralabials below; posterior loreal touching prefrontal and first supraocular above and second (barely) and third supralabials below; small, upper loreolabial touching first supraocular and posterior loreal; large,

triangular, lower loreolabial touching posterior loreal and fourth supralabial; scales of ocular ring small, two postoculars largest; uppermost postocular touching fifth supraocular; five supraoculars, first touching upper loreolabial, posterior loreal, prefrontal, median, and frontal (first supraocular divided into two scales on right side); fifth supraocular touching uppermost postocular, pretemporal and first temporal; pretemporal, touching fourth and fifth supraoculars, frontal, and parietal, followed by four (left) and five (right side) temporals that border parietal and postparietal; seven supralabials; four (left) and five (right side) infralabials; pretympenic scales variable in size, largest bordering temporal and auricular scales; five to seven small auricular scales; mental about as broad as long; three large pairs of postmentals, first pair touching medially; anteriormost pregular scale largest, between second pair of postmentals; 35 transverse rows (some intercalary from either side) of pregulars; 15 rows of pregulars between first pair of postmentals and anteriormost pregular fold; 17 rows between pregular folds, and four rows (curved from either side) of pregulars between posteriormost pregular fold and gular fold, excluding 13 enlarged scales on edge of gular fold; five rows of small scales in gular fold, anteriormost scales smallest.

Small, roundish, granular scales on back, sides, and limbs; some radials and femorals enlarged; 14 longitudinal rows of squarish ventrals at middle of body, lateralmost scales with curved outer edges and slightly smaller than adjacent ventrals; transverse rows of ventrals alternating along midline in some places, so that number is 32 on right and 34 on left side; two pairs of enlarged preanal scales, posteriormost pair largest; about 49 longitudinal dorsal scale rows at midbody; about 118 transverse rows of middorsal scales (from postparietals to level above posterior surface of thighs); 25 lamellae under fourth toe of left foot; seven femoral pores on each side; caudal scales rectangular, squarish proximally underneath tail.

*Coloration and pattern* (recently preserved, in alcohol): Dorsal ground color of head, body, limbs, and tail pale yellow-buff; sides of body whitish; ventral surfaces pale yellow-white; ground colors showing uneven distribution of minute black peppering under magnification; black peppering absent on postorbital head stripes, and mostly lacking proximally underneath tail and on chest and belly.

Dorsal surface having pattern of dark markings; dark brown spotlike markings on head, largest posteriorly; brown markings (paler than elsewhere) on limbs; dark brown-black markings on back, some markings lineate or of irregular shape; ground color of back less extensive than markings; dark brown-black markings on tail, tending to form ringed pattern; distinct, pale postorbital stripes extending posteriorly from upper margin of eye along juncture of temporals, and parietal and postparietal to small granular nuchal scales of neck; postorbital stripe with wide (as wide as pale stripe), continuous, brown-black lower border, but having border of two dark spots above; two,

pretympanic dark spots (right) or distinct, barlike mark (left side) between eye and ear opening; dark markings on side of neck and body paler and smaller than those dorsally; dark markings on side of head; labial region heavily suffused with dark punctations.

#### VARIATION

The general morphology of the nine paratypes closely approximates that of the holotype, except that the anterior preular fold is indicated by a fold of skin in OU 32848. The limbs seem to overlap more than in the holotype with the fourth toe reaching the region of the elbow when the limbs are adpressed to the body.

The measurements (in mm, means with ranges in parentheses) are based on the holotype and nine paratypes. The body length of the smallest specimen is 34.4. The body length of the largest female (holotype) is 56.8, and of the largest male is 50.8. Severed tails that have undergone complete regeneration are often difficult to distinguish from tails that have never been broken. The body length/tail length ratio of three specimens that appear to have original tails is 0.69 in one female with a body length of 51, and 0.74 and 0.75 in two males with body lengths of 50 and 51, respectively. The head length/body length ratio is 0.22 (0.21-0.24); the head width/body length ratio is 0.16 (0.15-0.17); the head width/head length ratio is 0.72 (0.68-0.79); and the head depth/head length ratio is 0.38 (0.35-0.42).

The squamation of the paratypes resembles that of the holotype. The size of the small interpostparietal is often variable; the scale is either lacking or very small, or in LACM 55957, it is especially elongate. Four specimens have either one or two small intercalary scales at the rear of the interparietal; in LACM 55961 the intercalary scale touches the small interpostparietal, and in LACM 55964 the two scales nearly touch. In LACM 55963 the postparietals are completely separated by a large interpostparietal. The nasals, prefrontals, frontals, and postparietals touch medially in all specimens. An incomplete longitudinal suture partly divides the posterior loreal (right side) in LACM 55961. All specimens have minutely pustulose head scales. The supraoculars are five, in one case four (second and third supraoculars fused). There is often one (sometimes two) intercalary scale between the first and second supraoculars and the adjacent median head scales; the intercalary scale seems to represent a fragment of the first supraocular. The temporals, variable in size, are usually five, in some cases four or six. The supralabials are usually seven, in one case six, and the infralabials are usually five, in one case four, and in another six. The largest postmentals are usually three, in one case four.

The transverse rows of ventrals average 32.8 (31-34), excluding the two (usually) or three rows (each of two scales) of enlarged preanals, and small intercalary rows, usually in the chest region. The longitudinal rows of dorsal granular scales across the middle of the back average 49.6 (48-52), and the

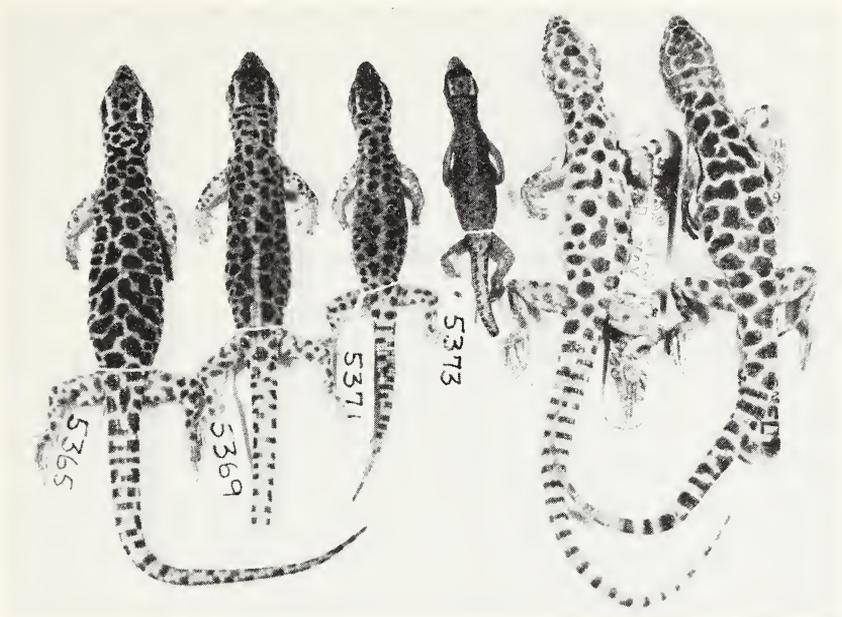


Figure 1. Comparison of dorsal pattern of *Xantusia h. bolsonae* and *X. h. henshawi*; four individuals of *bolsonae* at left and two individuals of *henshawi* at right; museum numbers of specimens from left to right: LACM 55956 (holotype), LACM 55960, LACM 55962, LACM 55964, CAS 57852, CAS 58089.

femoral pores average 6.9 (6-8). The femoral pores in females are often not well developed being marked by shallow depressions. The average number of transverse rows of preguarals between the anterior preguaral fold and gular fold is 20.8 (19-23), and of the enlarged scales on the gular fold is 11.8 (10-13).

The nine paratypes resemble the holotype in general features of pattern. All specimens have distinct pale postorbital stripes, which are accentuated by lacking microscopic black peppering and by having blackish borders that may be narrowly interrupted, especially the upper border. The black peppering is usually lacking proximally on the underside of the tail, is lacking or diffusely scattered on the underside of the head, and is mostly lacking on the chest and belly. The pattern on the neck and back of the largest specimens consists of small, irregularly shaped, dark blotches (generally intermeshed in jigsaw fashion) with the total area of blotching about equal to or slightly exceeding that of the ground color. However, ontogenetic variation is suggested since the corresponding pattern of the smallest specimen (LACM 55964, 34 mm body length) is obscure, consisting of small, mostly punctate, dark markings. See Figure 1 for variation in dorsal pattern.

Living individuals had pale yellow to buff ground color on the back, with the color somewhat more intense on the head. The tails were pale yellow, whereas the limbs and sides of the body were white. The dorsal markings on head, body, limbs and tail were dark brown-black. The ventral surfaces were white with the belly and tail tinged with yellow, especially ventrolaterally. The irises were orange with black reticulations concentrated anteriorly and posteriorly.

*Etymology:* The name *bolsonae* refers to the geographic position of this race in a southern outlier of the Bolson de Mapimí.

#### COMPARISONS AND RELATIONSHIPS

Based on gross morphological similarities there are two distinct species of *Xantusia*—*vigilis* and *henshawi*. Hitherto, *X. vigilis* contained six subspecies, *vigilis*, *gilberti*, *wigginsi*, *utahensis* (Savage, 1963:35), *sierrae* (Bezy, 1967a), and *arizonae* (Bezy, 1967b). *Xantusia extorris* closely resembles *X. vigilis*, but because of its geographic isolation and because of the status of the morphologically similar *arizonae* as a distinct species at that time, *extorris* was considered a distinct species (Webb, 1965). The degree of morphological difference between the subspecies of *X. vigilis* and between *X. henshawi* and *X. vigilis* indicates that relationships within the genus are best expressed by considering *X. extorris* as a subspecies of *X. vigilis*, and the isolated population described herein as *bolsonae* as a subspecies of the previously monotypic *X. henshawi*.

The distinct species, *X. henshawi*, is most readily distinguished from the other species in the genus, *X. vigilis*, by 14 longitudinal rows of ventral scales (instead of 12), and a dorsal pattern of relatively large, black blotches (instead of small dark dots).

The 108 specimens examined from throughout the range of *X. h. henshawi* do not seem to show any geographic variation, except in the number of femoral pores, and possibly in the number of temporals. In 54 specimens from the northernmost part of the range in the vicinity of the San Jacinto Mountains, Riverside County, California, the femoral pores average 11.9 (8-16), whereas the femoral pores in 54 specimens from the other localities to the south average 9.7 (7-12); the combined number of femoral pores averages 10.7. The number of temporals shows a slight increase from north to south. In populations to the north the number averages 5.2 (4-8), whereas the temporals in other populations to the south average 5.9 (4-7); the combined average number of temporals is 5.6. There seems to be no significant geographic difference in the number of dorsal granules across the back (62.8, 56-71), transverse rows of ventral scales (32.7, 30-36), enlarged scales on edge of gular fold (10.3, 7-14), transverse rows of pregonials between the anterior pregonial and gular folds (22.6, 19-29), infralabials (5.1, 4-7), supralabials (6.2, 5-8), in the ratio, head width/body length (0.18, 0.16-0.28), and in dorsal pattern. The average

body length of the 10 largest males is 60.4 (59-62), and of the 10 largest females is 65.3 (63-68).

*Xantusia h. bolsonae* has fewer longitudinal rows of dorsal granules (49.6, 48-52) than *X. h. henschawi* (62.8, 56-71). The average number of femoral pores is fewer in *X. h. bolsonae* (6.9, 6-8) than in *X. h. henschawi* (10.7, 7-16). The number of supralabials is usually seven in *X. h. bolsonae* (95%) rather than six as in *X. h. henschawi* (72%; the frequency of seven supralabials is 25%). In some specimens of *X. h. henschawi* it is difficult to determine which scale is the last supralabial. *Xantusia h. bolsonae* seems to have a slightly narrower head in relation to body length (head width/body length averaging 0.16, 0.15-0.17) than *X. h. henschawi* (0.18, 0.16-0.28). The two lateralmost longitudinal scale rows of the belly have a few scattered dots but are mostly devoid of microscopic black peppering in *X. h. bolsonae*. The ventral black peppering is extensive in *X. h. henschawi* but is diffuse or absent medially and most concentrated laterally; the two, and often the four, lateralmost scale rows are usually liberally black-peppered in *X. h. henschawi*. The postorbital stripes are distinct in all specimens of *X. h. bolsonae*; when present in *X. h. henschawi* the stripes are often indistinct. A comparison of the dorsal patterns on the back is difficult to evaluate, but generally the pattern is of relatively smaller, more often irregular-shaped, dark markings in *X. h. bolsonae* than in *X. h. henschawi* (see comparison in Fig. 1). *Xantusia h. bolsonae* may be a smaller subspecies (maximum size, 57) than *X. h. henschawi* (maximum size, 68).

*Comparative material examined of X. h. henschawi* (108 specimens): Baja California: 14 specimens—CAS 11932, 57294-96, 57455-58; LACM 36542-44, 36555-56, 36564. California. Imperial County: 20 specimens—CAS 22574-75, 57846-59; LACM 52668-71. Riverside County: 54 specimens—LACM 3769-72, 3774-76, 14513, 14519, 14524-26, 14528-29, 14531-49, 22370-73, 22376, 22381-84, 22389, 22391-92, 22395, 22397, 26800, 52672-77. San Diego County: 20 specimens—CAS 22017-18, 22566, 22581-85, 58083, 58086, 58089, 58093-94, 64298; LACM 52678-83.

#### GEOGRAPHIC RANGE AND HABITAT

The ten known specimens of *X. henschawi bolsonae* are from within about a one-half mile radius, 6-6.5 road miles (Mexican Highway 40) NE Pedriceña, Durango, México. The nearest localities for *X. henschawi*, some 800 miles to the northwest, are in southern California and adjacent northern Baja California (see map 72 in Stebbins, 1966). The extent of geographic range of *X. h. bolsonae* is not known. Apparent habitat was intensively examined only at the type locality. Perhaps *X. h. bolsonae* is restricted, at least in Durango, to the general desert habitat south of the Río Nazas where *X. vigilis extorris*, *Sceloporus maculosus*, and *Cnemidophorus inornatus paululus* also have restricted distributions in Durango.

The general desert habitat in this part of the Chihuahuan Desert has been



Figure 2. Type locality of *Xantusia henshawi bolsonae*, 6-6.5 road miles NE Pedriceña, elevation 4400 ft., Durango. Photographs taken August 25, 1969. Top: General view of hills and low mountains showing isolated, small, andesitic outcrops. Bottom: Outcrop of large weathered boulders of andesite.

described elsewhere (Webb, 1965). The general area is of relatively low elevation and physiographically is part of the extensive Bolson de Mapimí to the north; the topography is mostly irregular consisting of hills and low mountains. At the type locality there is a series of low hills with rock outcrops (Fig. 2). The principal vegetation covering the low hills includes lechuguilla (*Agave lecheguilla*), a maguey (*Agave* sp.), a treelike yucca (*Yucca* sp.), ocotillo (*Fouquieria splendens*), cholla (*Opuntia* sp.), small prickly pear (*Opuntia* sp.), and leatherplant (*Jatropha cuneata*). A shrubby legume (resembling *Mimosa*) and a small-leaved shrub (resembling *Rhus*) are often associated with the rock outcrops.

Rock outcrops in the area are not extensive and generally form either a cluster of large boulders (Fig. 2) or a rim-rock escarpment of limited extent up to 10 feet in height. *Xantusia h. bolsonae* is associated with these igneous outcrops; the rock is best described as a porphyritic andesite (with phenocrysts of biotite and feldspar) and may have either a gray or pink hue. Most of the rock exposures in this desert are gray dolomitic limestone; these outcrops frequently are extensive and have rough corrugated surfaces. Although collecting activities were limited, *X. henshawi* was not found to be associated with the limestone. The andesite weathers mostly into large chunks. The lizards were found in both vertical and horizontal crevices. They occurred in some horizontal crevices that had small amounts of soil. All individuals occurred singly, and were observed only after moving large chunks of andesite by using a large crowbar. Temperatures at 2 pm on August 24 were: rock surface in sun, 48° C; air in sun, 37° C; and air in shade of rock crevice, 34° C. Three species of rock-dwelling *Sceloporus*—*S. poinsetti*, *S. jarrovi*, and *S. maculosus*—are associated with both the andesite and limestone outcrops. One specimen of *S. poinsetti* and one of *X. henshawi* were found in the same rock crevice.

*Xantusia h. bolsonae* is sympatric with *X. vigilis extorris* in eastern Durango; one specimen of *X. vigilis* was found under a fallen yucca a few feet below an andesitic outcrop. Both populations are disjunct from the species in the southwestern United States and northwestern Mexico. The two Durangan populations occur east of the continental divide, and their ranges appear to be limited to the west by grasslands at higher elevations. The morphological differences between the two subspecies of *X. henshawi* seem to be greater than those between *X. vigilis extorris* and *X. vigilis gilberti* (the subspecies that *extorris* most closely resembles).

#### RESUMEN

Dies especímenes del género *Xantusia* de la habitación del desierto en el este de Durango, México, estan descritos como una nueva subespecie del previo monotípico *X. henshawi*. La población de Durango de *X. henshawi* es

conocida solamente por el tipo local; individuos ocurren en grietas y hendiduras en las pretuverancias de andesita ígnea.

*Xantusia extorris* es ahora considerada como una subespecie de *X. vigilis*.

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THE BIRDS OF THE KALINZU FOREST,  
SOUTHWESTERN ANKOLE, UGANDA

By HERBERT FRIEDMANN AND JOHN G. WILLIAMS



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*Managing Editor*

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## THE BIRDS OF THE KALINZU FOREST, SOUTHWESTERN ANKOLE, UGANDA

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**ABSTRACT:** The Kalinzu Forest, southwestern Ankole, Uganda, had never been explored zoologically before our field team worked there late in 1969. The forest is being cut down rapidly, and the present report on its avifauna may well be the final as well as the first account of its bird life. In all some 123 species are here recorded, and indicate that the Kalinzu Forest is (or was) a meeting place for some montane forest birds with the lowland forest species of western Uganda.

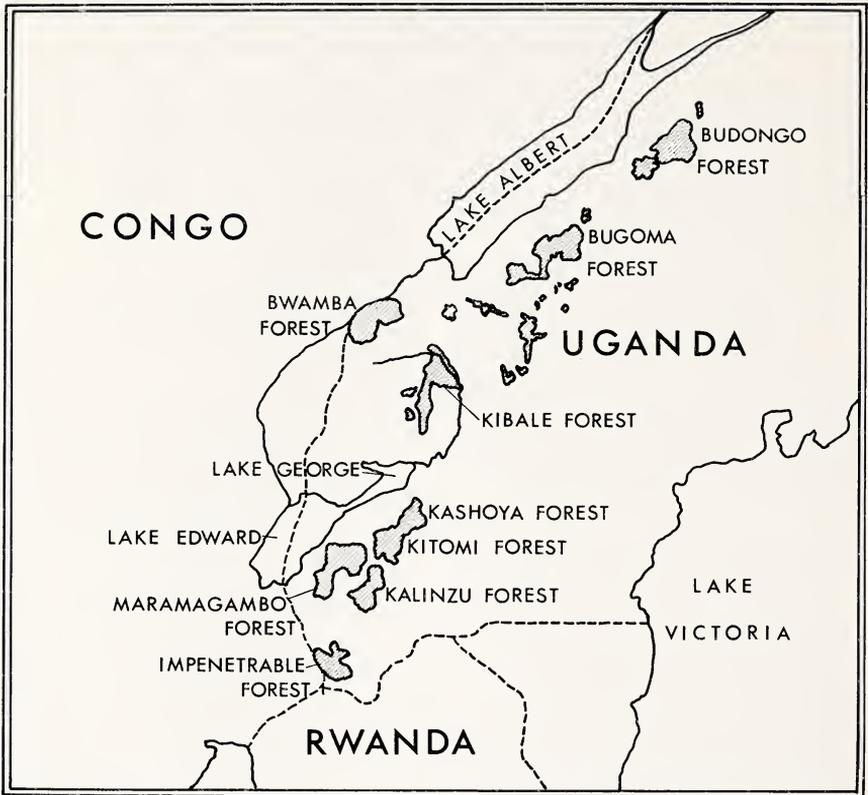
The Kalinzu Forest, a medium altitude (5000 feet) moist, evergreen forest, in southwestern Ankole Province, western Uganda, lies a short distance to the south of Lake George and to the east of Lake Edward, at 0° 25' S, 30° 05' E. It is close to, but 1400 feet higher than, the larger Maramagambo Forest, which extends to the border between Ankole and Kigezi, the extreme southwestern province of Uganda.

The Kalinzu Forest had never been explored zoologically before, and, indeed there seem to be no Kalinzu bird records in print. The survey on which the present report is based was carried out under sponsorship of National Science Foundation Grant GB-7787, by a team led by Robert M. Glen and Andrew Williams. Their stay in the Kalinzu covered just a month; their first specimens were collected on October 27, the last on November 26, 1969. The collection consists of 433 specimens of 121 species of birds, and also sight records of two more species. This comprises the first, and quite possibly, the last, collection to be made in that forest.

In the original plan submitted to National Science Foundation in 1966 for the survey of the terrestrial vertebrates of the isolated forests of western Uganda it was pointed out that these areas have, or may be expected to have, faunas that are west African rather than east African in their main affiliations, and, as such, they form the easternmost outliers of the ranges of many Congolese species. It was also stressed that there is an unfortunate urgency in the survey as most of these forests are being cut down at an alarming rate to make room for agriculture, and that if the survey were postponed by even a few years, it might be too late, and our potential knowledge of the original, natural distributional limits of many of these sylvan species would be thereby restricted forever.

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Forests of western Uganda.

The Kalinzu Forest may be taken as an extreme instance of the urgency for collecting data before it is too late; it is an area in which there is reason to think the survey was accomplished literally at the last opportunity. In a letter from the field, dated November 17, 1969, Robert M. Glen wrote as follows: ". . . The Kalinzu is probably the poorest forest we have yet collected. Vast areas, almost the whole forest, have been worked for timber with the majority of the remaining non-timber trees poisoned by the forestry department . . ." He was informed by the area forest officer, ". . . who spent two days in our camp, that we are seeing the last of the forest in its present state, since it is his intention, and that of the department, to utilize all standing timber as charcoal to supply a nearby tea factory which is at present being erected. Within a relatively short space of time . . . all vegetation will be of a secondary nature only."

It must be emphasized that it is not our intention to deplore what is happening to original, natural environments, as these changes are probably

inevitable, and no criticism of the trend is here implied. We merely wish to stress the need for gathering information about such areas while it is still possible to do so.

The following catalog of Kalinzu birds may well be smaller than it would have been if made five or ten years earlier, but we must be grateful that it was still possible to report so many kinds of birds. The fact that the forest lies at an altitude of 5000 feet makes it a meeting place of many lowland forest species with a smaller number ordinarily considered highland forest birds. Among the latter may be mentioned *Pycnonotus masukensis kakamegae*, *Coracina caesia pura* and *Erithacus aequatorialis*, all of which were collected, and *Tauraco johnstoni* and *Nectarinia purpureiventris*, which were seen, but not obtained.

The name Kalinzu Forest has previously been used for the lowest level of the Impenetrable Forest, in southwestern Kigezi Province, as was pointed out recently by Keith *et al.* (1969: 9-10). While it is unfortunate that this ambiguous application of the name exists, it must be clear that the Kalinzu Forest with which this paper deals is quite a different area, in Ankole Province, some 40 miles north-north-east of the nearest edge of the Impenetrable Forest, and at an altitude of 1500 feet higher than the lowest levels of the latter.

In the following annotated list we have kept to a minimum discussions of different systematic treatment by different authors, as our real purpose is merely to record what birds are known to occur (possibly by the time this paper appears, what are known to have occurred) in the Kalinzu Forest. By and large, we follow White (1960-1965) in nomenclature, and in the recognition or rejection of subspecies, except where more recent revisions have been issued, principally in the volumes completing the Check-list of Birds of the World begun by the late J. L. Peters. The order of the passerine families follows that of Chapin (1953, 1954).

#### ACCIPITRIDAE

##### *Polyboroides typus* Smith

On November 26 an African harrier hawk flew into a tree in an area in the Kalinzu Forest where several mist nets had been placed. It landed among a troop of monkeys of several species, all of which made a tremendous racket, but which dispersed as the hawk was shot. It proved to be an adult male, testes not enlarged; bill black, the base and soft parts whitish; iris dark brown; feet yellow; weight 720 grams; stomach empty.

##### *Accipiter tachiro sparsimfasciatus* (Reichenow)

One specimen, male, testes not enlarged, November 19; bill black, cere and gape greenish yellow; basal ring gray; iris yellow; feet yellow; weight 227 grams; stomach empty. This goshawk was caught in a net in open undergrowth in an area of remaining natural forest.

*Hieraaetus africanus* (Cassin)

Cassin's hawk-eagle is still generally considered a rare bird everywhere in its range, chiefly because it is rare in museum collections, yet three examples were obtained in eleven days, November 13 to 23, suggesting that in the Kalinzu Forest it is by no means uncommon. The three examples, two males and one female, were in non-breeding condition; bill black, the base gray, the soft parts, cere, and gape pale yellow; ring at base pale gray; iris medium brown to brownish cream; feet pale yellow; weight, female 1153 grams; males 938 and 1049 grams; all stomachs were empty. One of these birds was shot out of a tall tree, and while the collector's assistants were searching for it in the undergrowth, another one, probably its mate, flew into the same tree and was also collected. The other example was caught in a trap baited with a small chicken. The Kalinzu Forest is the second area in Uganda from which this hawk is now known, the other being the Impenetrable Forest in the extreme southwestern part of the country. It may be worth noting that in the Impenetrable Forest this hawk must also be common as our collectors in 1969 noted (but did not collect) the species on 21 occasions during two months in the field.

Keith and Twomey (1968: 537-538) considered it significant that their single male specimen from the Impenetrable Forest had an unusually long tail, 248 mm, as compared with 225 and 234 mm in two topotypical male birds from Gabon. Our two Kalinzu males have tails 228 and 231 mm long, the female 266 mm. Our males therefore agree in this dimension with Gabon examples and negate any suspicion that the eastern population of the species may prove to be a race characterized by its tail length.

## RALLIDAE

*Sarothrura elegans* (Smith)

One buff-spotted crane, a female with the ovary much enlarged, was collected on October 30, when it flew into the camp at night, apparently attracted by one of the pressure lamps hanging in the mess tent. It had the bill blackish gray, the lower base whitish; iris dark brown; feet dark brown; eye skin gray; weight 44.5 grams; stomach contents grit and small beetle fragments.

*Sarothrura pulchra centralis* Neumann

The white-spotted crane was not obtained in the Kalinzu Forest, but on November 8 an adult male was taken in the nearby Maramagamambo Forest, 3600 feet (as compared with 5000 feet at Kalinzu). It showed only slight gonadal swelling; bill black; iris dark brown; feet dark gray; weight 46 grams; stomach contents insect fragments.

## COLUMBIDAE

*Columba unicincta* Cassin

The afep pigeon is represented by an unsexed adult taken on November 21; bill gray, paling to whitish gray at the tip; iris orange-red; feet pale gray; weight 379 grams; stomach contents seeds of small fruits. The bird was seen feeding in a fruiting tree in an open area of the forest.

*Streptopelia semitorquata* (Rüppell)

Two adults with enlarged gonads, one male, one female, were collected on November 14, from a flock of several red-eyed doves feeding on the small berry-like fruits of a tall tree. Bill dull black, the gape pinkish in the male, dull maroon in the female; iris dark red; bare skin dull crimson to dull maroon; feet dull pale maroon; weight 162.5 grams (female), 192.5 grams (male); stomach contents seeds of small fruits.

*Turtur tympanistria* (Temminck)

One male with enlarged testes, November 13; bill black; soft parts dark dull maroon; iris very dark brown; bare skin dark gray; feet dull maroon; weight 75 grams; stomach contents seeds and grit.

*Treron australis gibberifrons* (Madarasz)

This green pigeon was met with twice, on November 12 and 16. On each day an adult male was taken, the second of which had large testes; bill pale gray; soft parts and cere dull orange; iris bright metallic sky-blue; feet orange-red; weight 225 and 226.5 grams; stomach contents small fruits.

## MUSOPHAGIDAE

*Tauraco schutti emini* (Reichenow)

On October 29 one male of this black-billed lourie was collected in a patch of secondary forest which had recently been felled; testes not enlarged; bill black, the lower base red; iris dark brown; feet black; bare eye skin red; weight 267 grams; stomach contents fruit seeds.

*Tauraco johnstoni* (Sharpe)

Robert Glen saw, but was unable to collect, what “. . . was certainly a Ruwenzori turaco . . .”, which would establish a new minimal altitude for this montane bird. A specimen would not only have been welcome to corroborate the identification, but also to determine which of the two races occurs in the Kalinzu Forest.

## CUCULIDAE

*Cuculus clamosus gabonensis* Lafresnaye

An almost adult female in the pale-bellied "mabirae" type of plumage of this forest cuckoo was taken on November 25; maxilla black; mandible slightly grayish; iris dark brown; feet white with pale gray scales; weight 87 grams; stomach contents hairy caterpillars. This specimen has the chin, throat and upper breast pale rufescent barred fairly broadly with blackish; the lower breast and abdomen whitish cream with only a small number of incomplete fuscous cross bars, especially toward the sides of the breast and abdomen, the under tail coverts unmarked cream.

*Chrysococcyx cupreus cupreus* (Shaw)

The emerald cuckoo undoubtedly occurs in every forest in Uganda. In the Kalinzu an adult female with an enlarged ovary was taken on November 2; maxilla blackish gray; mandible below greenish; iris dark brown; eye ring apple-green; feet blue-gray; weight 38 grams; stomach contents caterpillars. A few of the abdominal feathers have a pronounced yellowish wash in their pale areas—a slight variation in the direction of the richly yellow abdomen of the male.

*Ceuthmochares aereus aereus* (Viellot)

This cuckoo is represented in the collection by two males, one with large, the other with small, gonads, November 14 and 22; bill lemon-yellow; iris chestnut-brown to dark red; feet black; bare skin behind eye blue, in front of eye apple-green; weight 56 and 66 grams; stomach contents caterpillars, grasshoppers and beetles. These birds were found feeding in creeper-covered bush in mixed, exploited forest.

## STRIGIDAE

*Glaucidium tephronotum medje* Chapin

Three examples, two males and one female, of this owl were taken November 1, 22, and 26, respectively. It follows that the species must be fairly common in the Kalinzu Forest, and in the forests of western Uganda generally, as six more specimens from the Bwamba, Kibale, and Impenetrable Forests are now in the Los Angeles County Museum of Natural History. One of the present individuals was kept alive for some days and was heard to give a rather mournful sounding, whistled *poop* several times in rapid succession. This owl was caught in mist nets in the undergrowth in both primary forest and in areas where the trees had been heavily exploited. All three examples were in non-breeding state; bill pale greenish yellow to dull apple-green; cere yellow to greenish yellow; iris bright yellow (with gray flecks in one of the males); feet

yellow; eyelids olive; weight 83.5, 94, and 103 grams (the female the heaviest); stomach contents insect fragments and one green beetle. There is much individual variation among these owls, especially in the amount of rufescence on the underparts, and in the degree of difference between the dark grayish of the crown and occiput and the brown of the back, the distinction being more marked in some individuals than in others. As we pointed out (Friedmann and Williams, 1968: 15) some of the dorsal variability is probably due to wear as the brown feathers of the back have dark grayish tips when fresh, and as these are abraded, the brown color becomes correspondingly more prominent.

Because of the scarcity of specimens of this owl in most museum collections, the measurements of the nine examples now in Los Angeles form a useful addition to those discussed by Keith and Twomey (1968: 540-541). Our eight males have wing lengths of from 112 to 119 mm; tail lengths 80 to 88 mm; our one female, wing, 115 mm, tail, 85 mm.

#### APODIDAE

##### *Apus affinis affinis* (Gray)

This swift is fairly common in the Kalinzu area, where three males were taken November 1, 4, and 6. Two of them had enlarged gonads, the third showed only slight testicular swelling; bill black; iris dark brown; feet black; weight 25 to 28 grams; stomach contents flying insects. The collectors noted that this species was nesting under the eaves of the forestry department rest house at the edge of the forest.

##### *Chaetura sabini* Gray

Sabine's spine-tailed swift appears to be commoner and more widely distributed in western Uganda than was formerly thought. Five females were taken in the Kalinzu area October 31 to November 10, and others have been reported or collected in the Bwamba, Budongo, and Kibale Forests as well. Of our present examples only one showed much gonadal enlargement, the others had small ovaries; bill black; iris dark brown; feet maroon to maroon-gray; toes blackish; weight 16.5 to 18 grams; stomach contents small flying insects. These specimens were shot from groups flying over the swampy forest together with other swifts and with black rough-winged swallows (*Psalidoprocne*).

In an earlier paper we (Friedmann and Williams, 1968: 16) noted that the wing length of our sole Kibale specimen was only 110.9 mm, which seemed to uphold the validity of the supposedly short winged race *ogowensis*. Our present five examples have wing lengths varying from 114 to 126 mm, and they, in turn, make it more probable that *ogowensis* is not a recognizable subspecies. The use of a binomial for this swift thus appears to correctly reflect our knowledge of its variability.

## TROGONIDAE

*Apaloderma narina brachyurum* Chapin

Two male trogons, taken on the same day, November 25, differ in that in one the feathers of the rump and the upper tail coverts are somewhat bluer, less greenish than in the other; one had enlarged testes, the other showed only slight gonadal swelling; bill greenish gray becoming yellow at the base; iris chestnut-brown; feet pale flesh-brown; bare skin around eye apple-green; weight 68 and 70 grams, respectively; stomach contents caterpillars, one butterfly and other insect fragments. The birds were flying after insects about 20 feet from the ground, but the presence of caterpillars in their stomachs is evidence that not all of their food is caught on the wing.

## ALCEDINIDAE

*Halcyon malimbica malimbica* (Shaw)

Two specimens of this kingfisher were taken on November 18 and 19, one of each sex; the female with large ovary, the male with slightly swollen testes; bill crimson-red, the mandible and the lower base blackish; iris dark brown; feet orange, scales brownish; weight 89 and 92.5 grams, respectively; stomach of the female held a blue-green tree frog while that of the male was empty.

## MEROPIIDAE

*Merops gularis australis* (Reichenow)

One male and two females of this bee-eater were taken October 28 to November 4, all in non-breeding state; bill black; iris red; feet black; weight 30 to 34 grams; stomach contents beetles and one wasp. On November 8 another male was taken in the nearby Maramagambo Forest, 3600 feet.

## CORACIIDAE

*Eurystomus gularis neglectus* Neumann

Two male rollers with small gonads and one female with enlarged ovary collected November 10 to 16. The males are in a changing state of plumage with a mixture of blue and maroon-brown on the abdomen; bill yellow; iris dark brown; feet yellowish brown, the toes darker; weight 99 (female) to 117.5 grams (males); stomach contents termites and flying black ants. These birds were seen catching small insects on the wing in the open, exploited forest.

## PHOENICULIDAE

*Phoeniculus bollei jacksoni* (Sharpe)

Two wood hoopoes were taken October 30 and November 4, the former unsexed, the latter a male; bill orange-red to deep pinkish crimson; iris dark brown; feet red; weight 48 and 55 grams; stomach contents beetle larvae and other insect remains.

## BUCEROTIDAE

*Bycanistes subcylindricus subquadratus* Cabanis

One male hornbill in breeding condition, taken November 14; bill dull scaly brown, with base and half of casque pale gray; iris rich reddish brown; bare skin dull black; feet scaly black; weight "over 1600 grams"; stomach contents fruits. The collectors noted many more single birds (males?) than pairs, which seemed to suggest that the females were already holed up in their nests.

## CAPITONIDAE

*Lybius hirsutus ansorgei* (Shelley)

The hairy-chested barbet is fairly common in the Kalinzu forest. Three examples were collected October 31 to November 22; all with slight gonadal enlargement; bill black; iris dark brown; feet black; weight 45 to 49 grams; stomach contents berries and fruit seeds. These specimens were collected in the undergrowth in an unspoiled area of natural forest.

*Gymnobucco bonapartei cinereiceps* Sharpe

The brown barbet was numerous and four specimens were taken November 13 to 19, three of them with large gonads, one with small ones; bill blackish horn; iris cream to yellowish white; feet black; weight 62 to 67 grams; stomach contents green fruits. A female, November 19, was shot at a nesting (?) hole in a dead tree.

*Buccanodon duchaillui duchaillui* (Cassin)

On November 10 three adults, two females, 1 unsexed, were collected; this was the only time the field team met with this barbet. The birds were in non-breeding state; bill black; iris dark brown; feet dark gray; weight 33 to 36.5 grams; stomach contents small fruit seeds. All were netted in the undergrowth in a heavily exploited part of the forest.

*Pogoniulus scolopaceus aloysii* (Salvadori)

This little tinker bird was common in the Kalinzu. Specimens were obtained October 28, November 14, and November 20, the first and the last were in breeding condition; bill black; iris cream to grayish yellow; feet dark gray; weight 15.5 to 17 grams; stomach contents insect fragments and small fruit seeds. Found in the undergrowth in exploited forest areas.

*Pogoniulus bilineatus mfumbiri* (Ogilvie-Grant)

The commonest tinker bird in Kalinzu; seven examples, October 29 to November 19; non-breeding condition; bill black; iris dark brown; feet blackish; weight 10.5 to 13.5 grams; stomach contents fruit seeds and insect fragments.

*Trachyphonus purpuratus elgonensis* Sharpe

This brightly colored species was one of the commonest barbets in the Kalinzu. Large numbers were caught in the mist nets (and released) where they were catching flying termites as they escaped from the ground. Five specimens were taken October 30 to November 12; four of them with small, one with large, gonads; bill lemon-yellow; iris dark red; feet blackish gray; weight 72 to 85 grams; stomach contents fruit and fruit seeds.

INDICATORIDAE

*Indicator exilis pachyrhynchus* (Heuglin)

The least honey guide is represented in the collection by one adult male, with enlarged testes, taken October 30; bill black, the lower base whitish; iris dark brown; eye skin dark gray; feet olive-gray; weight 21.5 grams; stomach entirely filled with beeswax. It was collected when it came to a spot where a number of sunbirds were excitedly mobbing a snake. Although this was the only example noted, there is every reason to assume that this honey guide is no less numerous in the Kalinzu than it is in the other western Uganda forests. The local abundance of small barbets, of at least two species of *Pogoniulus*, would assure an ample supply of hosts for this brood parasite as well as for the next species.

*Indicator willcocksii willcocksii* Alexander

That this forest honey guide occurs in the Kalinzu is of interest in rounding out our concept of its range in western Uganda, where it is already known from the Impenetrable and the Kibale Forests. It does not occur in the Bwamba woodlands, which are at too low an altitude, as its range seems to be above 4200 feet. Three specimens, one male and two females, were taken in the Kalinzu on October 27, November 13, and November 23, respectively; all were in non-breeding state; bill black, the lower base pale pinkish gray; iris dark brown; feet olive-gray; weight 16 and 17 grams in the females, 20.5 grams in the case of the male; stomach contents entirely beeswax in two, beeswax and small insect fragments in the third.

In an earlier paper we (Friedmann and Williams, 1968: 17-18) described seven specimens from the Impenetrable and Kibale Forests as being slightly paler and with more of a yellowish tone below and less heavily streaked on the crown than were the available Cameroon and Congo specimens, and we raised the possibility of an eastern subspecies of *I. willcocksii*. The Kalinzu birds merely add to the variability, or the inconstancy of coloration as noted in the western Uganda population, and thereby tend to negate the idea of an eastern race of this honey guide. Furthermore, as we pointed out in the earlier paper, it would be necessary to see specimens from localities all across the Congo before it would be possible to ascertain where, if anywhere, such a division might be made.

## PICIDAE

*Campethera nivosa herberti* (Alexander)

Inasmuch as the buff-spotted woodpecker is known from many forested areas throughout Uganda, it is no surprise to find it in the Kalinzu as well. On November 22, two males were collected as they were watched searching for insects on a dead branch sticking up out of the undergrowth in an undisturbed area of primary forest. Both birds showed only slight gonadal enlargement; bill horn black becoming brown on the basal part of the mandible; iris dark brown; bare eye skin olive-gray; feet olive; weight 35 and 39 grams; stomach contents insect fragments.

*Campethera tullbergi taeniolaema* Reichenow and Neumann

The fine-banded woodpecker is a very common bird in the Kalinzu Forest. Our collectors obtained ten specimens from October 30 to November 8, all in non-breeding condition; bill horn-black to dark gray, the basal part of the maxilla pale gray; iris bright crimson to deep chestnut; eye skin gray; feet olive; weight 48 to 55 grams; stomach contents ants in all cases. These woodpeckers were found feeding along long stems in the undergrowth in areas where the forest had been heavily exploited.

*Dendropicus fuscescens lepidus* (Cabanis and Heine)

The cardinal woodpecker was met with on November 23 when one adult male was collected as it was pecking on one of the upper branches of a dead forest tree that had been poisoned by the forestry department as part of its scheme to remove the remnants of the Kalinzu to make way for agriculture. It is not known if the methods used to poison non-timber trees affects the edibility of the insects still found on the latter, and, so, in turn, the birds that feed on them; but the question is a real one. The specimen obtained had the bill dark horn-gray above, paler toward the base on the mandible; iris red-brown; eye skin dark gray; feet olive; weight 25 grams; stomach contents beetles and beetle larvae.

*Mesopicos xantholophus* (Hargitt)

The yellow-crested woodpecker occurs in many Ugandan forests and its presence in the Kalinzu is therefore not surprising. One male and two unsexed specimens were collected, October 31 to November 25; bill dark horn-gray, paler on the mandible; iris red-brown to deep crimson; eye skin dark gray; feet olive-gray; weight 57.5 to 66 grams; stomach contents beetle larvae. The birds were noted feeding extensively on spurge stems (*Neobutonia*), which apparently house a great many beetles. Robert Glen wrote that he had observed many species of beetles, including even the very large goliath beetle, frequenting these spurge stems.

*Mesopicos elliotii elliotii* (Cassin)

Elliot's woodpecker is generally considered to be fairly uncommon in the forests of Uganda, but it must be common in Kalinzu, as four specimens were obtained in less than a week, October 30 to November 4; all in non-breeding state; bill blackish horn, paling to gray on the mandible; iris dark brown to deep crimson; eye skin brown to dark gray; feet olive; weight 34.5 to 38 grams; stomach contents ants, caterpillars and beetle larvae.

## EURYLAEMIDAE

*Smithornis capensis meinertzhageni* van Someren

The African broadbill is common in Kalinzu; five specimens, four males, one female, all in non-breeding state, were collected, November 8 to 22; maxilla black; mandible whitish gray to pale pink; iris dark brown; feet pale olive-yellow to olive; weight 23 to 27.5 grams; stomach contents insects, mainly small beetles. These birds were all netted in the dense undergrowth in natural forest areas.

## HIRUNDINIDAE

*Hirundo rustica rustica* Linnaeus

One male example of the European barn swallow, a winter visitor to Uganda, was collected on November 16; weight 20 grams; stomach contents small flies.

*Psalidoprocne pristopectera ruwenzori* Chapin

One male, with large testes, collected November 14, has a short tail (77.5 mm) well within the variational range of *ruwenzori*; bill black; iris dark brown; feet dark brown; weight 11.5 grams; stomach contents insect fragments.

## MOTACILLIDAE

*Motacilla cinerea cinerea* Tunstall

One female gray wagtail was taken November 16; ovary small; bill blackish horn; iris dark brown; feet pale brown; weight 16.5 grams; stomach contents insect fragments.

*Motacilla capensis wellsii* Ogilvie-Grant

Common in the open areas about the Kalinzu Forest. From October 29 to November 13 four examples were secured, two males with large gonads, one female with a small ovary, and one of unrecorded sex; bill black; iris dark brown; feet blackish gray; weight 19 to 25.5 grams; stomach contents insect remains.

## TIMALIIDAE

*Trichastoma fulvescens ugandae* (van Someren)

This brown babbler would seem to be relatively uncommon in Kalinzu, judged by the fact that only a single example was obtained, as compared with four or five of *T. rufipennis* and *T. albipectus*. One male in non-breeding state was obtained November 4; maxilla black; mandible gray; iris brown; feet dark gray; stomach contents beetles and small snails. The bird was caught in a mist net in the dense undergrowth in an area of heavily exploited forest.

*Trichastoma pyrrhoptera pyrrhoptera* (Reichenow and Neumann)

One specimen, a non-breeding male, November 8; maxilla black; mandible pale gray; iris chestnut; feet gray; weight 25 grams; stomach contents beetles and small snails.

*Trichastoma rufipennis rufipennis* Sharpe

Common in the Kalinzu Forest, where four specimens were caught in mist nets placed in the undergrowth of natural, undisturbed forest, November 13 and 14; all were in non-breeding state; maxilla black; mandible blue-gray; gape yellow; iris dark brown; feet dark gray, the toes paler; weight 21 to 26 grams; stomach contents insect fragments and small snails.

*Trichastoma albipectus* (Reichenow)

Like the previous species this one is also numerous in the Kalinzu Forest, where it occurs with the very similar *T. rufipennis*. Five specimens, four males, one of which had enlarged gonads, and one female, were taken November 1 to 23; maxilla black; mandible pale gray; gape yellow; iris brown to reddish brown; feet opaque pale gray in some cases with a pinkish or a pale violet tinge; weight 28 to 32 grams; stomach contents small beetle fragments and parts of one millipede. This species was caught in nets in both natural and exploited forest.

## PYCNONOTIDAE

*Pycnonotus barbatus tricolor* (Hartlaub)

This ubiquitous bulbul is represented in the collection by an adult male in non-breeding state, taken on November 19 outside the forest; bill black; iris dark brown; feet black; weight 45 grams; stomach contents fruits.

*Pycnonotus masukensis kakemegae* (Sharpe)

The Kalinzu Forest would seem to be at the lower level of the range of this bulbul, which is chiefly a bird of the highland forests. Between October 28 and November 21 four males and one female were collected; gonads ranging

from small to much enlarged; bill blackish above, dark gray below; iris red-brown; feet blue-gray; weight 25 to 27 grams; stomach contents insect fragments, and, in one case, small fruits. These birds were collected in natural or little exploited forest areas. The Kalinzu is the only area from western Uganda other than the Impenetrable Forest from which we have received examples of this species; it might have been expected in the Kibale Forest, but our collectors did not meet it there.

*Pycnonotus virens holochlorus* (van Someren)

One female in non-breeding condition, November 4; bill brownish black; iris dark gray; feet yellow-brown; weight 21.5 grams; stomach empty; netted in undergrowth in heavily exploited forest.

*Pycnonotus gracilis ugandae* (van Someren)

Common in the Kalinzu; six specimens, four males and two females, all with small gonads, were taken October 30 to November 22; bill black; iris dark brown; feet olive-gray; weight 19 to 22 grams; stomach contents fruit seeds, insects and insect larvae.

*Pycnonotus curvirostris curvirostris* (Cassin)

Another common Kalinzu bird; seven examples October 29 to November 24; gonads varying from small to large; bill dark horn gray to blackish, more yellowish brown at tip; iris chestnut-brown to red-brown; feet olive; weight 23.5 to 26 grams; stomach contents fruit seeds and insect fragments.

*Pycnonotus latirostris eugenius* (Reichenow)

As might have been expected this bulbul proved to be numerous in the Kalinzu Forest. Seven specimens were obtained October 28 to November 14, three of them with enlarged gonads, four with small ones; bill black, tomium and gape yellow; iris dark gray-brown; feet brownish yellow; weight 25.5 to 29 grams; stomach contents fruit seeds and insect remains. The yellow-whiskered bulbul was found (netted) chiefly in undergrowth in heavily exploited areas of the forest.

*Pycnonotus gracilirostris congensis* (Reichenow)

Very common. Seven examples were taken in the Kalinzu Forest and two more in the nearby Maramagambo Forest, October 28 to November 19. A long series of this bulbul from many of the western Uganda forests suggests the use of the name *congensis* rather than the recognition of *chagwensis*. In this allocation we follow White (1962: 78) rather than Rand (1960: 256). The birds were mostly in non-breeding state, but one female, November 2, had an enlarged ovary; bill black; iris brick-red to crimson; feet black; weight 29 to 37

grams; stomach contents insect fragments entirely. These slender-billed bulbuls were noted feeding in the tree tops in the ironwood climax forest.

*Baeopogon indicator indicator* (Verreaux)

One male in non-breeding state, October 28; bill black; iris white; feet dark gray; weight 47 grams; stomach contents ants; collected in a heavily exploited area of the forest.

*Phyllastrephus hypochlorus* (Jackson)

Apparently fairly common in the Kalinzu Forest; three specimens, November 8 to 18; all with small gonads; bill black above, grayish below with whitish sides at the tip; iris brown; feet gray; weight 21 to 28 grams; stomach contents insect fragments.

*Phyllastrephus fischeri sucosus* Reichenow

Very common in the Kalinzu; seven examples were collected, October 28 to November 22; gonads ranging from small to much enlarged; bill blackish horn to black, the tomium and mandible paler; iris gray to yellow-gray to pale brown; feet gray; weight 20 to 27 grams; stomach contents ants and other insect fragments. These birds were netted in the undergrowth in heavily exploited areas of the forest.

*Phyllastrephus xavieri xavieri* (Oustalet)

Xavier's bulbul was found to be common in the Kalinzu, where four specimens were obtained October 31 to November 24; all with small gonads; bill black, tomium and gape yellow, mandible gray at base; iris gray to grayish cream; feet dark gray, the toes paler; weight 25.5 to 27 grams; stomach contents insect remains. These birds were caught in nets in the undergrowth in the heavily exploited areas of the forest.

*Bleda syndactyla woosnami* Ogilvie-Grant

Very common in the Kalinzu; seven specimens taken November 4 to 21; all but one with small gonads; bill black above, pale gray below; iris dark red to reddish brown; feet brownish gray to pinkish gray; weight 40 to 49 grams; stomach contents beetles and other insect fragments.

*Criniger calurus emini* Chapin

This bulbul was found to be very common and seven specimens were obtained November 4 to 22; gonads ranging from small to much enlarged; bill black above, blue-gray below and with the tomium whitish in some but not in all individuals; iris chestnut to crimson; feet gray to dark blue-gray; weight 23 to 31 grams; stomach contents beetles and other insect fragments. All these

specimens are definitely *C. calurus* and not *C. ndussumensis*, as all have broad bills and lack any grayish on the lores.

CAMPEPHAGIDAE

*Coracina caesia pura* (Sharpe)

The Kalinzu Forest (5000 feet) must be close to the lower level of the range of this cuckoo-shrike, which does not occur in the lower Bugoma, Bwamba or Kibale Forests. Two females, both in non-breeding condition, were taken November 20 and 22. Both were in late stages of molt and both were in nearly complete adult plumage; bill black; iris dark brown; feet black; weight 49 and 50 grams; stomach contents caterpillars and other insect remains.

*Campephaga phoenicea petiti* Oustalet

One adult male, testes much enlarged, taken on November 25; bill black; gape rich yellow; iris dark brown; feet black; weight 34 grams; stomach contents caterpillars. The yellow gape of the male is conspicuous in the field.

MUSCICAPIDAE

*Muscicapa adusta pumila* (Reichenow)

One male of this little flycatcher, testes not enlarged, was taken November 7; bill black above, the basal half of mandible cream; iris dark brown; feet black; weight 7.5 grams; stomach contents beetles.

*Muscicapa griseigularis* (Jackson)

This flycatcher is fairly common in the Kalinzu Forest; three males and one female, all with small gonads, were collected November 4 to 18; maxilla black; mandible gray; iris dark brown; feet gray; weight 10.5 to 13 grams; stomach contents small beetle and other insect fragments. These birds were caught in mist nets in the undergrowth of both natural and exploited areas of the forest.

*Muscicapa comitata* (Cassin)

Another common bird, of which four specimens were taken November 2 to 14, two of each sex, all with small gonads; bill black; iris dark brown; feet black; weight 14 to 15 grams; stomach contents small beetle fragments.

*Artomyias fuliginosa* J. and E. Verreaux

This dusky brown flycatcher was found to be very numerous in the Kalinzu; six specimens were collected November 1 to 13; four with enlarged gonads, the other two unsexed because of damage; bill black; iris dark brown; feet black; weight 17 to 19 grams; stomach contents beetle fragments. One of the unsexed birds is subadult, molting into adult plumage, but still has the

upper parts and the breast dotted with white, the abdominal feathers with buffy grayish white ends, and also with the gape whitish. The birds perch on bare branches of tall forest trees from which they make frequent sorties to capture insects. They resemble martins when on the wing.

*Fraseria ocreata ocreata* (Strickland)

Common in the Kalinzu Forest; four specimens taken October 30 to November 5; two of each sex, all in non-breeding state; bill black; iris dark brown; feet blackish; weight 37.5 to 40 grams; stomach contents beetle fragments. Three of these forest flycatchers were noted as being collected while they were catching termites on the wing, but the fact remains that only beetles were found in their stomachs!

*Megabyas flammulata aequatorialis* Jackson

Another common Kalinzu species; six specimens taken, three females, two males, October 28 to November 6; all with small gonads; bill black; iris red; feet dull brownish pink to maroon; weight 27.5 to 31 grams; stomach contents beetle fragments, and, in one case, lepidopteran eggs. These birds were seen feeding in trees and were also netted in the undergrowth in exploited parts of the forest. On November 8 an immature male, molting into adult plumage, was collected in the nearby, but lower (3600 feet), Maramagambo Forest.

*Bias musicus musicus* (Vieillot)

Fairly common flycatcher. One of each sex collected, October 31 and November 9 in the Kalinzu, and two others, one of each sex, November 8 in the Maramagambo Forest; bill black; iris yellow; feet pale yellow; weight 21 to 22 grams; stomach contents beetles and other insect fragments, including flying insects.

*Batis molitor* (Hahn and Kuster)

This flycatcher was met with only once, on November 6, when a pair were seen running along branches of low trees in search of food. Both birds were in non-breeding state; bill black; iris pale green, lower ring yellow; feet black; weight 11 and 12 grams; stomach contents small beetles.

*Platysteira castanea castanea* Fraser

Very common in the Kalinzu Forest; seven examples were taken, October 28 to November 25; gonads large in one, small in the others; bill black; iris chestnut to dark maroon; feet dull maroon; weight 12 to 16 grams; stomach contents insect, largely beetle, fragments. The eye wattles in the females seem to be slightly darker in life than those of the males. These wattle-eyes were caught largely in nets in the undergrowth, close to the ground, in relatively unmolested areas of natural forest.

*Platysteira blissetti jamesoni* (Sharpe)

One male, with enlarged testes, taken October 28 and one female, with a small ovary, November 13; bill black; iris dark maroon; feet maroon to dull violet-maroon; weight 10.5 to 11 grams; stomach contents insect fragments, beetles in one case. Netted near a small stream in natural forest.

*Platysteira concreta graueri* (Hartert)

This wattle-eye must be very numerous in the Kalinzu Forest, as six specimens were collected November 4 to 21, three of each sex; one of the females with much gonadal enlargement, the other individuals with small gonads. The males illustrate the plumage polymorphism of this species, described by Prigogine (1969), as one of them has the entire underparts bright yellow while the other two have the whole area bright chestnut; the three females have the chin, throat and breast bright chestnut, the abdomen and under tail coverts yellow, the two being sharply demarcated; bill black; iris very dark maroon-brown with a white inner ring; wattles pale yellow-green; feet dark blue-gray; weight 12.5 to 15 grams; stomach contents small insect, largely beetle, fragments. Although this wattle-eye has been reported from the Semliki Valley on the west side of the Congo-Uganda border, and from Kakamega in western Kenya, we are not aware of any Uganda locality other than Bwamba and Kalinzu Forests.

*Trochocercus nigromitratus* (Reichenow)

Two specimens, October 28 and November 13, represent this flycatcher; bill black; iris dark brown; feet gray to dark blue-gray; weight 10 to 11.5 grams; stomach contents beetle and other insect fragments.

*Terpsiphone viridis ferreti* (Guerin)

This paradise flycatcher is very common in the Kalinzu Forest; thirteen specimens were obtained October 28 to November 25. The series illustrates the polymorphic nature of the species, two of the females have the entire upper parts, wings and tail dark bluish gray; all the others are reddish brown backed birds but with much variation in the darkness of the blue-gray underparts, which range from fairly pale blue-gray to almost blackish blue. The only males with elongated central rectrices also had enlarged testes; bill dark blue-gray to pale cobalt-blue, the tip and tomium blackish; iris dark brown; feet blue-gray to dark blue-gray; eye skin dark blue-gray; weight 12 to 16.5 grams (one female marked 22 grams); stomach contents small beetle and other insect fragments.

One of the dark bluish gray backed females was seen together with, and apparently following, a red backed, long tailed male (also collected), a good indication that what we are dealing with here is polymorphism and not a confusion of two different taxa.

## TURDIDAE

*Alethe poliocephala carruthersi* Ogilvie-Grant

This thrush was common in the Kalinzu Forest; five specimens were taken November 1 to 13; gonads small in four, large in one; bill black; iris deep chestnut to dark "soft" brown; feet opaque gray, with or without a pinkish tone; weight 25 to 34 grams; stomach contents small beetle and other insect fragments, one snail. The brown-chested alethe was found in both unspoiled and in heavily exploited parts of the forest.

*Erithacus aequatorialis* (Jackson)

Fairly common; four specimens taken, October 31 to November 5; all in non-breeding state; bill black; iris dark brown; feet silvery gray to pale brownish gray; toes yellowish; weight 14 to 19.5 grams; stomach contents insect fragments, mainly beetles. These akalats were caught in nets in the undergrowth in heavily exploited areas of the forest.

*Sphenoeacus mentalis mentalis* (Fraser)

One specimen, a female with an enlarged ovary, was taken November 19; maxilla black above, the tomium and mandible pale gray; iris pale brown; feet pale gray; weight 36 grams; stomach contents insect fragments. The bird was shot while it was skulking in scrub grassland at the edge of the forest.

*Neocossyphus poensis praepectoralis* Jackson

Abundant in the Kalinzu Forest; nine examples were collected November 4 to 21; one female with an enlarged ovary, the other specimens in non-breeding state; bill black; iris dark brown; feet whitish flesh to flesh pink; weight 45 to 60 grams; stomach contents ants and small beetles. These birds were taken in mist nets in the undergrowth and also shot high up in the forest trees.

*Stizorhina fraseri vulpina* Reichenow

Fairly common in the Kalinzu; three specimens were taken October 29 to November 8; all with non-breeding gonads; bill black, the base brownish in a female; iris dark brown; feet pale brown to pinkish brown; weight 37 to 39 grams; stomach contents entirely beetles.

## SYLVIIDAE

*Schoenicola platyura alexinae* (Heuglin)

The great-tailed warbler was met with once, on November 12, when two males were collected, one with small and one with large testes; bill black above, pale gray below; iris brown; feet gray with a brownish wash; weight 16.5 and 17 grams; stomach contents small insect fragments.

*Prinia leucopogon reichenowi* (Hartlaub)

The white-chinned prinia was found to be numerous in the Kalinzu where six specimens were collected November 1 to 10; gonads ranging from small to large; bill black; iris chestnut; feet pale pinkish brown; weight 11.5 to 13.5 grams; stomach contents insect fragments. Most of these examples were netted in the undergrowth in heavily exploited areas of the forest.

*Apalis jacksoni jacksoni* Sharpe

One specimen, October 28, a male in non-breeding state; bill black; iris brown; feet flesh-brown; weight 10 grams; stomach contents small flies and small insect larvae.

*Apalis rufogularis nigrescens* (Jackson)

This warbler is represented in the collection by two specimens, collected November 11 and 16; one a male, the other with sex unrecorded; bill black; iris chestnut to pale brown; feet dull pinkish brown; toes paler; weight 9 and 10 grams; stomach contents small insects and insect larvae. In their dark brownish dorsal coloration these specimens agree with *nigrescens* from the Kibale, Bugoma and Bwamba Forests, and not with the more grayish backed *kigezi* of the Impenetrable Forest.

*Bathmocercus cerviniventris vulpinus* Reichenow

Very common; seven specimens, October 30 to November 21; gonads small to much enlarged; bill black; iris dark brown; feet dark blue-gray; weight 15.5 to 19.5 grams; stomach contents small insect fragments. The black-faced rufous warbler was netted largely in the undergrowth in heavily exploited parts of the forest.

*Camaroptera chloronota toroensis* (Jackson)

Very common; eight specimens, October 28 to November 23; all in non-breeding state; bill black above, pale horn to whitish gray below; iris pale brown to gray-brown; feet pale brown; weight 8 to 13 grams; stomach contents insect fragments.

*Camaroptera brachyura tincta* (Cassin)

This little warbler was as numerous as the preceding species; six examples were taken October 29 to November 21; most were in non-breeding state, but one male, November 6, had enlarged gonads; bill black; iris pale brown; feet pale pinkish brown; weight 11 to 12.5 grams; stomach contents insect fragments.

*Sylvietta leucophrys chloronota* Hartert

One specimen, a non-breeding female, was taken November 10; bill pale

horn-brown, pinkish at the base; iris chestnut; feet deep pink; weight 10 grams; stomach contents insect fragments.

*Hylia prasina prasina* (Cassin)

The green hylia was taken once in the Kalinzu Forest, November 13, and a second example was collected in the Maramagambo Forest, November 8; both in non-breeding state; bill black, the tomium and gape yellow; iris dark brown; feet olive to olive-gray; weight 15 and 16 grams; stomach contents insect matter.

LANIIDAE

*Tchagra minuta minuta* (Hartlaub)

This shrike was not collected in the Kalinzu Forest, but on November 8 two birds, one of each sex, were taken in a grass covered glade in the nearby Maramagambo Forest; the male had large testes, the female had a small ovary; bill black; iris pale maroon; feet gray; weight 31 and 36 grams; stomach contents grasshoppers and beetles.

*Laniarius luhderi luhderi* Reichenow

This bush-shrike was common in the Kalinzu Forest; seven specimens were taken October 28 to November 10; gonads ranging from small to much enlarged; bill black; in immature birds it is blackish horn above, paling to pale blue-gray basally on the mandible; feet gray to bluish gray; weight 41 to 47.5 grams; stomach contents grasshoppers, beetles and other insect remains.

*Telophorus bocagei jacksoni* (Sharpe)

This shrike is not uncommon in the Kalinzu Forest; two females were collected on October 30 and November 19; bill black; iris dark brown; feet dark gray; weight 27 grams each; stomach contents insect larvae.

*Lanius collurio phoenicuroides* (Schalow)

This winter visitor from Eurasia is represented by one immature individual, taken on November 7; bill horn-gray, the tip blackish; iris very dark brown; feet gray black; weight 26.5 grams; stomach contents small grasshoppers. It was shot in secondary growth in one area of forest that had been exploited.

*Lanius mackinnoni* Sharpe

Not uncommon; three specimens, October 30, November 7 and 8; all in non-breeding state; bill black; iris dark brown; feet black; weight 34 to 37 grams; stomach contents caterpillars, grasshoppers and beetle fragments.

## ORIOLIDAE

*Oriolus brachyrhynchus laetior* Sharpe

One adult male of this oriole was taken in the Kalinzu Forest, November 16, and three immature birds were collected in the Maramagambo Forest, on November 8; bill of adult dull pinkish brown-horn; of immature birds blackish, pinkish brown basally; iris wine-red in adult male, dull red to dark grayish brown in the others; feet blue-gray; weight 48 to 56 grams; stomach contents fruits, small seeds, caterpillars and insect fragments.

*Oriolus larvatus percivali* Ogilvie-Grant

One adult male with enlarged gonads was taken on October 31, in a mist net in the undergrowth in an area of heavily exploited forest; bill metallic deep pink; iris dark crimson; feet dark gray; weight 74 grams; stomach contents caterpillars.

## PARIDAE

*Parus funereus funereus* (Verreaux)

This tit was common in the Kalinzu, where five examples were collected October 31 to November 2. All were in non-breeding state; bill black; iris red in four cases, yellow-brown in one; feet slate gray; weight 23 to 27 grams; stomach contents caterpillars, beetle larvae and small insect remains.

## STURNIDAE

*Poeoptera stuhlmanni* (Reichenow)

Two specimens of this starling, a male with large gonads and a female in non-breeding condition, were taken on October 30 and 31; bill black; iris dark brown; with outer ring yellow; feet black; weight 39 (female) and 44 (male) grams; stomach contents remains of fruits.

*Poeoptera lugubris* Bonaparte

Five adult males, November 2 to 14, with gonads ranging from small to much enlarged; bill black; iris bright yellow; feet black; weight 42 to 43 grams; stomach contents fruit fragments, seeds, beetles and other small insect remains.

Keith (1968) has recently described a race of this starling, *P. l. webbi*, from the Impenetrable and Kibale Forests, on the basis of greater wing length and a bluish sheen to the purple gloss of the feathers in the male. He gives the wing length of males of nominate *lugubris* as 89 to 96 (average 93.13 mm), of *webbi* as 94 to 99 (average 97.23 mm). Our five Kalinzu males bridge this difference as they have wing lengths of 93 to 97 (average 95 mm). In color they agree with our series of *webbi* but there is some slight individual variation in the amount of blue or purple. No examples of nominate *lugubris* from Gabon have been available for comparison and we therefore use a binomial

for our specimens. We cannot avoid the conclusion that *webbi* is a poorly marked form, if a valid one.

*Onychognathus walleri elgonensis* (Sharpe)

Four examples of this race of Waller's chestnut-winged starling, two males and one female with large gonads and one female with a small ovary, were taken November 4 to 14; bill black; iris crimson-red with the inner ring dark brown; feet black; weight 70 to 82 grams; stomach contents small green fruits and fruit seeds. These birds were seen feeding in a fruiting *Symphonia* tree.

*Lamprotornis splendidus splendidus* (Vieillot)

This starling was fairly common in the Kalinzu Forest; one male and two females, all with enlarged gonads, were collected on October 31, November 12 and 14; bill black; iris yellow-white to cream; feet black; weight 120 to 135 grams; stomach contents fruits and seeds.

ZOSTEROPIDAE

*Zosterops senegalensis toroensis* Reichenow

Two specimens of this common white-eye, one of each sex, taken on November 19, agree with a series of *toroensis* from the Kibale and Bwamba Forests; bill black; iris dark brown; feet gray; weight 11 grams each; stomach contents insect fragments.

NECTARINIIDAE

*Anthreptes fraseri axillaris* (Reichenow)

Common in the Kalinzu; six examples of this sunbird were collected October 31 to November 18; gonads ranging from small to large; bill black to dark brown above, pinkish white below; iris brown to reddish brown; feet olive to olive-gray to gray-brown; weight 10 to 13 grams; stomach contents insect remains. This species was found chiefly in natural, undisturbed areas of the forest.

*Anthreptes rectirostris tephrolaema* (Jardine and Fraser)

This sunbird was found to be very common in the Kalinzu Forest, where eight specimens were obtained, October 30 to November 19, and one in the Maramagambo Forest, November 8; of five males four had large gonads, while of four females none showed gonadal swelling; bill black; iris red-brown to dark brown; feet black; weight 10 to 12 grams; stomach contents insect fragments, small spiders and bits of fruit. The gray-chinned sunbird was found both in natural and in heavily exploited areas of the forest.

*Anthreptes collaris garguensis* Mearns

Our collectors met with this sunbird only on October 31 and November 1; on each day they obtained a single example, so the bird may not be very numerous in the Kalinzu; bill black; iris dark brown; feet black; weight 8.5 grams; stomach contents insect remains.

*Nectarinia olivacea ragazzii* (Salvadori)

The olive sunbird was found to be very numerous in the Kalinzu, and eleven examples were collected November 2 to 18; gonads ranging from small to large; bill black above, the base of the mandible dull yellow to pinkish brown; feet dark brown to black; weight 9 to 12.5 grams; stomach contents insect fragments.

*Nectarinia verticalis viridisplendens* (Reichenow)

This sunbird was also very common in the Kalnizu Forest; six males and one unsexed, but probably female by plumage, were collected November 1 to 10; gonads varying from small to large; bill black; iris dark brown; feet black; weight 12 to 15 grams (one marked 26.5 grams, probably an error for 16.5 grams); stomach contents insect fragments, small insect larvae.

*Nectarinia rubescens rubescens* (Vieillot)

Common in the Kalinzu; seven specimens October 30 to November 11; gonads small to large; bill black; iris dark brown; feet black; weight 10.5 to 12.5 grams; stomach contents insect fragments. The green-throated sunbird was seen chiefly feeding in fairly tall trees.

*Nectarinia bouvieri* (Shelley)

This sunbird was met with but once, on November 24 when an adult male with large testes was collected; bill black; iris dark brown; feet black; weight 10 grams; stomach contents very small insect fragments. The bird was found in the small scrub-bush of a grass covered hillside at the edge of the forest.

*Nectarinia purpureiventris* (Reichenow)

The purple-breasted sunbird, a species primarily of highland forest, was seen several times in the Kalinzu by Williams, but he was unable to collect one.

*Nectarinia kilimensis kilimensis* Shelley

One female, ovary enlarged, was taken on November 25; bill black; iris dark cream; feet black; weight 16 grams; stomach contents insect fragments.

## PLOCEIDAE

*Amblyospiza albifrons melanota* (Heuglin)

One adult male of this heavy-billed weaver in breeding condition was taken November 13 from a small flock seen in the undergrowth of an exploited area of the forest; bill horn-black; iris dark brown; feet grayish black; weight 47 grams; stomach contents seeds.

*Ploceus nigricollis nigricollis* (Vieillot)

Common in the Kalinzu; three males and four females were collected, October 31 to November 25, all in non-breeding state; bill black; iris dark brown; feet dark gray; weight 21.5 to 29 grams; stomach contents small beetles, green caterpillars and other insect fragments. Several of these specimens were caught in mist nets in the undergrowth in exploited areas of the forest.

*Ploceus melanogaster stephanophorus* (Sharpe)

This weaver was very common in the Kalinzu; nine specimens were taken October 28 to November 24; one male with large gonads, all the others with small ones; bill black; iris dark brown; feet dark gray; weight 20.5 to 25 grams; stomach contents insect remains, including beetles and small caterpillars. Four of the specimens are molting into full adult plumage. A number of these black-billed weavers were caught in nets in the undergrowth in a heavily exploited area of the forest, where they came, together with other species, to feed on flying termites as they emerged from the ground.

*Ploceus superciliosus* (Shelley)

Not taken in the Kalinzu, but on November 8 one (unsexed) example was collected in the Maramagambo Forest; bill black above, pale gray below; iris dark brown; feet pale brown; weight 21 grams; stomach contents grass seeds.

*Ploceus insignis insignis* (Sharpe)

This weaver was met with but once, on November 2, when one adult of each sex, both in non-breeding state, were taken; bill black; iris red-brown in male, bright brick-red in female; feet pale brown; weight 28 grams each; stomach contents insect fragments. The birds were searching for food among the moss and lichen on a small tree.

*Malimbus rubricollis rubricollis* (Swainson)

This malimbe was common in the Kalinzu Forest; four examples were collected October 31 to November 2; all in non-breeding condition; bill black; iris dark red-brown; feet black; weight 39 to 45 grams; stomach contents insect fragments.

## ESTRILDIDAE

*Parmoptila woodhousei jamesoni* (Shelley)

The Kalinzu Forest is an additional Uganda locality for this Congolese flower pecker. One adult male, with enlarged testes, was taken on November 13; bill black; iris very dark red-brown; feet pale buffy brown; weight 10 grams; stomach contents small black ants.

*Nigrita fusconota fusconota* Fraser

This negro finch was met with but once in the Kalinzu, on November 25, when a male with large testes and a female in non-breeding state were taken; bill black; iris dark brown; feet dark gray; weight 8 and 9.5 grams; stomach contents very small insects.

*Nigrita canicapilla schistacea* Sharpe

This species was not uncommon in the Kalinzu; four specimens were taken on October 30 and 31, but then no more were encountered although the collectors were there for nearly a month; one of our birds was in breeding condition; the others were not; bill black; iris orange-red; feet dark brown; weight 19 to 20 grams; stomach contents small seeds and insect fragments.

*Nesocharis ansorgei ansorgei* (Hartert)

It was something of a surprise to find this little waxbill fairly common in the Kalinzu Forest; five specimens were taken October 30 to November 7; all in non-breeding state; bill black, pale gray at base; iris dark brown; feet blackish; weight 8.5 to 10 grams; stomach contents small crushed grass seeds. The birds were found in the tall undergrowth in areas of forest that had been heavily exploited. The Kalinzu Forest is an additional locality to those mentioned by the senior author (Friedmann, 1968) in his discussion of this little weaver finch.

*Spermophaga ruficapilla ruficapilla* (Shelley)

As in so many west Ugandan forests, this bird was found to be common in the Kalinzu; six examples were collected, October 29 to November 10; all in non-breeding condition; bill black with metallic blue wash, the tomium pinkish orange; iris dark brown; feet dark brown to dark gray-brown; weight 19.5 to 26.5 grams; stomach contents seeds and grit.

*Lonchura bicolor poensis* (Fraser)

Although this mannikin is not a typical forest bird, the one example obtained was collected in a mist net in an exploited part of the forest; bill pale gray; iris dark brown; feet dark gray; weight 10 grams; stomach contents grass seeds.

## FRINGILLIDAE

*Serinus frontalis frontalis* Reichenow

This little finch is represented by a single example collected November 12; bill horn brown above, pale horn below; iris dark brown; feet brown; weight 13 grams; stomach contents insects and small seeds. It was taken in the scrub undergrowth at the edge of the forest.

*Serinus burtoni tanganjicae* Granvik

Fairly common in the heavily exploited parts of the Kalinzu Forest. Three specimens were taken November 4 to 20; gonads small to large; bill horn-brown, paler below; iris medium to dark brown; feet pale to dark brown; weight 30 to 32 grams; stomach contents seeds and flower buds.

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# CONTRIBUTIONS IN SCIENCE

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TWO NEW SPECIES OF CATFISHES OF THE GENERA  
*NANNORHAMDIA* AND *IMPARALES* (FAMILY  
PIMELODIDAE) FROM CENTRAL AMERICA

By WILLIAM A. BUSSING



LOS ANGELES COUNTY MUSEUM OF NATURAL HISTORY • EXPOSITION PARK  
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TWO NEW SPECIES OF CATFISHES OF THE GENERA  
*NANNORHAMDIA* AND *IMPARALES* (FAMILY  
PIMELODIDAE) FROM CENTRAL AMERICA

By WILLIAM A. BUSSING<sup>1</sup>

ABSTRACT: Two new species of pimelodid catfishes, *Nannorhamdia lineata* and *Imparales panamensis*, are described from Costa Rica and Panama respectively. *Nannorhamdia* is recorded for the first time in Central America and each species represents a relict population. The relationships are discussed and habitats described for each species.

Recent collections by Horace Loftin (1965) in Panama and by Albert Greenberg in Costa Rica have revealed two undescribed species of small pimelodid catfishes of the genera *Nannorhamdia* and *Imparales*. The former was previously known only from South America, whereas Miller (1966) included *Imparales* sp. in his checklist of Central American fishes. In 1967 Oscar Blanco B. and I obtained additional specimens of the Costa Rican *Nannorhamdia*. More specimens of *Imparales* were collected in 1967 in the Chucunaque and Balsas drainages of Panama by members of the Battelle Memorial Institute, Pacific Northwest Laboratory (Battelle NW) as part of their sub-contractual work for the Interoceanic Sea Level Canal Feasibility Study. Material from all these sources was used in this study.

***Nannorhamdia lineata*, new species**

Figure 1

*Holotype*: LACM 30688-1 (♀, 74.1 mm SL), Costa Rica: Puntarenas Prov., Quebrada 36 (elev. 80 m) 12 km W of Pueblo Río Claro at Interamerican Highway; 5 January 1967; collectors W. Bussing, Oscar Blanco B.

*Paratypes*: UCR 111-10 (18, 48.5-71.7 mm SL), same data as holotype; LACM 30688-2 (3, 51.8-69.9 mm SL), same data as holotype; BMNH 1967.9.29.1-2 (2, 64.0-68.2 mm SL), same data as holotype; USNM 204694 (2, 58.4 and 69.5 mm SL), same data as holotype; USNM 194230 (1, 57.0 mm SL) Costa Rica: Puntarenas Prov., Río Salamá Nuevo (?) at Interamerican Highway; 21 January 1963; collector Albert Greenberg.

Type specimens are deposited in the British Museum (Natural History) (BMNH), Los Angeles County Museum of Natural History (LACM), Museo de Zoología, Universidad de Costa Rica (UCR) and the United States National Museum (USNM).

*Comparative Material*: *Nannorhamdia nemacheir* (Eigenmann and

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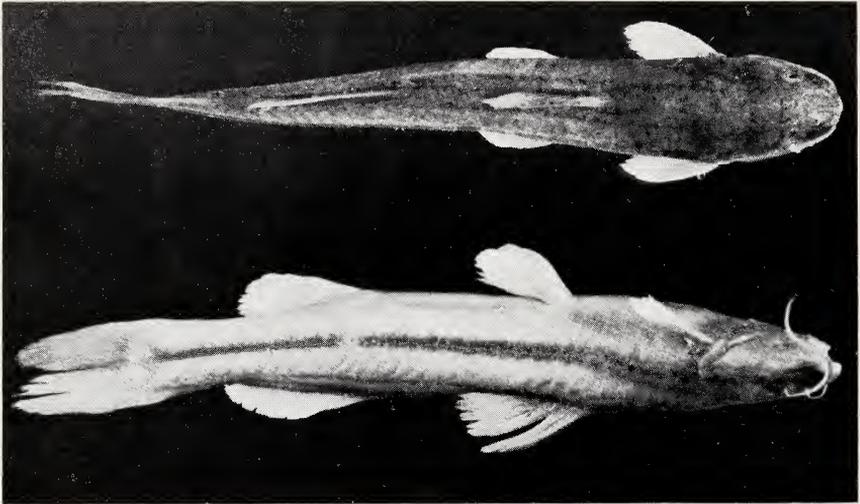


Figure 1. *Nannorhamdia lineata*, new species, lateral view of holotype LACM 30688-1, 74.1 mm SL; dorsal view of paratype UCR 111-10, 71.1 mm SL.

Fisher), USNM 121167 (30, 33.8-68.5 mm SL), Venezuela: Río San Juan at bridge, tributary to Río Motatán; 17 and 20 March 1942; collector L. P. Schultz. UCR 318-1 (6, 30.3-55.1 mm SL), Colombia: Río Salado, ca. ¼ mile upstream from junction with Río Truandó; 27 August 1967; collector H. Loftin. *Cetopsorhamdia nasus* (Eigenmann and Fisher), USNM 86816 (1, 62.5 mm SL), Bolivia: Tumupasa; December 1921; collector N. E. Pearson.

*Diagnosis:* A *Nannorhamdia* with pronounced lateral stripe extending from the tip of snout to caudal base; short maxillary barbels not passing pectoral fin base; subequal caudal lobes; 8-11 total gill rakers; 7-9 principal (branched rays plus one simple ray) anal fin rays; no prominent dorsal blotches on body contrasting with ground color; all pectoral and dorsal fin elements unserrated.

The new species is immediately separated from *N. guttatus* Pearson, *N. benedettii* Fernández Yépez, *N. stictnotus* Fowler and *N. nemacheir* Eigenmann and Fisher by its lateral stripe and short maxillary barbels; from *N. guttatus* and *N. benedettii* it also differs in having fewer anal rays (7-9 vs. 10-12). From *N. macrocephala* Miles it differs in having fewer anal rays (7-9 vs. 13) and lacking dorsal and pectoral spines with denticulations on the posterior borders. It differs from *N. schubarti* Gomes principally in having fewer gill rakers (8-11 vs. 9-15), shorter maxillary barbels (22.4-26.8 vs. 32.1-55.5), shorter first dorsal ray (14.3-16.9 vs. 19.4-24.6) and shorter first pectoral ray (13.3-15.4 vs. 16.7-20.0).

The new species is closest to *N. spurrellii* of the Río San Juan drainage,

Colombia. The latter is distinguished from *N. lineata* by its narrower inter-narial distance, interorbital distance and caudal peduncle depth, much longer maxillary and mental barbels, higher gill raker count and much more prominent lateral stripe. Mr. Alwyne Wheeler (*personal communication*, 1968) reported that the type specimen of *N. spurrellii* is quite round-bodied and does not seem to have shrunk, thus discounting unnatural proportional differences due to preservation.

*Description:* Head slightly depressed, snout bluntly rounded. Narrow fontanel in middorsal line extending from before eyes to base of occipital process. Mouth subterminal, snout projecting. Villiform teeth in bands on both jaws; premaxillary patches slightly wider laterally, but without posteriorly projecting angles; dentary patches wider medially, very narrow laterally; no teeth on vomer or palatines. Nostrils wide apart, anterior ones tubular and in line with bases of maxillary barbels; posterior nostrils with an anterior flap and lying equidistant between anterior nostril and margin of eye. Maxillary barbels the longest, one pair lying in a groove along the snout and extending along the first third or half of the length of pectoral fin; two pairs of mental barbels, their bases in a straight line, outer pair reaching to or slightly beyond origin of pectoral fin; inner pair extending three-fourths the distance to pectoral origin. No ontogenetic variation in barbel length on specimens in the present size range.

Caudal fin well forked, shortest median rays slightly longer than half the length of the longest rays; upper lobe slightly longer and more pointed than lower. First dorsal ray soft, not extended into a filament, margin of fin truncate; origin slightly in advance of pelvic fin origin. Anal fin margin rounded; origin directly below adipose origin. Adipose fin short, slightly longer than anal; height about 4.5 times in length. Pelvic fins short, rounded; arising below third or fourth dorsal ray. First pectoral ray soft, not extended into a filament; appressed fin not quite reaching a vertical through dorsal origin. Anus between middle of length of pelvic fins.

*Counts:* The counts and body proportions in percent of standard length of the holotype and nine paratypes of *N. lineata* from Quebrada 36 are recorded below, followed by data for the type of *N. spurrellii* in parentheses. Data for the type specimen of *N. spurrellii* Regan (BMNH 1913.10.1.41; Río Condoto, San Juan drainage, Colombia) were kindly furnished by Alwyne C. Wheeler of the Zoology Department, British Museum of Natural History. Proportional measurements of the single specimen from Río Salamá Nuevo, Costa Rica, which in some cases fall slightly out of the range given below due to its shrunken condition, are not included.

Dorsal rays i,6; i,5-6 (i,6). Anal v,8; iv-v,6-8 (ii,6). Pectoral i,9; i,8-9 (i,9). Pelvic i,5; i,5 (i,5). Branched caudal rays 15, 15-16 (15). Gill rakers of holotype 2 + 7 and 1 + 8, total 9; paratypes 1-2 + 7-10, total 8-11 (*N. spurrellii* 2 + 10, total 12).

TABLE 1

Comparison of holotype and 16 paratypes of *Imparales panamensis* and holotype of *I. mariai*. Proportions expressed in thousandths of standard length.

	<i>Imparales panamensis</i>			<i>I. mariai</i>	
	Holotype USNM 204692	Paratypes <sup>1</sup>	Paratypes <sup>2</sup> USNM 204693	Paratype USNM 204693	Holotype USNM 121251
Standard length (mm)	62.3	36.5-55.0	23.4-71.5	38.2	38.5
Head length	189	180-207	192-239	223	184
Head width	144	131-175	144-175	165	127
Snout length	67	64-71	65-94	84	65
Eye to posterior nostril	18	13-18	15-19	18	13
Internarial distance	35	38-41	31-43	45	26
Mouth width	71	58-82	66-98	84	—
Eye diameter	30	31-44	28-43	34	21
Interorbital, fleshy width	51	42-54	41-64	68	52
Postorbital length of head	104	89-109	100-124	118	104
Body depth	130	91-106	118-143	118	112
Caudal peduncle, least depth	80	71-88	80-88	92	78
Caudal peduncle, length	255	224-269	212-262	230	205
Predorsal distance	305	317-342	248-353	343	343
Prenal distance	639	648-679	614-693	652	652
Tip of snout to anus	413	426-498	411-491	455	440
Prepectoral distance	178	160-186	178-235	207	171

TABLE 1 (cont.)

Preadipose distance	637	625-689	610-674	644	623
Prepelvic distance	358	369-402	356-418	387	377
Anus to anal fin origin	223	216-239	192-223	196	226
First dorsal ray, length	143	116-162	138-179	152	127
First pectoral ray, length	130	132-148	122-171	133	104
Longest pelvic ray, length	144	133-162	112-171	157	132
Longest anal ray, length	116	122-135	107-136	141	99
Upper caudal lobe, length	342	260-358	256-322	285	338
Lower caudal lobe, length	209	179-211	184-243	215	221
Shortest caudal ray, length	128	122-151	127-153	147	114
Dorsal fin base, length	117	112-134	116-138	123	—
Anal fin base, length	136	116-147	127-159	141	—
Adipose fin, length	321	261-315	282-336	314	356
Adipose fin, height	35	33-47	33-43	39	29
Maxillary barbel, length	233	221-310	231-397	301	353
Outer mental barbel, length	152	132-190	133-214	152	195
Inner mental barbel, length	127	91-147	96-179	102	130

<sup>1</sup>Based on 6 specimens from LACM 30689-1, LACM 30690-1, UCR 321-1, UCR 322-1

<sup>2</sup>Based on 9 specimens

*Proportions:* Standard length (mm) 74.1, 48.7-71.7 (62.5); head length 23.0, 21.6-24.0 (23.2); head width at pectorals 16.6, 16.7-18.3 (19.4); snout length 9.5, 8.7-10.1 (8.8); distance from eye to posterior nostril 3.2, 2.9-3.7 (2.9); distance between nostrils 3.9, 3.7-4.7 (3.4); mouth width 9.4, 8.8-10.3 (8.8); eye diameter 3.4, 3.3-4.1 (3.7); fleshy interorbital distance 7.7, 7.3-8.8 (6.2); postorbital distance 10.9, 10.6-11.3 (10.7); greatest body depth 17.8, 16.8-20.4 (17.1); caudal peduncle depth 9.7, 9.7-10.8 (6.9); caudal peduncle length 21.2, 19.0-21.9 (21.6); predorsal distance 36.0, 36.6-39.3 (36.0); preanal distance 68.8, 66.7-70.9 (67.2); prepectoral distance 19.3, 19.2-21.6 (21.6); prepelvic distance 38.8, 40.2-43.1 (42.7); preadipose distance 66.2, 65.8-69.7 (67.2); distance between tip of snout and anus 45.9, 46.7-49.6 (48.0); distance between anus and anal fin origin 23.6, 20.5-23.7 (20.5); length of first (simple) ray of dorsal fin 15.1, 14.3-16.9 (13.6+); length of first pectoral ray 14.7, 13.3-15.4 (16.8); longest pelvic ray 14.0, 14.2-16.2 (15.7); longest anal ray 13.8, 12.5-15.2 (13.3); longest ray upper lobe of caudal fin 20.2, 19.5-24.0 (16.0+); longest ray of lower lobe of caudal fin 19.3, 16.2-23.4 (22.4+); shortest middle ray of caudal fin 12.1, 11.9-14.2 (10.4); length dorsal fin base 11.9, 11.1-12.2 (13.6); length anal fin base 12.5, 10.6-12.9 (11.2); total length adipose fin 23.4, 20.6-23.9 (20.8); height of adipose fin 4.6, 3.8-4.7 (3.2); length of maxillary barbel 23.6, 22.4-26.8 (35.7); length of outer mental barbel 15.8, 14.7-17.5 (19.2); length of inner mental barbel 10.8, 11.4-12.6 (12.8).

*Coloration:* In alcohol, specimens brownish above, pale below. A black stripe running from maxillary barbel origin through the eye and extending along midside to caudal base; stripe diffuse on cheek and operculum and near caudal base, well defined and about equal to eye diameter in width along rest of body. Predorsal area and interval between dorsal and adipose fins slightly darker than area immediately along these fin bases. Dorsal and caudal fin rays dusky; anal fin pale; paired fins with scattered melanophores only on proximal half. Maxillary barbels pigmented on upper surface.

*Dimorphism:* Sexual dimorphism is evident in the size of individuals. The three smallest specimens measured (48.7-55.3 mm SL) are males. The seven larger examples (58.6-74.1 mm SL) are females. None of the ten specimens examined in detail were in breeding condition although they were mature individuals. The shape of the genital papilla was usually, but not always, consistent with sex. A tubular papilla was found on all three males and one female. The six other females had thicker, more conical papillae.

*Etymology:* The specific name, *lineata*, refers to the prominent lateral stripe of the species.

*Relationships:* Specimens of this small Costa Rican catfish clearly fall within the limits of *Nannorhamdia* Regan. The specimens also bear a close resemblance to species of *Cetopsorhamdia* Eigenmann and Fisher, but differ in having eyes with free dorsal margins. Schultz (1944a) pointed out that

"The state of preservation determines to a large extent whether the rim of the orbit is free from the eye dorsally." Although the present well preserved forms clearly present a free orbital rim, they were compared to the eleven species of *Cetopsorhamdia* and were shown to differ from them in other characteristics as well.

*Nannorhamdia* was described by Regan (1913) as lacking dorsal and pectoral spines. Eigenmann (1922), however, separated *Nannorhamdia* from *Cetopsorhamdia* on the basis of the former's "spines." Schultz (1944a) has clarified this confusion by showing how the flexible distal segments of the first pectoral ray may fracture and produce a fairly sharp spine. The species described by Miles (1943) as *Nannorhamdia macrocephala* should be reexamined. It was described as notorious for inflicting painful wounds with its short, pungent dorsal and pectoral spines.

The anus-origin of anal fin distance could prove useful in distinguishing species of *Nannorhamdia* from *Cetopsorhamdia*. In *N. lineata*, *spurrellii* and *nemacheir* the distance between anus and anal fin origin is 17.5-25.1 percent of SL. In *C. nasus*, *shermani*, *picklei* and *orinoco* the anus-origin of anal fin distance is 10.1-14.0 percent of SL.

*Habitat*: The type locality is Quebrada 36, a small tributary of the Río Esquinas flowing into the upper Golfo Dulce in southern Costa Rica. The region receives over 4.5 meters of precipitation annually. The stream is one to four meters wide with shallow rapid areas and small pools no deeper than 0.5 meter. The current is moderate and flows over a bottom of gravel and sand. Grasses line the shore. At the time of collection, the water temperature was 27° C and visibility good.

Twenty-two species of fishes were collected at this site by poisoning with Pro-Noxfish. Four other species of siluriform fishes were taken: *Rhamdia wagneri*, *Pimelodella chagresi*, *Hypostomus plecostomus* and *Pygidium striatum*.

### ***Imparales panamensis*, new species**

#### Figure 2

*Imparales* sp, Miller, 1966: 786 (name only; Panama)

*Holotype*: USNM 204692 (♂, 62.3 mm SL), Panama: Veraguas Prov., creek crossing road on S side of Santa Fe (elev. 305 m); 9 February 1962; collectors H. Loftin and E. L. Tyson; original field no. HL-106.

*Paratypes*: USNM 204693 (40, 23.4-71.5 mm SL), same data as holotype; LACM 30689-1 (3, 45.2-51.7 mm SL), Panama: Darien Prov., Río Membrillo tributary to Río Chucunaque; 22 March 1967; collector Battelle NW; LACM 30690-1 (1, 55.0 mm SL), Panama: Darien Prov., Río Chucunaque at Uala; 17 March 1967; collector Battelle NW; UCR 321-1 (1, 44.7 mm SL), Panama: Darien Prov.; Río Congo, tributary to Río Chucunaque;

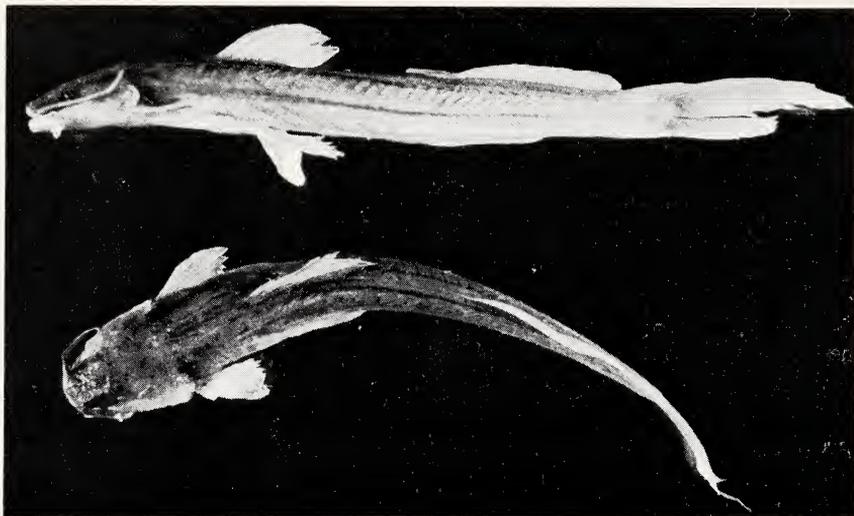


Figure 2. *Imparales panamensis*, new species, lateral view of holotype USNM 204692, 62.3 mm SL; dorsal view of paratype USNM 204693, 63.8 mm SL.

24 March 1967; collector Battelle NW; UCR 322-1 (1, 36.5 mm SL) Panama: Darien Prov.; Quebrada Coho, tributary to Río Congo; 8 March 1967; collector Battelle NW.

*Diagnosis:* The species is distinguished from its only known congener, *Imparales mariai* Schultz, by a series of proportional differences and at least two meristic distinctions. *Imparales panamensis* is characterized by its shorter adipose fin (26.1-33.6 vs. 35.6 percent of SL), which is not confluent with the caudal fin at any age in the present size range; greater head width (13.1-17.5 vs. 12.7 percent of SL); greater distance between nostrils (3.1-4.5 vs. 2.6 percent of SL); longer first branched anal ray (10.7-14.1 vs. 9.9 percent of SL); shorter maxillary barbels (22.1-31.0 vs. 35.3 percent of SL); more pectoral rays i,7-8 vs. i,6); fewer average gillrakers (3-7, usually 5 vs. about 7).

*Description:* Head wide, strongly depressed. Mouth terminal, snout slightly rounded in dorsal view. Narrow fontanel in middorsal line extending from before eyes to base of occipital process. Occipital process short. Villiform teeth in bands on both jaws; premaxillary patches of equal width throughout; dentary patches wider medially; no vomerine or palatine teeth. Anterior nostrils tubular; posterior nostrils with a fleshy flap on anterior border. Eyes small, located on middle of length of head on largest specimens or just in front of middle of head on smaller individuals. Pelvic insertion below base of third or fourth dorsal element; pectoral fin tip reaches a vertical with the base of the first or second dorsal ray. Adipose origin over base of second to fourth anal

element. Both lobes of caudal fin rounded; upper lobe nearly half again as long as the lower lobe. Anus between middle of length of pelvic fins. Lateral line complete.

Maxillary barbels reaching slightly beyond middle of pectoral fin; outer mental barbels not extending beyond posterior margin of pectoral base; inner mental barbels not extending beyond the anterior margin of pectoral base. Bases of four mental barbels in a straight line.

The smallest mature individual examined was a female of 46.8 mm SL. No sexual dimorphism with respect to size was evident, although mature males reveal a consistently longer and more pointed urogenital papilla. This papilla arises about an eye's diameter behind the anus. Several adult specimens from USNM 204693 were in breeding condition.

*Counts:* Proportional measurements for *I. panamensis* and *I. mariai* are presented in Table 1. Counts for the holotype are followed by the range for 17 paratypes from USNM 204693, LACM 30689-1, LACM 30690-1, UCR 321-1 and UCR 322-1. Dorsal fin rays i,6; i,6 (i,6). Anal vii,5; v-vii,5-7 (v,7). Pectoral i,7; i,7-9 (i,6). Pelvic i,5; i,5 (i,5). Branched caudal rays 15, 13-15 (13). Gill rakers 1 + 4 and 0 + 3 on holotype; 0-1 + 3-7 on paratypes; (1-2 + 5-6 on *I. mariai*). Total gill rakers 3-5 on holotype; 3-7 on paratypes; (about 7 on *I. mariai*).

*Coloration:* Specimens in alcohol dark brown above, gradually paling below. Predorsal and humeral areas slightly darker than surrounding regions. All fin rays brown, interradial membranes clear or with few scattered melanophores; adipose fin brown. Maxillary barbels brown; mental barbels pale.

*Etymology:* The specific name, *panamensis*, refers to the principal known distribution of the species.

*Remarks:* The generic description of *Imparales* Schultz (1944b) is amended to read: pelvic insertions under base of first to third branched dorsal ray; adipose fin confluent or not with caudal fin; either adipose or anal fin origin opposed or one or the other slightly in advance; anal fin of five to seven simple soft rays followed by five to seven branched rays; lateral line complete or possibly incomplete.

Although the differences between the Panamanian species and *I. mariai* are not great, I believe that the former merits specific rank for two reasons. *I. panamensis* shows little intraspecific variation throughout its range and it is expected that when further specimens of *I. mariai* are available they will still be consistently separable from *I. panamensis* by the diagnostic characters. The Cordillera Oriental extends to the sea in northern Colombia and forms an effective barrier between the faunas of the Amazon, the Orinoco and the Maracaibo basins on the east, and of the Magdalena and Atrato basins on the west. It is not surprising then to find divergences between the Panamanian and the Río Meta (Orinoco drainage) populations of *Imparales*.

*Distribution:* *I. panamensis* occurs from west of the Canal Zone to near

the Colombian border on the Pacific slope and in the Río Chagres Basin on the Atlantic versant. It was collected in only one locality west of the Canal in Veraguas Province. The other specimens included in this study were taken in extreme eastern Panama in the Río Chucunaque and Río Congo drainages. The following collections of *Imparales*, presumably *I. panamensis*, were not available to me. Dr. Loftin (1965) identified specimens of *Imparales* from a small stream in the Río Chagres system, and more recently from several other streams in the same drainage. He also identified as *Imparales*, specimens collected by Battelle NW in the Río Balsas, Darien Province in March 1967.

The type locality near Santa Fe is a swift flowing stream with a maximum width of 7 meters and depths to 1 meter. Large and small rocks and sand cover the bottom. At the time of collection, the water was clear. The site, at the foot of Cerro Tuto, is a tributary of the Río Santa María which runs southwesterly for some distance and then swings east to empty into the Golfo de Parita, a part of the Golfo de Panamá.

Twelve other species of fishes were collected with the holotype. The siluriform fishes, *Pimelodella chagresi* and *Pygidium striatum* were among those taken.

*Discussion:* The presence of disjunct Middle American populations of *Nannorhamdia* and *Imparales* gives clear evidence of a former, much larger range for these genera; the center of dispersal of both genera is northern South America. The genus *Imparales* is formerly known from one other species collected in the Río Meta, Colombia. Other species of *Nannorhamdia* are known from the Atrato, Magdalena, San Juan and Orinoco drainages of Colombia as well as Venezuela, Brazil and Bolivia.

The presence of these now relict populations suggests a once more favorable environment in Middle America which allowed these small catfishes to extend at least as far north as Costa Rica and Panama. It is not yet obvious what environmental factors presently restrict the distribution of stenoeicous forms such as *I. panamensis* and *N. lineata*.

#### ACKNOWLEDGMENTS

I wish to express my appreciation to Horace Loftin for bringing to my attention his collections of *Imparales*, Greenberg's specimen of *Nannorhamdia* and for collecting and furnishing additional comparative material; to Alwyne C. Wheeler (BMNH) for supplying complete data for the type specimen of *N. spurrellii* and for comparing it with paratypes of *N. lineata*; to William L. Templeton and John M. Dean, directors of the Battelle NW study, Oscar Blanco B., Albert Greenberg and Edwin L. Tyson for collecting material used in the study; and to the University of Costa Rica for supporting this study.

#### RESUMEN

Se determinaron dos nuevas especies de barbudos pequeños (Familia

Pimelodidae) de colecciones recientes de Costa Rica y Panamá. *Nannorhamdia lineata*, restringida a la cuenca del Río Grande de Térraba, presenta como forma más cercana en parentesco a *N. spurrellii* de la cuenca del Río San Juan, Colombia. Esta última se distingue de *N. lineata* por las siguientes características: distancia internasal, interorbital, y profundidad del pedúnculo caudal menores; mayor número de branquiespinas y banda oscura lateral muy prominente.

*Imparales panamensis* se colectó en el Río Santa María, Provincia de Veraguas. Se distingue de *I. mariai* del Río Meta, Colombia por diferencias proporcionales y por presentar mayor número de radios pectorales y menos branquiespinas.

Las dos especies nuevas representan poblaciones reliquias cuya distribución anterior fue más amplia y continua con sus antepasados sudamericanos en una época más favorable para su expansión.

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THE SOCIAL WASPS OF LOWER CALIFORNIA, MEXICO  
(Hymenoptera: Vespidae)

*By* ROY R. SNELLING

LOS ANGELES COUNTY MUSEUM OF NATURAL HISTORY • EXPOSITION PARK  
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*Editor*

# THE SOCIAL WASPS OF LOWER CALIFORNIA, MEXICO (Hymenoptera: Vespidae)

By ROY R. SNELLING<sup>1</sup>

ABSTRACT: There are four genera of social Vespidae in Lower California: *Vespula* (two species), *Polistes* (seven species), *Mischocyttarus* (two species) and *Polybia* (one species). One new species, *Mischocyttarus fisheri*, is described from the Sierra Laguna and the genus *Polybia* is newly recorded from Lower California. Keys for all species are included, most species are illustrated and distribution data are given in full.

The social wasps of Lower California have never been the subject of a comprehensive study. Until relatively recently there has been very little material available; the only collection of note was that housed at the California Academy of Sciences, collected by A. E. Michelbacher and E. S. Ross in 1938 and by E. S. Ross and G. E. Bohart in 1941. This material was reported on, in part, by R. M. Bohart (1949) who described several new endemic *Polistes*. In subsequent years one additional *Polistes* was recorded from Lower California by Snelling (1955) and two species of *Vespula* were noted to be present by Bohart and Bechtel (1957).

None of the above studies was devoted exclusively to the wasps of this region, nor did they contain keys for these species. The present study has two purposes: to enumerate the species of social wasps of Lower California and to provide means for their identification through a series of keys. Most species are illustrated here and their distributions, as far as known, are indicated.

The Lower California peninsula is divided into two political regions: the State of Baja California in the north and the Territorio de sur de Baja California in the south. I have departed from customary procedure in the southwestern United States by referring to the region involved as Lower California, rather than Baja California. The use of Lower California in American entomological literature dates at least as far back as 1875, and has been frequently used in subsequent years, so that the precedent is well-established. Furthermore, I feel that the existence of a discrete state of Baja California is a source of possible confusion. Within the text Lower California refers to the peninsula as a whole and Baja California to the state in the northern portion of the peninsula. The dividing line between the two political regions, 28° N, is also an approximate boundary for some of the species. This study includes the species of the entire peninsula and of the islands in the Gulf of California. The collection data for each species are cited from north to south and are broken down by region, as follows: *Baja Calif.* (Estado de Baja California), *Terr. Sur* (Territorio de sur de Baja California) and *Golfo de Calif.* (islands in the Golfo

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de California). Excluded from this study are the Revillagigedo Islands, located some 300 miles south of Cabo San Lucas. One social wasp, *Polistes dorsalis clarionensis* R. Bohart, is reported from these islands.

In northern Baja California the fauna is essentially an extension of that of southern California. East of the escarpment of the Sierra Juarez the wasps are typically lower Sonoran Desert species extending south to about Bahia San Luis Gonzaga. Here only *Polistes* is found: the ubiquitous *P. fuscatus centralis* Hayward and *P. major palmarum* Bequaert, a species restricted to native palm grove canyons. West of the crest of the Sierra Juarez the species are those of the chaparral of southern California: *Vespula pensylvanica* (Saussure), *V. sulphurea* (Saussure), *P. fuscatus aurifer* Saussure, *P. dorsalis californicus* R. Bohart and, probably, *Mischocyttarus flavitarsis* (Saussure). One anomalous species, *Polybia diguetana* (du Buysson), is present in this area. This is known from a single collection of two specimens taken at Ensenada and may be an accidental introduction.

The area between Bahia San Luis Gonzaga and El Arco at 28° N is poorly represented in the material studied. The peninsular form of *P. f. centralis* is common; *P. major slevini* R. Bohart is found at Bahia de Los Angeles and *P. rossi* R. Bohart is found at Cataviña. The latter two are rare, however, this far north. From 28° N southward, they become more common. This area seems to be the northern limit of *P. exclamans lineonotus* R. Bohart although it may occur further north along the Gulf side of the peninsula. The fauna, from 28° N, remains essentially unchanged to the south except in the mountains of the Cape Region. Here, *Polistes dorsalis californicus* and *Mischocyttarus fisheri*, new species are found. The subtropical element of mainland Mexico is not reflected in the Cape Region. The lack of this element is of interest since some other groups of insects show definite affinities with the fauna of the adjacent mainland. The ants of Lower California, now being studied, exhibit distributional characteristics similar to those of the vespids.

#### KEY TO GENERA OF SOCIAL VESPIDAE IN LOWER CALIFORNIA

1. Abdomen petiolate, the first segment more than twice as long as broad, the second segment abruptly swelling at base . . . . . 2  
 Abdomen sessile or subsessile, the first segment as broad or broader than long, the second not swelling abruptly at base . . . . . 3
2. Third and fourth segments of mid and hind tarsi asymmetrical, inner apical lobe distinctly longer than outer; mesepisternum divided above by an oblique suture into upper and lower plates . . . . . *Mischocyttarus*  
 Third and fourth segments of mid and hind tarsi symmetrical; mesepisternum not divided above . . . . . *Polybia*
3. First tergite broadly convex in lateral view; clypeal apex narrow, pointed in front view . . . . . *Polistes*

First tergite vertically truncate on basal one-half or more; clypeal apex broad, concave or truncate . . . . . *Vespula*

#### KEY TO SPECIES OF *VESPULA* IN LOWER CALIFORNIA

Occipital carina of female and worker complete from inferior mandibular articulation to near top of eye; sternite VII of male broadly and shallowly emarginate apically; mesoscutum all dark; female and worker with scape black beneath . . . . . *pensylvanica* (Saussure)

Occipital carina of female and worker not reaching inferior mandibular articulation; sternite VII of male narrowed apically, not emarginate; mesoscutum with two prominent longitudinal lines; scape yellow beneath . . . . . *sulphurea* (Saussure)

#### ***Vespula (Vespula) pensylvanica*** (Saussure)

*Vespa pensylvanica* Saussure, 1857. Stettin. Entomologische Zeitung 18: 117. ♀.

*Vespa occidentalis* Cresson, 1874. Trans. Amer. Ent. Soc. 5: 100. ♀, ♀.

*Vespula pensylvanica*, Bequaert, 1932. Ent. Amer., n.s. 12: 95-97. ♀, ♀, ♂.

*Vespula pennsylvanica* [sic], Miller, 1961. Canad. Ent. 93 (Suppl. 22): 13-15. ♀, ♀, ♂.

This common western yellow-jacket is found in northern Baja California. Bohart and Bechtel (1957) have recorded this species from Agua Caliente, and I have seen the following.

SPECIMENS EXAMINED: Baja California.: 5 ♀ ♀, Arroyo Santo Tomas, June 22, 1963 (E. L. Sleeper; LBSC); 5 ♀ ♀, Aguajito Spring, Valle de la Trinidad, Mar. 17, 1936 (C. F. Harbison; SDM); 1 ♀, San Felipe, Apr. 27, 1953 (W. R. Lower; LACM) [note: this female was most probably taken in the Sierra Juarez, west of San Felipe. It seems quite unlikely this species occurs in such an arid habitat as San Felipe]; 14 ♀ ♀, El Progreso, El Tajo Can., Sierra Juarez, Sept. 10, 1958 (F. S. Truxal & J. R. Northern; LACM).

#### ***Vespula (Vespula) sulphurea*** (Saussure)

*Vespa sulphurea* Saussure, 1854. Etudes sur la Famille des Vespides 2: 137. ♀.

*Vespula sulphurea*, Bequaert, 1932. Ent. Amer., n.s., 12: 111-112. ♀, ♀, ♂.

I have seen no specimens of this very distinctive wasp from Baja California, but Bohart and Bechtel (1957) state that it is found there, and their map indicates a record inland from Bahia San Quintin. This species should occur in the Sierra San Pedro Martir and Sierra Juarez, probably south to about Valle de la Trinidad.

KEY TO SPECIES AND SUBSPECIES OF *Polistes* IN LOWER CALIFORNIA

1. Malar area about twice as long as distance between antennal sockets; prepectal suture present, sometimes indistinct; sternite VII of male without median tubercle . . . . . 2  
 Malar areas as long as, or less than, distance between antennal sockets; prepectal suture always absent; sternite VII of male with or without median tubercle . . . . . 3
2. At least 75 percent (usually much more) of scutellum yellow; propodeum usually immaculate, rarely with two small median spots near flange; malar area darker than adjacent portions of clypeus. . . *major slevini* R. Bohart  
 No more than 25 percent of scutellum yellow; propodeum with two prominent longitudinal stripes on lower two-thirds or three-fourths; malar area yellow, concolorous with clypeus . . . . . *major palmarum* Bequaert
3. In dorsal view, tergite I distinctly broader than long; mesopleura below uniformly finely and closely punctate, without scattered large punctures; sternite VII of male with median tubercle . . . . . 4  
 In dorsal view, tergite I a little longer than broad; mesopleura below finely punctate, with slightly shiny interspaces, and distinct, scattered larger punctures; sternite VII of male without median tubercle . . . . .  
 . . . . . *exclamans lineonotus* R. Bohart
4. Males, antennae thirteen segmented . . . . . 5  
 Females, antennae twelve segmented . . . . . 8
5. Clypeus separated from inner eye margin by a distance less than an ocellar diameter, frequently contiguous with eyes for a short distance; aedeagus with teeth of variable size . . . . . 6  
 Clypeus separated from inner eye margin by a distance exceeding an ocellar diameter; aedeagus with teeth of uniform size. . . . .  
 . . . . . *dorsalis californicus* R. Bohart
6. Lateral ocelli separated from inner eye margin by two or more times diameter of anterior ocellus; apical four segments of antennae not pruinose beneath, distinctly polished; propodeal striae usually fine, close; lamella of propodeal valve yellow . . . . . 7  
 Lateral ocelli separated from inner eye margin by about 1.3 times diameter of anterior ocellus; apical four segments of antennae largely delicately pruinose beneath, apical segment sometimes slightly shiny; propodeal striae usually quite coarse; lamella of propodeal valve largely translucent ferruginous . . . . . *rossi* R. Bohart
7. Ground color of thorax largely black . . . . . *fuscatus aurifer* Saussure  
 Ground color of thorax largely ferruginous . . *fuscatus centralis* Hayward
8. Ground color of thorax largely ferruginous . . . . . 9  
 Ground color of thorax largely black . . . . . *fuscatus aurifer* Saussure

9. Propodeum usually with 20 or more fine, transverse striae; but sometimes with a few coarse striae; longitudinal yellow stripes usually present on propodeum; flanges of propodeal valve yellow; angle of clypeal apex usually about 95°; clypeus as broad or broader than long . . . . . 10  
 Propodeum with 15-20 coarse striae, rarely finely striate; longitudinal yellow stripes of propodeum absent; flanges of propodeal valve largely translucent ferruginous; angle of clypeal apex usually about 90°; clypeus slightly longer than broad. . . . . *rossi* R. Bohart
10. Tergite I with quadrate median ferruginous mark; if tergite II largely yellow, posterior margin of ferruginous mark is transverse and lateral yellow area is broadly confluent with apical yellow band . . . . .  
 . . . . . *dorsalis californicus* R. Bohart  
 Tergite I largely ferruginous with yellow apical and lateral margins; if with a quadrate median mark, then ferruginous mark of tergite II acuminate behind or lateral yellow area separated from apical band as a large spot . . . . . *fuscatus centralis* Hayward

#### ***Polistes major palmarum* Bequaert**

Figures 1g; 2g, n.

*Polistes major palmarum* Bequaert, 1936. Ent. News 47: 11. ♀.

This light red and yellow wasp has previously been known from Riverside and San Diego Counties of California, where it occurs in natural palm groves. Nests are usually constructed beneath the fronds of the palms. The Baja California records are all from habitats similar to those in California.

SPECIMENS EXAMINED: *Baja Calif.*: 2 ♀♀, San Matias Pass, 8 mi. S., May 16, 1960 (E. L. Sleeper; LBSC); 14 ♀♀, Cañon de Guadalupe, Sierra Juarez, May 2-3, 1964 (R. R. Snelling, E. M. Fisher; LACM); 1 ♀, El Tajo Cañon, Sierra Juarez, Sept. 9, 1957 (J. Roberds; LACM); 2 ♂♂, 5 ♀♀, same locality, Sept. 11, 1958 (J. R. Northern; LACM).

#### ***Polistes major slevini* R. Bohart**

Figures 1f; 2f, m; 3d

*Polistes major slevini* R. Bohart, 1949. Pan-Pacific Ent. 15: 103. ♂ ♀.

This form is similar to the foregoing subspecies, but the ferruginous color is darker, the propodeum usually lacks yellow stripes and the scutellum is either wholly yellow or with two small ferruginous spots in the middle. As with *P. m. palmarum*, this subspecies is found in the vicinity of natural palm groves and frequently nests under the living fronds.

SPECIMENS EXAMINED: *Baja Calif.*: 2 ♀♀, Bahia de los Angeles, 1 mi. S., June 11, 1967 (E. L. Sleeper & E. M. Fisher; LBSC); 1 ♀, Santa Gertrudis, April 23, 1940 (C. F. Harbison; SDM). *Terr. Sur.*: 1 ♂, San Ignacio, June 17-18, 1967 (E. L. Sleeper & E. M. Fisher; LBSC); 1 ♀, La Virgen (shrine),

Sept. 14, 1959 (C. F. Harbison; SDM); 2 ♂♂, 1 ♀, Rancho El Coyote, May 23, 1961 (R. Maynard & J. Honey; LACM); 1 ♀, Bahia Concepcion, April 24, 1958 (E. Y. Dawson; LACM); 1 ♀, Loreto, Sept. 29, 1959 (C. F. Harbison; SDM); 1 ♂, 2 ♀♀, Rancho Potrero, May 9, 1959 (D. Patterson; UCR), "wasps living in palm head"; 1 ♀, La Paz, 13 mi. W., Nov. 11, 1965 (W. Ewart & R. C. Dickson; UCR), on *Tecoma stansburyi*; 2 ♀♀, La Paz, 10 mi. NW, Oct. 6, 1941 (E. S. Ross & G. E. Bohart; CAS); 5 ♀♀, La Paz, June 3, 1921 (E. P. Van Duzee; CAS); 1 ♀, same locality, June 26, 1967 (E. L. Sleeper & E. M. Fisher; LBSC); 1 ♀, La Paz, 20 kilo. SE, Nov. 11, 1952 (C. B. Heller; SDM); 1 ♀, Todos Santos, 10 mi. N., Dec. 26, 1958 (H. B. Leech; CAS); 4 ♀♀, Todos Santos, Aug. 12, 1919 (J. R. Slevin; CAS); 1 ♀, same locality, Sept. 16, 1959 (C. F. Harbison; SDM); 1 ♀, same locality, Dec. 13, 1928 (A. E. Coburn; LACM); 1 ♂, Colonia Calles, Sept. 15, 1959 (C. F. Harbison; SDM); 1 ♂, 1 ♀, Triunfo, July 8, 1919 (G. F. Ferris; LACM); 1 ♀, same locality, July 7, 1939 (A. E. Michelbacher & E. S. Ross; CAS); 1 ♀, Las Animas, Sierra Laguna, Oct. 12, 1941 (E. S. Ross & G. E. Bohart; CAS); 1 ♀, Sierra Laguna, April 5-6, 1947 (CAS); 1 ♀, Agua Caliente, April 22, 1947 (LACM); 12 ♀♀, Boca de la Sierra, Mar. 5-6, 1969 (R. R. Snelling; LACM), mostly at aphid honeydew on native bamboo; 1 ♀, San Jose del Cabo, July 15, 1967 (E. M. Fisher; LBSC); 1 ♀, Cabo San Lucas, 3.4 mi. NE, Jan. 1, 1959 (H. B. Leech; CAS). *Golfo de Calif.*: 1 ♀, Punta Gordas, Isla Cerralbo, Mar. 20, 1953 (P. H. Arnaud; CAS); 1 ♀, Isla Partida, Apr. 17, 1958 (E. Y. Dawson; LACM); 3 ♀♀, Isla Espiritu Santo, Mar. 7, 1928 (T. Craig; CAS). In addition to the above localities, Bohart (1949) recorded a specimen from Las Parras, which I have not seen.

### ***Polistes exclamans lineonotus* R. Bohart**

Figures 1h; 2h, o; 3e

This slender wasp, with paired mesonotal stripes, is a distinctive element of the peninsular fauna. It is very common in the southern third; nests are frequently built in mesquite trees and, during the winter months, the trees may be liberally festooned with several years' accumulation of nests.

Unlike the nominate form, *P. e. lineonotus* is an aggressive wasp in the vicinity of the nests and stings very readily. Colonies, in the Cape Region, may persist throughout the year. I have seen populous nests (25 or more wasps) in this region in early March.

Because this wasp is nowhere in contact with the range of other subspecies of *P. exclamans*, its color pattern is quite stable. The paired mesoscutal stripes are almost invariably present in females. The ground color varies from light ferruginous to blackish, but the pleurae and propodeum seem always to be blackish. Generally, specimens from the Gulf islands have the ferruginous color replaced by blackish, but this condition is found in samples from the

peninsula. The male color pattern seems to parallel that of the females, but fewer males are available for study; there is a noticeable tendency in the males for a loss of mesoscutal stripes; the mesoscutum is concolorous ferruginous in about a third of the males seen.

**SPECIMENS EXAMINED:** *Baja Calif.*: 1 ♀, Santa Gertrudis, Apr. 24, 1940 (C. F. Harbison; SDM). *Terr. Sur*: 62 ♀♀, San Ignacio, June 17-18, 1967 (E. L. Sleeper & E. M. Fisher; LBSC); 1 ♀, Mulege, Feb. 27, 1969 (R. R. Snelling; LACM); 4 ♀♀, Mulege, May 14, 1921 (E. P. Van Duzee; CAS); 3 ♀♀, Puerto Escondido, Feb. 27, 1928 (T. Craig; CAS); 1 ♂ [Bahia] Agua Verde, May 26, 1921 (E. P. Van Duzee; CAS); 8 ♀♀, San Miguel Comondu, 2 mi. SW, June 23, 1967 (E. L. Sleeper & E. M. Fisher; LBSC); 2 ♀♀, San[to] Domingo, July 19, 1938 (A. E. Michelbacher & E. S. Ross; CAS); 22 ♀♀, San[to] Domingo, Oct. 23, 1941 (E. S. Ross & G. E. Bohart; CAS); 1 ♂, 3 ♀♀, Santo Domingo, Nov. 16, 1941 (F. Gander; SDM); 1 ♀, Santa Rita, 20 mi. SE, June 25, 1967 (E. L. Sleeper & E. M. Fisher; LBSC); 1 ♀, La Paz, 12 mi. W, Nov. 11, 1965 (W. Ewart & R. Dickson; UCR), on *Tecoma stansburyi*; 1 ♀, La Paz, June 4, 1921 (E. P. Van Duzee; CAS); 1 ♂, 9 ♀♀, La Paz, June 26, 1967 (E. L. Sleeper & E. M. Fisher; LBSC); 1 ♀, La Paz, June 28, 1919 (J. R. Slevin; CAS); 1 ♀, La Paz, July 7, 1953 (R. R. Snelling; LACM); 1 ♀, La Paz, Sept. 13, 1959 (C. F. Harbison; SDM); 1 ♀, La Paz, Oct. 9, 1955 (F. X. Williams; CAS); 1 ♀, San Bartolo, Oct. 24, 1941 (F. Gander; SDM); 1 ♂, 2 ♀♀, Todos Santos, 10 mi. N, Dec. 26, 1958 (H. B. Leech; CAS); 1 ♀, Todos Santos, Aug. 12, 1919 (J. R. Slevin; CAS); 7 ♀♀, Todos Santos, Sept. 14-16, 1959 (C. F. Harbison; SDM); 4 ♀♀, Colonia Calles, Sept. 15, 1959 (C. F. Harbison; SDM); 1 ♂, 4 ♀♀, Triunfo, July 8, 1919 (G. F. Ferris; LACM); 1 ♀, 4 ♀♀, between San Jose del Cabo and Triunfo (Albatross Expedition, 1911; AMNH); 1 ♀, [Rancho] Buena Vista, La Ribera, May 16, 1947 (LACM); 65 ♀♀, Boca de la Sierra, Mar. 5-6, 1969 (R. R. Snelling; LACM), 15 at nest in *Prosopis* tree, 11 at aphid honeydew; 11 ♀♀, Boca de la Sierra, June 27-28, 1967 (E. L. Sleeper & E. M. Fisher; LBSC); 3 ♀♀, Caduaña, 4.2 mi. W, Mar. 5, 1969 (R. R. Snelling; LACM); 1 ♀, Santa Anita, 4 mi. SW, Mar. 4, 1969 (R. R. Snelling; LACM); 1 ♂, 2 ♀♀, San Jose del Cabo, 5 mi. N, Nov. 8, 1951 (W. Ewart & R. Dickson; UCR); 6 ♂♂, 3 ♀♀, San Jose del Cabo, Nov. 11, 1952 (C. F. Harbison; SDM); 1 ♀, San Jose del Cabo, 1 mi. E, June 28, 1967 (E. M. Fisher; LBSC); 1 ♀, San Jose del Cabo, 11 mi. W, June 28, 1967 (E. M. Fisher; LBSC); 2 ♀♀, Cabo San Lucas, Mar. 16, 1953 (J. P. Figg-Hoblyn; CAS). *Golfo de Calif.*: 1 ♀, Isla San Jose, May 28, 1921 (E. P. Van Duzee; CAS); 2 ♀♀, Rancho Los Dolores, Isla San Jose, Aug. 11, 1965 (K. Lucas; CAS); 1 ♂, Isla Partida, Apr. 17, 1958 (E. Y. Dawson; LACM); 1 ♀, Isla Cerralbo, Apr. 9, 1966 (J. McLean; LACM); 9 ♀♀, Ruffo Rancho, Isla Cerralbo, Oct. 30, 1961 (R. C. Banks & M. Soule; CAS).

**Polistes fuscatus aurifer** Saussure

Figures 1c; 2c, j.

*Polistes aurifer* Saussure, 1853. Etudes sur la Famille des Vespides 2: 78. ♀.

*Polistes anaheimensis* Provancher, 1888. Addit. Corr. Faune Ent. Canada Hymen., p. 423. ♂ ♀.

*Polistes fuscatus aurifer*, Bequaert, 1940. Jour. N. Y. Ent. Soc. 48: 21.

*Polistes fuscatus montanus* Bequaert, 1940. *Op. cit.*, p. 26-27. ♀ ♂.

This subspecies barely enters Baja California from southern California where it is quite common. I have studied only two samples from Baja California, as noted below. These are from areas where *P. f. centralis* Hayward also is found and several specimens are intermediate between the two forms. The predominately black ground color of the thorax is partially replaced by ferruginous in these intermediates.

SPECIMENS EXAMINED: *Baja Calif.*: 11 ♀ ♀, Aguajito Spring, Valle de la Trinidad, March 20, 1936 (C. F. Harbison; SDM); 1 ♂, Cataviña, June 19, 1938 (A. E. Michelbacher & E. S. Ross; CAS).

**Polistes fuscatus centralis** Hayward

Figures 1a, b; 2a, b, i; 3a

*Polistes fuscatus centralis* Hayward, 1933. Proc. Utah Acad. Sci. 10: 143. ♀.

This is one of the commonest social wasps over most of the peninsula. It is apparently absent only from the northwestern area, west of the Sierra Juarez, where it is replaced by *P. f. aurifer*. The population over much of this area is characterized by an atypical color pattern present in both sexes. Specimens representing a more "typical" color pattern occur only in northeastern Baja California from the Mexicali area to Valle de la Trinidad. South of the Valle de la Trinidad the ferruginous ground color becomes much more extensive, especially on the abdomen. The tergites become largely ferruginous, often only with narrow apical yellow fasciae; small lateral yellow spots may be present on the second tergite. These specimens from the more arid regions also average much smaller than is usual and are easily confused with *P. d. californicus* R. Bohart. Some records here attributed to *P. f. centralis* have been previously thought to belong to *P. d. californicus*. These prior determinations were based upon isolated females. The large number of males now available have indicated that *P. d. californicus* is absent over much of the peninsula while *P. f. centralis* is abundant.

The small, largely ferruginous females here assigned to *P. f. centralis* differ slightly from *P. d. californicus* in their color pattern of the abdomen. The first tergite has a narrow apical yellow fascia often extending forward along the lateral margin; a lateral spot may or may not be present and it may

or may not be free of the apical fascia. In all specimens which I have studied of *P. d. californicus* from this area, there is a broad apical fascia joining a large, quadrate lateral spot, so that the first tergite has a small rectangular ferruginous mark on the mediobasal area. The second tergite of *P. f. centralis* is highly variable in its markings; it may be largely yellow, with the ferruginous area limited to the basal one-third or less. In these specimens the posterior margins of the ferruginous areas converge toward the midline so that the area is roughly triangular (fig. 1a). In specimens which are a little more extensively ferruginous, the ferruginous area is expanded beyond the point of convergence so that a poorly defined lateral yellow spot is demarked (fig. 1b). Still more extensively ferruginous individuals may have a free yellow spot or none at all. In *P. d. californicus* the ferruginous area is either truncate (fig. 1e) or oblique behind, almost always with a definitely quadrate or subquadrate lateral yellow spot which is always broadly attached to the apical fascia.

Structural characters which will reliably separate the females have not been found. A few trends do exist and, when used cautiously, may aid in coming to a correct determination. In *P. f. centralis* the genae, at the termination of the occipital carina, are usually no wider than the eye in profile. In about half the material examined, they are slightly narrower than the eyes. Rarely was an individual found in which the genae were wider than the eyes. In *P. d. californicus* about half the specimens had the genae and eyes of about equal width, while the genae were a little broader than the eyes in a great many specimens. In a few, the genae were narrower than the eyes (the measurements for *P. d. californicus* included samples from California; those of *P. f. centralis* were all from the peninsula).

The transverse propodeal striae tend to differ between the two wasps. Those of *P. f. centralis* are usually of variable size, with some coarser rugulae interspersed among the fine; there are often a few coarse rugulae near the spiracles. In *P. d. californicus* the rugulae are generally more uniform in size, finest above, near the spiracles, becoming gradually coarser below; coarser rugulae are rarely spaced among the fine, and are usually absent from the spiracular area.

The lateral propodeal lamella of *P. d. californicus* is usually evenly rounded onto the posterior, vertical surface, without a carina at the juncture of the two faces. That of *P. f. centralis* usually has a fine carina, at least on the inner half.

SPECIMENS EXAMINED: *Baja Calif.*: 1 ♀, Ejido Nayarit (about 21 mi. SE of Mexicali), July 14, 1953 (E. O. Johnson; LACM); 1 ♂, Mexicali, 36-42 kilom. S, June 29, 1953, (R. R. Snelling; LACM), on *Melilotus alba*; 3 ♀♀, Mexicali, 45 kilom. S, June 25, 1953 (R. R. Snelling; LACM), one with larva of *Alabama argillacea* (Hbn.), two from nest under eaves of dwelling; 1 ♀, El Mayor, June 15, 1952 (M. Cazier, W. Gertsch & R. Schrammel; AMNH); 1 ♀, Palacio, 20 mi. S, Apr. 1939 (C. D. Michener; CAS), on

*Larrea*; 5 ♀♀, San Jose Castillo, 12 mi. E, Nov. 11, 1960 (E. L. Sleeper; LBSC); 2 ♀♀, El Tajo Can., Sierra Juarez, Sept. 9, 1957 (J. Roberds; LACM); 13 ♀♀, Aguajito Spring, Valle de la Trinidad, Mar. 20, 1936 (C. F. Harbison; SDM); 16 ♀♀, Las Arrastras [de Arriola], 7 mi. N and 4 mi. S, June 8, 9, 1967 (E. L. Sleeper & E. M. Fisher; LBSC); 1 ♀, Mission Calamajue, 3.2 mi. S, June 10, 1967 (E. L. Sleeper & E. M. Fisher; LBSC); 1 ♀, Bahia de los Angeles, June 27, 1921 (E. P. Van Duzee; CAS); 3 ♀♀, Bahia de los Angeles, 1 mi. S, June 11, 1967 (E. L. Sleeper & E. M. Fisher; LBSC); 1 ♀, Santa Gertrudis, Apr. 23, 1940 (C. F. Harbison; SDM); 2 ♀♀, El Arco, June 16, 1967 (E. L. Sleeper & E. M. Fisher; LBSC). *Ferr. Sur*: 2 ♂♂, 2 ♀♀, El Arco Mine, 14, 30 & 40 mi. S, June 23, 1938 (A. E. Michelbacher & E. S. Ross; CAS); 6 ♂♂, San Ignacio, 15 mi. N, June 26, 1938 (A. E. Michelbacher & E. S. Ross; CAS); 2 ♂♂, San Ignacio, June 26, 1938 (A. E. Michelbacher & E. S. Ross; CAS); 17 ♂♂, 14 ♀♀, San Ignacio, June 17-18, 1967 (E. L. Sleeper & E. M. Fisher; LBSC); 1 ♂, 1 ♀, San Ignacio, 10 mi. E, Sept. 30, 1941 (E. S. Ross & G. E. Bohart; CAS); 8 ♀♀, Santa Rosalia, 17 mi. S, June 18, 1967 (E. L. Sleeper & E. M. Fisher; LBSC); 1 ♀, Mulege, May 15, 1921 (E. P. Van Duzee; CAS); 2 ♀♀, Mulege, 30 mi. S, June 21, 1967 (E. L. Sleeper & E. M. Fisher; LBSC); 1 ♂, Coyote Cove, Bahia Concepcion, Oct. 1, 1941 (E. S. Ross & G. E. Bohart; CAS); 1 ♂, Rancho El Coyote, Bahia Concepcion, June 23, 1961 (R. Maynard & J. Honey; LACM); 2 ♂♂, 2 ♀♀, Bahia Concepcion, east side, Apr. 24, 1958 (E. Y. Dawson; LACM); 1 ♀, Bahia Escondido, June 14, 1921 (E. P. Van Duzee; CAS); 1 ♂, 4 ♀♀, Puerto Escondido, Apr. 21, 1958 (E. Y. Dawson; LACM); 1 ♂, 6 ♀♀, Bahia Agua Verde, Apr. 20, 1958 (E. Y. Dawson; LACM); 1 ♀, San Miguel Comondu, 2 mi. SW, June 23, 1967 (E. L. Sleeper & E. M. Fisher; LBSC); 1 ♀, San Miguel Comondu, 19 mi. SW, June 23, 1967 (E. L. Sleeper & E. M. Fisher; LBSC); 1 ♀, Santa Rita, 20 mi. SE, June 25, 1967 (E. L. Sleeper & E. M. Fisher; LBSC); 8 ♀♀, La Paz, June 3-14, 1921 (E. P. Van Duzee; CAS); 2 ♂♂, 1 ♀, La Paz, June 28, 1919 (J. R. Slevin; CAS); 7 ♀♀, Bahia de los Muertos, Dec. 20, 1958 (H. B. Leech; CAS); 3 ♂♂, 3 ♀♀, San Antonio, July 12, 1919 (G. F. Ferris; LACM); 2 ♀♀, La Ribera, July 19, 1919 (G. F. Ferris; LACM); 1 ♀, Boca de la Sierra, Mar. 6, 1969 (R. R. Snelling; LACM), at aphid honeydew; 1 ♀, between San Jose del Cabo and Triunfo (Albatross Exped., 1911; AMNH); 1 ♀, San Jose del Cabo, 1 mi. E, July 15, 1967 (E. M. Fisher; LBSC). *Golfo de Calif.*: 1 ♂, Isla Monserrate, May 24, 1921 (E. P. Van Duzee; CAS); 2 ♀♀, Isla San Jose, Apr. 18, 1958 (E. Y. Dawson; LACM).

***Polistes dorsalis californicus* R. Bohart**

Figures 1e; 2e, 1; 3c

*Polistes hunteri californicus* R. Bohart, 1949. Pan-Pacific Ent. 15: 101.

♂ ♀.

Dr. Bohart examined the type of *Vespa dorsalis* Fabricius and found it to be a *Polistes*, identical to *P. hunteri neotropicus* Bequaert (*personal communication*). The Fabrician name has traditionally been applied to a eumenine species. But, since it is actually a *Polistes*, the name has priority over that of Bequaert so that the various forms attributed to *P. hunteri* Bequaert must now be transferred to *P. dorsalis*. The eumenine species takes its first available name, presumably *Odynerus crypticus* Say; this wasp is now placed in the genus *Euodynerus*.

While *P. d. californicus* is probably fairly abundant in the oak and chaparral areas of Baja California, it is absent over most of the peninsula. There are but three records for it in the Territorio Sur. Because of their distinctive facial structure the males of this wasp are easily separated from the forms of *P. fuscatus* (Fabricius) in the same area. The females are much less readily separated, however, and in the absence of males some records which might be attributed to this wasp have been assigned to *P. f. centralis*. In placing isolated females as *P. d. californicus* I have followed a fairly rigid, and possibly unrealistic, set of criteria. My justification is that the separation achieved is, so far as can now be demonstrated, supported by available males.

There are two specimens from the Cape region. The one from San Jose del Cabo is a perfectly typical male in all its markings. The second specimen, also a male, is from La Laguna, at an elevation of 5500 feet in the Sierra Laguna. In its structural features it seems inseparable from the other males of this wasp. Its ferruginous markings, however, are quite extensive and this specimen closely resembles some males of *P. f. centralis* with reduced yellow maculae.

SPECIMENS EXAMINED: *Baja Calif.*: 4 ♀♀, Aguajito Spring, Valle de la Trinidad, Mar. 20, 1936 (C. F. Harbison; SDM); 2 ♂♂, 6 ♀♀, El Tajo Can., Sierra Juarez, Sept. 11, 1958 (J. R. Northern; LACM). *Terr. Sur.*: 2 ♀♀, San Ignacio, June 17-18, 1967 (E. L. Sleeper & E. M. Fisher; LBSC); 1 ♂, La Laguna, Sierra Laguna, July 7-10, 1967 (E. M. Fisher; LBSC); 1 ♂, San Jose del Cabo, Nov. 11, 1952 (C. F. Harbison; SDM).

### ***Polistes rossi* R. Bohart**

Figures 1d; 2d, k; 3b

*Polistes rossi* Bohart, 1949. Pan-Pacific Ent. 25: 99-100. ♂ ♀.

This large, basically ferruginous wasp is apparently not common. The male is easily recognized by the large ocelli. The females are similar to the peninsular variant of *P. f. centralis*, but are larger, have an acute clypeal apex and a more coarsely striate propodeum. The propodeal character is subject to variation and some specimens have the striae uniformly as fine as those of *P. f. centralis*. A seemingly consistent feature of the females is that the lateral lamella of the propodeal valve is almost entirely clear ferruginous, rather than opaque yellow as in *P. f. centralis* and *P. d. californicus*.

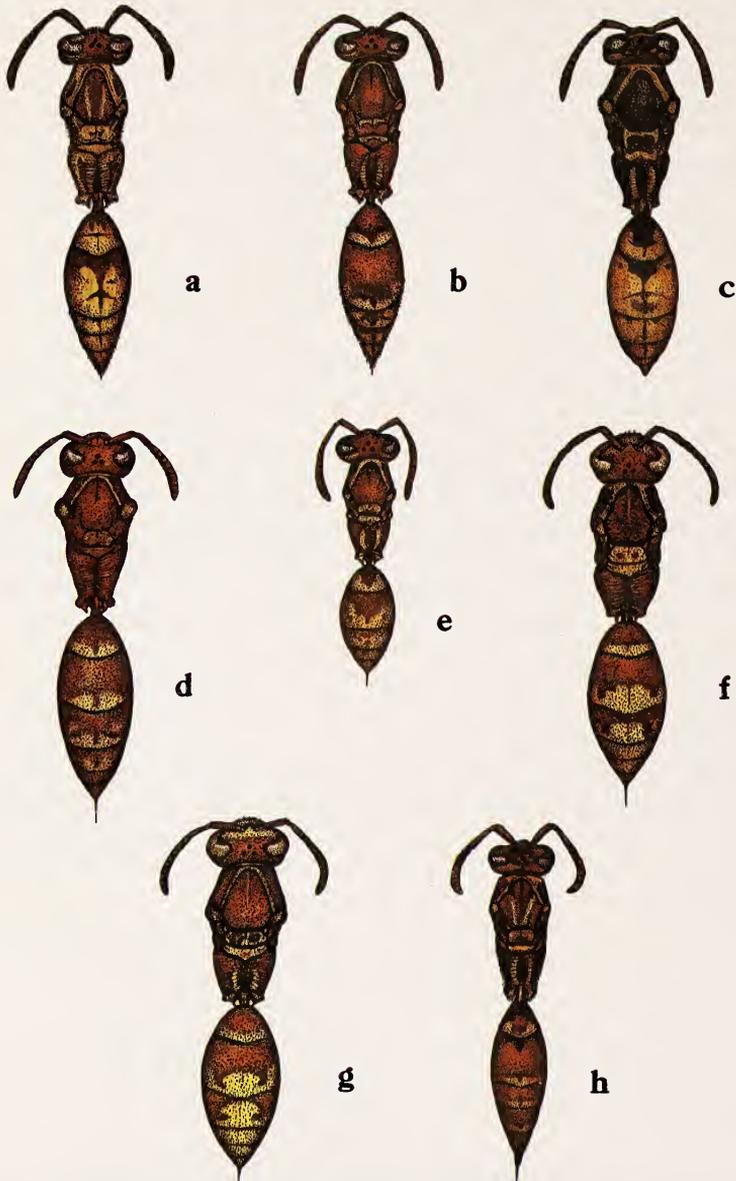


Figure 1. Dorsal aspect of *Polistes* females: a, *P. fuscatus centralis*, xanthic form; b, same, peninsular form; c, *P. fuscatus aurifer*; d, *P. rossi*; e, *P. dorsalis californicus*; f, *P. major slevini*; g, *P. major palmarum*; h, *P. lineonotus*. All figures drawn to same scale.



Figure 2. Heads of *Polistes* spp.: a, *P. fuscatus centralis*, ♀, xanthic form; b, same, ♀, peninsular form; c, *P. fuscatus aurifer*, ♀; d, *P. rossi*, ♀; e, *P. dorsalis californicus*, ♀; f, *P. major slevini*, ♀; g, *P. major palmarum*; h, *P. lineonotus*, ♀; i, *P. fuscatus centralis*, ♂; j, *P. fuscatus aurifer*, ♂; k, *P. rossi*, ♂; l, *P. dorsalis californicus*, ♂; m, *P. major slevini*, ♂; n, *P. major palmarum*; o, *P. lineonotus*, ♂. All figures drawn to same scale.

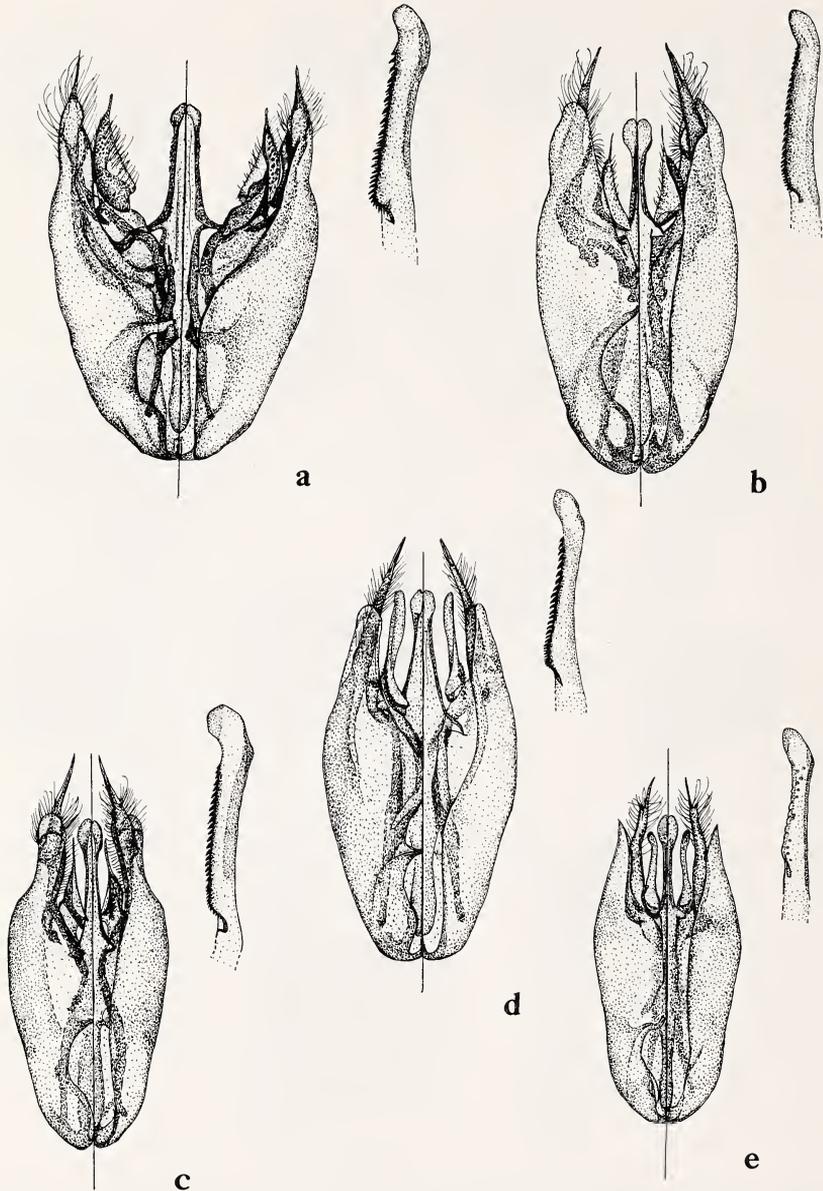


Figure 3. *Polistes* spp., male genitalia (right half dorsal aspect, left half ventral aspect) and lateral aspect of aedeagus (enlarged): a, *P. fuscatus centralis*; b, *P. rossi*; c, *P. dorsalis californicus*; d, *P. major slevini*; e, *P. lineonotus*. All figures drawn to same scale.

The habits of this uncommon wasp are largely unknown. It is regarded with considerable caution by inhabitants of areas where it occurs; the sting is said to be more painful than that of *P. e. lineonotus* or *P. f. centralis*. Nests are constructed on vertical rock faces of arroyos and washes, fully exposed.

**SPECIMENS EXAMINED:** *Baja Calif.:* 1 ♂, Cataviña, June 19, 1938 (A. E. Michelbacher & E. S. Ross; CAS); 2 ♀♀, Santa Gertrudis, Apr. 24, 1940 (C. F. Harbison; SDM); 1 ♀, El Arco, June 16, 1967 (E. M. Fisher; LBSC). *Terr. Sur.:* 1 ♀, El Arco, 15 mi. S, Aug. 26, 1959 (F. G. Werner; CAS); on mesquite; 2 ♂♂, El Arco, 20 mi. S, Sept. 30, 1941 (E. S. Ross & G. E. Bohart; CAS); 2 ♀♀ San Ignacio, 15 mi. N, July 26, 1938 (A. E. Michelbacher & E. S. Ross; CAS); 2 ♂♂, San Ignacio, 10 mi. E, Sept. 30, 1941 (E. S. Ross & G. E. Bohart; CAS); 5 ♀♀, Mulege, 30 and 37 mi. S, June 21, 1967 (E. L. Sleeper & E. M. Fisher; LBSC); 1 ♀, Coyote Cove, Bahia Concepcion, June 29, 1938 (A. E. Michelbacher & E. S. Ross; CAS); 1 ♀, Bahia Concepcion, Apr. 6-10, 1911 (Albatross Expedition, 1911; AMNH); 1 ♂, 2 ♀♀, Rancho El Coyote, Bahia Concepcion, June 23, 1961 (R. Maynard & J. Honey; LACM); 1 ♂, La Virgen Shrine, Sept. 14, 1950 (C. F. Harbison; SDM); 1 ♀, Canipole, Oct. 2, 1941 (E. S. Ross & G. E. Bohart; CAS); 1 ♂, Santo Domingo, Nov. 16, 1941 (F. Gander; SDM); 1 ♀, El Refugio, 15 mi. N, July 4, 1938 (A. E. Michelbacher & E. S. Ross; CAS); 1 ♀, La Paz, 22 mi. W, June 25, 1967 (E. L. Sleeper & E. M. Fisher; LBSC); 1 ♂, La Paz, Oct. 6, 1955 (F. X. Williams; CAS); 1 ♂, Todos Santos, 10 mi. N, Dec. 26, 1958 (H. B. Leech; CAS); 1 ♀, Boca de la Sierra, Mar. 6, 1969 (R. R. Snelling; LACM), at aphid honeydew; 1 ♀, Santa Anita, 4 mi. SW, Mar. 4, 1969 (R. R. Snelling; LACM); 5 ♀♀, San Jose del Cabo, 11 mi. W, June 28, 1967 (E. M. Fisher; LBSC). *Golfo de Calif.:* 1 ♀, Isla Espiritu Santo, Mar. 23, 1953 (P. H. Arnaud; CAS).

### ***Polistes carnifex* (Fabricius)**

*Vespa carnifex* Fabricius, 1775. *Systema entomologiae*, p. 365.

*Polistes carnifex*, Fabricius. 1804. *Systema piezatorum*, p. 272.

*Polistes onerata* Lepeletier, 1836. *Histoire naturelle des insectes, hymenopteres, suites a Buffon*, Paris, 1: 524.

*Polistes valida* Say, 1837. *Boston Jour. Nat. Hist.* 1: 389.

*Polistes transverso-strigata* Spinola, 1851. *Mem. Acad. Sci. Torino*, Ser. 2, 13: 78.

This wasp is one of the largest and most conspicuous *Polistes* in the Western Hemisphere. I recorded it (Snelling, 1955) from La Paz, Territorio Sur, where I collected a single female on the waterfront on July 7, 1953. Since that time there have been no subsequent captures of this species in this region. Consequently, it seems likely that the female which I captured represents an accidental introduction from the Mexican mainland; the species is common at Mazatlan, Sinaloa, and vessels from that port frequently travel to La Paz.

Until evidence to the contrary is advanced, I believe that *P. carnifex* should be dropped from the lists of peninsular vespids.

KEY TO SPECIES OF *MISCHOCYTTARUS* IN LOWER CALIFORNIA

Malar space nearly as long as width of antennal socket; mesopleurae without long, slender flexuous hairs; clypeal apex acute . . . . . *fisheri*, n. sp.

Malar space about one-half as long as width of antennal socket; mesopleurae with numerous long, slender flexuous hairs; clypeal apex obtuse . . . . . *flavitorsis* (Saussure)

***Mischocyttarus* (Kappa) *fisheri***, new species

Figure 4d-f

*Diagnosis:* This species belongs to the group of *M. flavitorsis* (Saussure) as defined by Richards (1945) and is most closely related to *M. flavitorsis* and *M. pallidipectus*. It differs from these and other members of the group by the following combination of features: malar space as long as diameter of antennal socket; pronotal furrow obtuse; pronotal keel obtuse over its entire length; first tergite longer than hind femora; propodeal furrow well defined; clypeus wider than long, with acute apex.

*Description:* Female/worker: Black; face below upper margin of ocular sinus light ferruginous, inner orbits and clypeal apex more yellowish; broad yellowish stripe along outer orbits to ocular summit, becoming light ferruginous behind; oblique occipital stripe, separated from outer orbital stripe by a narrow ferruginous occipital mark; scape and flagellum ferruginous, the flagellar segments infuscated over the apical six or seven segments; dorsal and anterior pronotal margins yellowish, remainder of pronotum light ferruginous; mesepisternum ventrally with large yellow mark behind front coxae; posterior half of prepectus yellow; scutum with two light ferruginous longitudinal stripes, coalesced over posterior third; scutellum ferruginous, lighter over anterior half; anterior half of postscutellum yellowish; two broad yellowish stripes on either side of propodeal midline; preapical ferruginous and narrower apical yellowish band on first tergite; subsequent tergites and sternites shading from blackish base to yellowish apical band, the greater part of the disc ferruginous; anterior femora with broad dorsal stripe and apical one-fifth ferruginous; mid and posterior femora ferruginous basally and yellowish apically, middle three-fourths blackish; remainder of legs ferruginous within, yellowish on outer surfaces. Wings brownish, with light ferruginous tones, veins and stigma ferruginous.

Head 1.17 times wider than long; clypeal width (between eyes) 1.2 times clypeal length; shortest malar length equal to diameter of antennal socket; interocellar distance one-third greater than diameter of anterior ocellus;

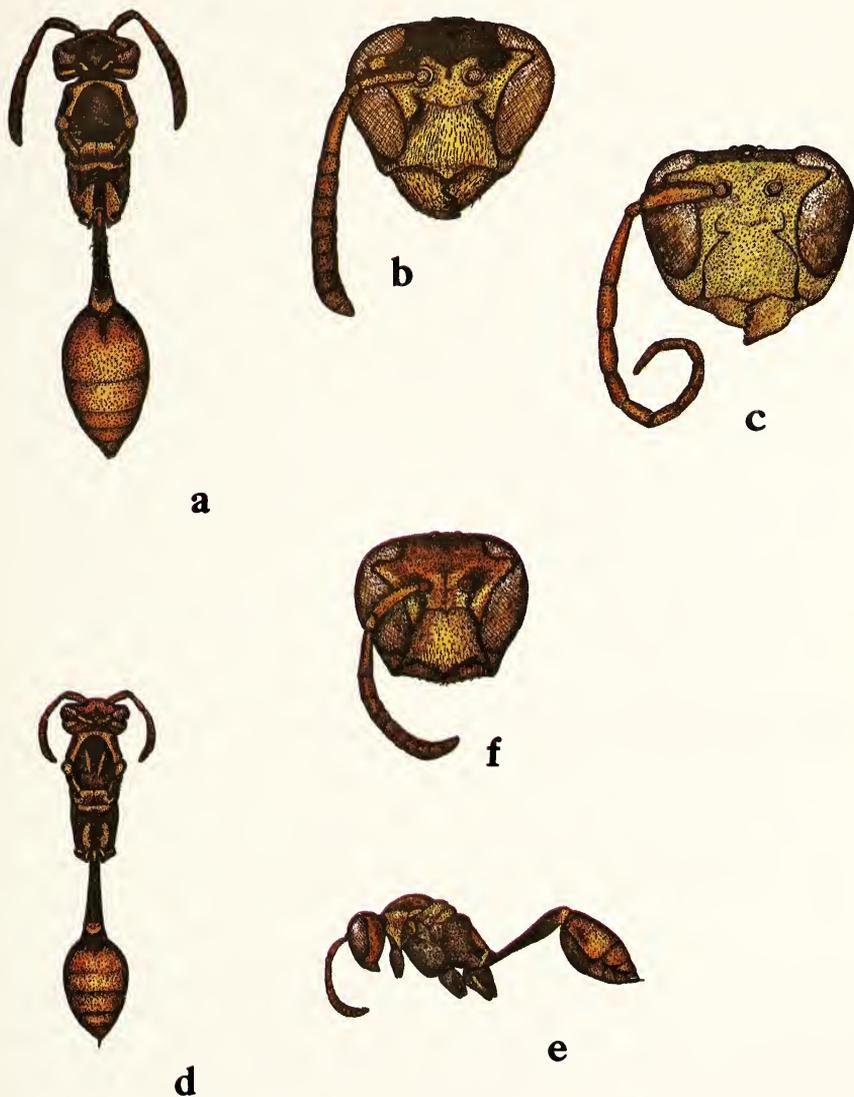


Figure 4. a-c, *Mischocyttarus flavitarsis*: a, female, dorsal aspect; b, female, head; c, male, head. d-f, *M. fisheri*: d, female, dorsal aspect; e, female, lateral aspect; f, female, head. All figures drawn to same scale.

ocellar-ocular distance about twice interocellar distance; postocellar distance about two and one-half times interocellar distance; scape 2.5 times longer than apical width, 1.36 times longer than first flagellar segment. Tentorial pits nearer antennal sockets than eyes. Frontal area dull, granulo-punctate. Upper three-fourths of clypeus finely, closely punctate, interspaces slightly shiny, apical one-fourth depressed, shinier, with numerous coarse, close punctures; apical margin acute. Eyes a little closer below than above, contiguous with clypeal margin for a distance subequal to antennal socket diameter. Gena slightly wider than eye in profile.

Thorax + propodeum about 1.6 times longer than wide in dorsal view, dull, everywhere granulo-punctate. Pronotum with anterior margin raised, but not reflexed, anterior furrow obtuse behind; lateral fovea present; keel, when viewed from above, gently and slightly curved, obtuse throughout. Postscutellum moderately flattened, its anterior margin below scutellum. Propodeum with narrow horizontal basal area, forming an angle with postscutellum, central furrow moderately broad and well defined, without central keel; dorso-lateral margin of valve plate acute. Mid tibial spurs about equal in length; third and fourth mid tarsal segments slightly asymmetrical; hind tarsi with inner lobe of third segment a little longer than outer lobe of fourth.

Tergite one a little longer than hind femora (10:9); anterior one-third, in dorsal view, with sides nearly parallel, then evenly expanded toward posterior margin, the latter about twice the basal width; spiracles hardly projecting in dorsal view, spiracular ratio about 5:7. Tergite two strongly expanded, slightly wider than long.

Entire body with very delicate suberect golden pubescence which does not obscure surface; mesopleura with scattered erect hairs about twice as long as the pubescence, but without obvious much longer hairs.

Length (front of anterior ocellus to margin of second tergite), 7.0-7.4 mm.; forewing 10.5-11.5 mm.

Holotype (Los Angeles County Museum of Natural History) and one paratype: La Laguna, 5500', Terr. Sur Baja California, July 7-10, 1967, collected by E. M. Fisher. The paratype is in the collection of California State College at Long Beach. This species is named for its collector, who has collected many interesting social Hymenoptera in Baja California.

Although closely related to both *M. flavitarsis* and *M. pallidipectus*, *M. fisheri* may be separated readily from both species by the lack of long, slender, flexuous hairs on the mesopleurae. From *M. flavitarsis* it may be further separated by the more acute clypeal apex and from *M. pallidipectus* by the slightly shining, less distinctly punctate tegulae. In *M. pallidipectus* the tegulae are dull and granulo-punctate. In the key to the species of this group by Richards (1945) *M. fisheri* fails at couplet 4 since it fails to agree fully with either alternative.

**Mischocyttarus (Kappa) flavitarsis flavitarsis** (Saussure)

Figure 4 a-c

*Polybia flavitarsis* Saussure, 1854. Etudes sur la Famille des Vespides 2: 199. ♀.

*Mischocyttarus flavitarsis*, Bequaert, 1932. Ent. Amer., n.s. 13: 119-129. ♀, ♀, ♂.

No specimens of this wasp have been seen from this area, nor are there published records of such occurrence. Since it does occur just north of Baja California, in San Diego County, California, it seems likely it will be found further south, in the chaparral areas of the Sierra San Pedro Martir and Sierra Juarez.

**Polybia diguetana** R. du Buysson

*Polybia occidentalis* var. *diguetana* R. du Buysson, 1905. Bulletin Societe entomologique France, 1905: 9. ♀, ♀, ♂.

*Polybia occidentalis* var. *parvula* Bequaert, 1944. Bull. Mus. Comp. Zool. 94: 287. (in part).

*Polybia diguetana*, Richards, 1951. Transactions Royal Entomological Society London 102: 138-140.

SPECIMENS EXAMINED: *Baja Calif.*: 2 ♀♀, Ensenada, June 10, 1950 (LACM).

These two specimens represent the first records for the genus *Polybia* in this area of Mexico and are a range extension of nearly 900 miles to the northwest into a very different type of habitat. Richards (1951) recorded *P. diguetana* from the states of Guerrero, Vera Cruz, Tabasco, Morelos, Oaxaca and Tamaulipas. I have a single female taken 39 mi. E of Villa Union, Sinaloa, on Aug. 27, 1960 by R. L. Westcott. This specimen and the two from Baja California compare favorably with samples from Vera Cruz (Cordoba, Presidio and Fortin de las Flores). This species is a member of the very difficult complex of *P. occidentalis* (Olivier), but the specimens from western Mexico do not differ from those of other areas and fit well the criteria established by Richards.

## ACKNOWLEDGMENTS

The material on which this study is based is mainly from four collections: California Academy of Sciences (CAS), through P. H. Arnaud; California State College at Long Beach (LBSC), through E. L. Sleeper and E. M. Fisher; Los Angeles County Museum of Natural History (LACM); San Diego Museum of Natural History (SDM), through C. F. Harbison. To each of the curators who made my study possible, I extend my sincere thanks. A few specimens from the American Museum of Natural History (AMNH) were loaned many years ago by M. A. Cazier, and I have seen several in the collections of the University of California at Riverside (UCR) which represent

records of interest. The figures were prepared by Ruth Ann DeNicola, to whom I continue to be grateful.

#### RESUMEN

Cuatro generos de Vespidae sociales se encuentran en Baja California: *Vespula* (dos especies), *Polistes* (siete especies), *Mischocyttarus* (dos especies) y *Polybia* (una especie). Una nueva especie, *Mischocyttarus fisheri*, de Sierra Laguna ha sido descrita y un nuevo genero, *Polybia*, ha sido recientemente descrito procedente de Baja California. Claves para todas estas especies con ilustraciones para cada especie y amplios factores de distribucion aqui se incluyen.

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VIRGINIA D. MILLER  
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ADDITIONS TO THE KNOWN AVIFAUNA OF THE  
BUGOMA, KIBALE, AND IMPENETRABLE FORESTS,  
WEST UGANDA

By HERBERT FRIEDMANN<sup>1</sup> AND JOHN G. WILLIAMS<sup>2</sup>

ABSTRACT: Distributional data on the birds of the isolated forests of western Uganda reported on in this paper add 38 species to the previously known avifauna of the Bugoma Forest, 91 to that of the Kibale Forest and 19 to that of the Impenetrable Forest. These are total figures for their respective areas as these have been given in the earlier literature, and they include a number of non-sylvan species that must have been collected immediately outside the true forests, although labeled as coming from within them. If we eliminate these from the additions to the avifauna of each of the three areas, we still have 26 species new to the Bugoma, 51 new to the Kibale and eight to the Impenetrable lists. Inasmuch as the new data on the bird life of the Bwamba, Kalinzu and Malabigambo Forests are treated in separate reports, they are omitted here. This is also true of the Budongo Forest, as the Museum has a collecting team working there at the present time. Included in the present report are the first specimen records from Uganda of *Francoelinus nobilis* and *Columba malherbii iriditorques*.

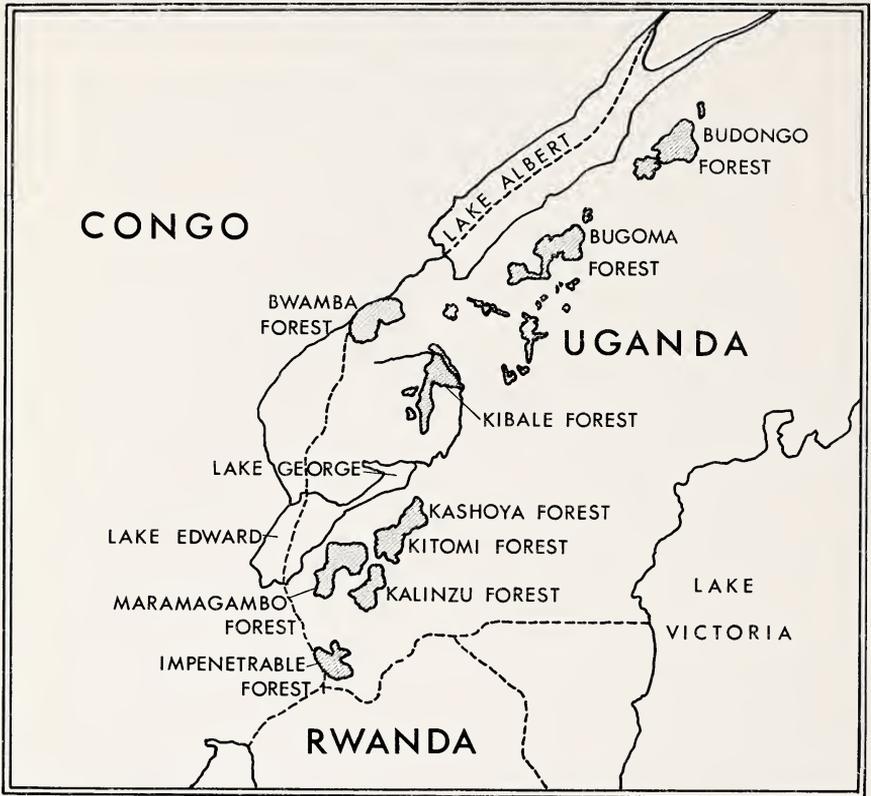
During the years 1966 to 1970, under the sponsorship of National Science Foundation (Grants GB-5107 and GB-7787), the Los Angeles County Museum of Natural History has been making zoological surveys of many of the dwindling, and, in some instances, disappearing, isolated forests of western Uganda. The purpose is twofold: to record, while it is still possible to do so, the occurrence of species in each of the forests; and to preserve in the Museum series of specimens of each taxon from each of these areas for future studies of incipient differentiation within each.

The forests surveyed are the Bwamba, Budongo, Bugoma, Impenetrable, Kalinzu, Kibale (Mpanga), Malabigambo (Sango Bay) and Ruwenzori. The resulting collections, preserved in the Museum in Los Angeles, are the largest and most comprehensive in any one institution, and it is hoped that all qualified students of central African birds will make use of them.

Separate reports have been written, and submitted to the press, on the birds of the lowland forests of Bwamba, in Toro Province, and of the hitherto unstudied, and now largely felled, Kalinzu, in south-western Ankole (now pub-

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Forests of western Uganda.

lished). Similarly a joint report (with Keith and Twomey) has been issued (1969) on the birds of the Impenetrable Forest in southwestern Kigezi. Also a report on the birds of the Sango Bay Forests, Buddu County, south of Masaka, considerably to the east of the true "west Uganda" area, has been issued by us (1969). While the joint report on the Impenetrable Forest was in press, the Museum received a second, very large collection of birds from that area which added a considerable number of species to its avifaunal record. The present paper is merely a brief report of the additions (represented by specimen records) to the previously known avifaunas of the Bugoma, Kibale and Impenetrable Forests. Inasmuch as a final survey is to be made shortly in the Budongo Forest, the material already on hand from that area will be held for inclusion in a separate paper together with the anticipated new data.

## BUGOMA FOREST

The Bugoma Forest appears to have been unvisited by collectors since van Someren's and Jackson's assistants worked there in the first two decades of this century. The forest extends from 1° 14' N to 1° 24' N, and from 30° 53' E to 31° 07' E, and it is one of the chain of disconnected sizable forests on the hills and the escarpment to the east of Lake Albert. This area ranges from about 3700 to 4500 feet in elevation; the lake itself lies in the deep Albertine trough at 2030 feet and is one of the lowest and hottest areas in Uganda.

The survey of the Bugoma Forest made for the Los Angeles County Museum of Natural History was accomplished from November 25 to December 18, 1967, inclusive, by A. L. Archer, R. Glen and A. Williams. In this period of a few weeks of intensive collecting some 669 specimens of 123 species of birds were obtained. Of these 123, 38 are additional to those listed by van Someren (1922; 1932) and by Jackson and Sclater (1938), and bring the total known Bugoma avifauna to 210 species. The 38 additions include 12 species that are not forest birds and that must have been collected immediately outside the true forest. All 38 are listed below, but the 12 non-sylvan species are marked by an asterisk. All the specimens taken in 1967 were collected in one area at an elevation of 3800 feet, and all are now in the collections of the Los Angeles County Museum of Natural History. It should be mentioned, in passing, that at least 25 or 30 species of those previously recorded from Bugoma are not forest birds either, but our concern here is limited to the species not mentioned by van Someren or by Jackson and Sclater.

## FAMILY ANATIDAE

\**Anas sparsa leucostigma* Rüppell

One male, one female, both in non-breeding state; Mwela; December 4 and 8.

## FAMILY RALLIDAE

*Sarothrura elegans* (A. Smith)

One male, testes enlarged; Mwela; December 7.

## FAMILY SCOLOPACIDAE

\**Tringa ochropus* (Linnaeus)

One male, one female; Mwela; December 1 and 8.

## FAMILY COLUMBIDAE

*Treron australis gibberifrons* (Madarasz)

Three specimens, all in non-breeding state; Mwela; December 2 and 4.

## FAMILY STRIGIDAE

*Ciccaba woodfordi nuchalis* Sharpe

Two males, testes not enlarged; Mwela; December 11 and 17.

## FAMILY ALCEDINIDAE

\**Ceryle maxima* (Pallas)

One female, non-breeding; Mwela; December 10.

## FAMILY MEROPIDAE

\**Merops pusillus meridionalis* (Sharpe)

One male, testes slightly enlarged; Mwela; December 15.

*Merops gularis australis* (Reichenow)

One male, testes slightly enlarged; Mwela; December 12.

## FAMILY PHOENICULIDAE

*Phoeniculus castaneiceps brunneiceps* (Sharpe)

Ten specimens, one with large, the rest with small, gonads; Mwela; November 27 to December 16.

## FAMILY BUCEROTIDAE

*Bycanistes cylindricus albotibialis* (Cabanis and Reichenow)

Two specimens, non-breeding; Mwela; November 28 and December 7.

*Bycanistes subcylindricus subquadratus* Cabanis

One male, testes small; Mwela; December 14.

## FAMILY CAPITONIDAE

*Pogoniulus scolopaceus aloysii* (Salvadori)

Thirteen examples, one with large, the rest with small, gonads; November 25 to December 16.

*Pogoniulus subsulphureus flavimentum* Verreaux

Nine specimens, four with large, five with small, gonads; November 26 to December 9.

## FAMILY INDICATORIDAE

\**Indicator variegatus* Lesson

Two males, one with large testes; December 18.

*Indicator minor riggenbachi* Zedlitz

Three male specimens, two with large testes; December 14, 17 and 18.

*Prodotiscus insignis insignis* Cassin

Four specimens, two with large and two with small gonads; November 28 to December 10.

## FAMILY HIRUNDINIDAE

*\*Hirundo rustica rustica* Linnaeus

Five examples; December 10 and 11.

## FAMILY MOTACILLIDAE

*\*Motacilla flava* Linnaeus

One specimen; December 15.

*\*Motacilla clara chapini* Amadon

One female, ovary small; December 8.

## FAMILY PYCNONOTIDAE

*Phyllastrephus xavieri xavieri* Oustalet

Two examples, non-breeding; November 29.

## FAMILY TURDIDAE

*Neocossyphus poensis praepectoralis* Jackson

Four examples, non-breeding condition; November 27 to December 12.

## FAMILY MUSCICAPIDAE

*Muscicapa caerulescens brevicauda* Ogilvie-Grant

Two specimens, non-breeding; December 3 and 4.

*Melaenornis edolioides lugubris* Hartlaub

One male, small testes; December 9.

## FAMILY SYLVIIDAE

*\*Phylloscopus trochilus* Linnaeus

Two examples; December 1 and 17.

*Camaroptera brachyura tincta* Cassin

Six specimens, all in non-breeding state; November 25 to December 16.

*Eremomela badiceps badiceps* Fraser

Nine specimens, two with large, seven with small, gonads; November 28 to December 15.

*Sylvietta virens baraka* Sharpe

Nine specimens, none in breeding state; December 4 to 16.

## FAMILY PARIDAE

*Parus funereus funereus* Verreaux

Two specimens, non-breeding; December 1.

## FAMILY STURNIDAE

*Onychognathus fulgidus harilaubi* Gray

One male, testes slightly enlarged; December 7.

## FAMILY ZOSTEROPIDAE

\**Zosterops senegalensis stuhlmanni* Reichenow

One, non-breeding; December 15.

## FAMILY NECTARINIIDAE

*Anthreptes rectirostris tephrolaema* Jardine and Frazer

Fifteen specimens, five with large, the rest with small, gonads; November 26 to December 14.

*Nectarinia seimundi traylori* Wolters

Five specimens, two with enlarged gonads; December 1 to 17.

*Nectarinia olivacea ragazzii* (Salvadori)

Ten examples, five with large, five with small, gonads; November 25 to December 13.

*Nectarinia rubescens rubescens* (Vieillot)

Three specimens, one with swollen gonads; December 5, 8 and 9.

## FAMILY PLOCEIDAE

\**Quelea erythrops* (Hartlaub)

One male, non-breeding; December 16.

## FAMILY ESTRILDIDAE

*Clytospiza montieri* (Hartlaub)

One male with large testes, one female with small ovary; December 14.

*Nigrita fusconota fusconota* Fraser

Eleven examples, four with enlarged gonads, the rest with small ones; November 27 to December 17.

\**Lonchura bicolor poensis* (Fraser)

Seven specimens, all in non-breeding state; December 5 to 16.

## KIBALE FOREST

The Kibale Forest is considerably higher than the Bugoma, averaging about 6000 feet in elevation. It lies some 35 miles to the south of Fort Portal, Toro Province, and extends from 0° 2' N to 0° 40' N, and from 30° 19' E to 30° 32' E. In the older literature, as well as in some recent papers, it appears under the name Mpanga Forest.

In the senior author's account of the Knudsen-Machris 1963 Expedition (Friedmann, 1966: 7-11) a complete list was given of all the birds collected in the Kibale by that group as well as those reported previously by Ogilvie-Grant (1910) in his report of the British Museum's Ruwenzori expedition of 1905-1906 and by Jackson and Sclater (1938), as well as a few other species mentioned by van Someren (1922) and by Chapin (1932 to 1954). In all, these sources yielded a total of 113 species of birds, including a few that are not forest dwelling forms. The survey of the Kibale Forest made for the Los Angeles County Museum of Natural History in November and December, 1966, by A. L. Archer, R. Glen and A. Williams, resulted in a collection of 939 specimens of 185 species, of which 91, or almost half, are additional to the 113 kinds reported earlier. This great increase is a reflection on the fragmentary state of previous knowledge of the avifauna which obviously was even more superficial and incomplete than was thought at the time our field party began its work in that forest. Of the 91 species here added to the Kibale fauna, about half are not birds of the forest itself, but must have been collected immediately outside its limits. Even discounting these, which are marked with asterisks, the increase in the number of sylvan species is so large as to suggest that the present list is now probably fairly close to an adequate faunal summary.

## FAMILY CICONIIDAE

\**Ciconia abdimii* Lichtenstein

One male, testes small; November 4.

## FAMILY ACCIPITRIDAE

\**Circaetus cinerascens* (Müller)

One male, non-breeding state; December 10.

\**Accipiter tachiro sparsimfasciatus* (Reichenow)

One male, testes slightly enlarged; December 14.

*Buteo rufofuscus augur* (Rüppell)

One male, nonbreeding condition; December 9.

*Lophoetus occipitalis* (Daudin)

One female, ovary small; November 12.

*Stephanoaetus coronatus* (Linnaeus)

One female, ovary much enlarged; December 8.

*Hieraaetus dubius* Smith

One male, testes small; December 4.

\**Pernis apivorus apivorus* (Linnaeus)

One female; November 4.

\**Elanus caeruleus caeruleus* (Desfontaines)

One male, testes small; December 10.

## FAMILY FALCONIDAE

\**Falco tinnunculus rufescens* (Swainson)

One female, ovary small; December 3.

## FAMILY NUMIDIDAE

*Guttera edouardi sethsmithi* Neumann

Four downy chicks; November 27.

## FAMILY RALLIDAE

*Sarothrura elegans* (A. Smith)

One immature female; December 8.

## FAMILY SCOLOPACIDAE

\**Tringa ochropus* Linnaeus

Four females; November 12 to 25.

\**Tringa hypoleucos* Linnaeus

One male; December 5.

## FAMILY COLUMBIDAE

*Columba arquatrix arquatrix* Temminck and Knip

Three examples, gonads somewhat enlarged in two; November 4 to 11.

*Columba albinucha* Sassi

One male, testes slightly enlarged; November 13.

\**Streptopelia semitorquata* (Rüppell)

Three females, all with small ovaries; November 4, 5 and 12.

\**Turtur tympanistria* (Temminck and Knip)

Six specimens, gonads small or slightly enlarged; November 5 to December 6.

*Treron australis gibberifrons* (Madarasz)

One male, testes small; December 7.

## FAMILY PSITTACIDAE

*Psittacus erithacus erithacus* Linnaeus

One male with testes considerably enlarged; November 7; one female, ovary small; November 19.

## FAMILY MUSOPHAGIDAE

*Tauraco schutti emini* (Reichenow)

Seven examples, with gonads slightly enlarged in one, small in the others, one of which is a chick; November 7 to December 5.

## FAMILY CUCULIDAE

*\*Centropus superciliosus loandae* Grant

One female, ovary large; November 17.

## FAMILY STRIGIDAE

*Glaucidium tephronotum medje* Chapin

Two males, testes small; November 29 and December 10.

## FAMILY CAPRIMULGIDAE

*\*Caprimulgus pectoralis nigriscapularis* Reichenow

One male, testes small; November 29.

## FAMILY APODIDAE

*\*Chaetura sabini* Gray

One unsexed example; November 7.

*\*Chaetura ussheri sharpei* Neumann

Four specimens, all non-breeding state; November 6 and 7.

## FAMILY ALCEDINIDAE

*\*Ceryle maxima* (Pallas)

Two specimens, a male with small testes; November 27; a female with a large ovary; December 14.

*Alcedo quadribrachys guentheri* Sharpe

Three examples, all in non-breeding condition; November 19 to December 7.

*Halcyon malimbica malimbica* (Shaw)

Three specimens, the gonads slightly enlarged in one and small in the other two; November 4 to 22.

## FAMILY MEROPIDAE

*\*Merops albicollis* Vieillot

Three specimens, all in non-breeding condition; November 22 and 23.

*Merops gularis australis* (Reichenow)

Four specimens, gonads slightly enlarged in one, small in the others; November 28 to December 12.

## FAMILY CAPITONIDAE

*Lybius hirsutus ansorgei* (Shelley)

Seven specimens, one with large gonads, the others small; November 5 to December 13.

*Buccanodon duchaillui duchaillui* (Cassin)

Seven specimens, all in non-breeding state; November 29 to December 10.

*Pogoniulus bilineatus mfumbiri* (Ogilvie-Grant)

Fourteen examples, mostly with small gonads, three with large ones; November 4 to 10.

## FAMILY INDICATORIDAE

*Indicator conirostris conirostris* (Cassin)

Two adult females, one with a large, the other a small, ovary, and one young male; November 11, 12 and 20.

*Indicator exilis pachyrhynchus* (Heuglin)

Six examples, two with large, the others with small, gonads; November 13 to December 8.

*Indicator willcocksii willcocksii* Alexander

Five specimens, all with small gonads; November 10 to December 11.

## FAMILY PICIDAE

*Campethera caroli* (Malherbe)

Seven examples, all in non-breeding state; November 5 to December 12.

*Mesopicos xantholophus* (Hargitt)

Three female specimens, one with the ovary large, the others small; November 5 to December 8.

## FAMILY HIRUNDINIDAE

*\*Riparia riparia riparia* (Linnaeus)

Six examples, all in non-breeding state; November 8 to December 3.

*\*Hirundo rustica rustica* Linnaeus

Four specimens, gonads small; November 17, 18 and December 7.

\**Hirundo angolensis* Bocage

Three specimens, all in non-breeding state; November 17 and December 3.

\**Hirundo senegalensis saturator* Bannerman

One male, testes small; November 27.

\**Hirundo griseopyga griseopyga* Sundevall

Five specimens, gonads small; November 24.

\**Psalidoprocne albiceps albiceps* Sclater

Four examples, gonads small; November 14.

## FAMILY MOTACILLIDAE

\**Motacilla cinerea cinerea* Tunstall

Two specimens, gonads small; November 12.

\**Motacilla alba vidua* Sundevall

One male, testes not enlarged; November 17.

\**Anthus trivialis trivialis* Linnaeus

Seven examples, all in non-breeding state (Eurasian migrants); November 19 to December 10.

## FAMILY TIMALIIDAE

*Malacocincla albipectus* (Reichenow)

Three specimens, gonads small in each; November 7, December 8 and 12.

## FAMILY PYCNONOTIDAE

*Phyllastrephus fischeri sucosus* Reichenow

Six examples, gonads small to somewhat enlarged; November 5 and 6, December 6.

## FAMILY TURDIDAE

\**Saxicola rubetra* Linnaeus

One female, ovary small; December 9.

\**Saxicola torquata axillaris* (Shelley)

One male, testes small; December 7.

\**Cercotrichas hartlaubi* (Reichenow)

One male, testes slightly enlarged; November 18.

*Cossypha polioptera polioptera* Reichenow

One female, ovary small; November 5.

*Zoothera camaronensis prigoginei* Hall

Two males, non-breeding state; December 12.

## FAMILY MUSCICAPIDAE

*Muscicapa cassini* Heine

Four males, all in non-breeding condition; November 17, 19, 20 and 22.

*Muscicapa caerulescens brevicauda* Ogilvie-Grant

Six specimens, gonads slightly enlarged in one, small in the others; November 6 to December 12.

*Muscicapa griseigularis* (Jackson)

Four examples, all with small gonads; November 6 to December 7.

*Bias musica musica* (Vieillot)

Four specimens, all with small gonads; November 8 and December 4.

*Trochocercus albiventris* Sjostedt

Two specimens, in non-breeding state; November 11 and 27.

*Terpsiphone rufiventer somereni* Chapin

Fifteen examples, one with large gonads, three with gonads somewhat enlarged, the rest with small ones; November 10 to December 13.

## FAMILY SYLVIIDAE

*\*Sylvia borin* (Boddaert)

Two specimens, gonads small; November 5 and 9.

*\*Cisticola hunteri chubbi* Sharpe

Four males, all in non-breeding state; November 13 to December 12.

*\*Cisticola galactotes amphilecta* Reichenow

Three specimens, gonads small; November 17, 21 and 25.

*\*Cisticola natalensis strangei* (Fraser)

Two specimens, gonads small; November 17 and 20.

*Sylvietta virens baraka* Sharpe

One female, ovary small; November 19.

## FAMILY LANIIDAE

*Malaconotus bocagei jacksoni* (Sharpe)

One female, ovary small; November 23.

\**Lanius mackinnoni* Sharpe

One female, ovary small; November 12.

\**Lanius collurio phoenicuroides* (Schalow)

Three examples, gonads small; November 19, 22 and 24.

## FAMILY STURNIDAE

*Poeyoptera lugubris webbi* Keith

Fourteen specimens, gonads small in all; November 3 to December 11. This subspecies is a poorly marked race, but, if recognized, will be the local race.

*Onychognathus walleri elgonensis* (Sharpe)

One male, testes small; November 7.

*Onychognathus fulgidus hartlaubii* Gray

Two specimens, gonads small; November 11 and 22.

\**Cinnyricinclus leucogaster leucogaster* (Gmelin)

One male; November 11.

## FAMILY NECTARINIIDAE

*Nectarinia rubescens rubescens* Vieillot

One male, testes small; November 5.

*Nectarinia chloropygia orphogaster* (Reichenow)

Seven specimens, all in non-breeding condition; November 18 to 22.

*Nectarinia cuprea cuprea* (Shaw)

One male, testes small; November 27.

## FAMILY PLOCEIDAE

*Ploceus nigricollis nigricollis* (Vieillot)

Ten examples, one with large, the rest with small gonads; November 18 to December 6.

*Ploceus pelzelni pelzelni* (Hartlaub)

Two specimens, gonads small; December 3.

*Ploceus melanocephalus capitalis* (Latham)

Three males, gonads small or slightly enlarged; November 17.

*Ploceus superciliosus* (Shelley)

Two females, ovary small; November 27.

*Quelea cardinalis cardinalis* (Hartlaub)

Eight specimens, all in non-breeding state; November 18, 21 and 23.

\**Euplectes gierowii ansorgei* (Hartert)

One male, testes small; November 25.

\**Euplectes axillaris phoeniceus* (Heuglin)

One male, testes small; December 9.

\**Euplectes capensis crassirostris* (Ogilvie-Grant)

One female, ovary large; November 18.

## FAMILY ESTRILDIDAE

*Cryptospiza reichenovii australis* Shelley

Six examples, all with small gonads; November 7 to 13.

*Pirenestes ostrinus ostrinus* (Vieillot)

Seven specimens, one with large gonads, the others with small; November 18 to 24.

\**Estrilda paludicola roseicrissa* Reichenow

Four specimens, all with small gonads; November 17 and 20.

*Estrilda nonnula nonnula* Hartlaub

Six specimens, all with small gonads; November 11 to 22.

*Estrilda astrild peasei* Shelley

Seven examples, all in non-breeding state; November 17.

*Lagonosticta rubricata congica* Sharpe

Two specimens, gonads small or slightly enlarged; November 24.

\**Lonchura cucullata cucullata* (Swainson)

One male, gonads small; November 17.

## IMPENETRABLE FOREST

As stated in the introductory portion of this paper the Museum received a second, very extensive collection of birds from the Impenetrable Forest at a time when it was too late to include the new data in the joint report by Keith et al. (1969) on that area.

Besides containing additional examples of many rarities (*Pseudocalyptomena*, *Hemitesia*, *Graueria*, *Parmoptila*, etc.), the new collection, comprising over 1300 specimens in all, included a significant number of species additional to those included in the report or that were listed in it without the firm basis of actual specimen records. There is no need to publish an annotated

catalog of this new collection as it largely duplicates the first one, made in 1967, under National Science Foundation Grant GB-5107, and it seems sufficient to note here merely the birds not previously recorded from the area, plus brief mention of a few of the rarities on which the new information adds to the data in the previous literature. The 1969 summary report by Keith et al. was based on Twomey's sizeable 1960 collection, now in the Carnegie Museum, Pittsburgh, on Keith's smaller 1962 material and observations, on J. G. Williams' notes and on the large collection made in 1967 by A. L. Archer and A. Williams for the Los Angeles County Museum of Natural History.

The combined report listed 265 kinds of birds; to these the present paper adds 19 more as well as supplying specimen records for six species included in the earlier paper on the basis of sight records only.

#### FAMILY PHASIANIDAE

##### *Fringillus nobilis* Reichenow

Listed in the 1969 report on the basis of sight records only by Keith. We now have five specimens taken in the Bwindi and Rohizha areas, between 7000 to 7500 feet, May 13 to June 11. In the van Somerens' Bwamba report (1949: 22) this francolin was listed on sight and sound records only. Our present examples appear to be the first actual specimen records from within the political boundaries of Uganda. We have had no specimens from elsewhere in the range of the species to compare with our Impenetrable Forest birds and cannot, therefore, comment on the validity of the supposed Ruwenzori race *F. n. chapini*. We note that Hall (1963: 134) found the width of the grayish edges on the chestnut feathers of the breast and upper abdomen to vary individually, although the limited Ruwenzori material available to her had these edges consistently narrow. In our birds there is enough variation to cause us to doubt the advisability of recognizing a race based on this character. More posteriorly the variation is even more marked on the abdominal feathers. One of our adult males has the middle of the abdomen much more grayish than the other; two females show the same difference between them.

##### *Fringillus squamatus schuetti* Cabanis

One specimen, 7600 feet; Rohizha area; May 25.

##### *Coturnix chinensis adansonii* Verreaux

One specimen, 5300 feet; Itama area; July 11.

#### FAMILY RALLIDAE

##### *Sarothrura pulchra centralis* Neumann

One specimen, 5300 feet; Itama area; June 25. Stuart Keith (personal communication) January 23, 1970) informed me that he recently realized

that he actually had the voice of this rail in the background of a tape recording of *Sylvietta virens* that he made in the Impenetrable Forest in 1962. Regardless of whether such a tape recorded sound might be accepted as a basis for adding a species to the known avifauna of a locality, we do now have an unquestionable specimen record of the white-spotted crane.

FAMILY COLUMBIDAE

*Aplopelia larvata jacksoni* Sharpe

Five specimens, 5300 to 7000 feet; Itama, Rohizha and Bwindi areas; May 24 to June 25.

*Columba malherbii iriditorques* (Cassin)

One specimen, 5300 feet; Itama area; June 18. The identification of this specimen was kindly checked for us by Mr. M. A. Traylor of the Field Museum, as no examples were immediately available for comparison in Los Angeles. This is the first specimen record for Uganda. Keith (1968: 5) attempted to identify as *iriditorques* a call on a tape recording he made in Bwamba under the assumption that it was *Columba delegorguei*, which he later found does not occur there.

FAMILY CUCULIDAE

*Cercococcyx mechowii* Cabanis

Seven specimens, 5300 feet; Itama area; May 22 to July 7. Previously listed from the Impenetrable Forest by Keith et al. (1969: 12) on the basis of sight records only, made at 3500 and 5000 feet.

FAMILY STRIGIDAE

*Ciccaba woodfordi nuchalis* Sharpe

Two specimens, 5300 and 7500 feet; Itama and Ruhizha areas; June 5 and 21. Listed by Keith et al. (1969: 12) binomially on sight records only, at 3500 to 7000 feet.

FAMILY APODIDAE

*Apus myoptilus chapini* Prigogine

One specimen, 5300 feet; Itama area; July 16. Listed by Keith et al. (1969: 12) on sight records only at 5000 feet.

FAMILY ALCEDINIDAE

*Halcyon leucocephala leucocephala* (Müller)

One specimen, 5300 feet; Itama area; July 11. Listed binomially on sight records only by Keith et al. (1969: 12).

FAMILY CORACIIDAE

*Eurystomus gularis neglectus* Neumann

One specimen, 5300 feet; Itama area; July 1.

## FAMILY INDICATORIDAE

*Indicator minor riggenbachi* Zedlitz

Two specimens, 7500 feet; Ruhizha area; May 30, June 6. In their 1969 paper on the Impenetrable Forest avifauna, Keith et al. (1969: 14) listed, on the basis of a sight record only, *Indicator conirostris* from 3500 feet. We doubt if this can be considered a valid observation as *conirostris* and *riggenbachi* are very similar in appearance. There is, however, no reason why both of these birds may not occur there.

*Indicator pumilio* Chapin

One specimen, 7000 feet; lower bamboo zone; June 12. This diminutive honey guide was listed by Keith et al. (1969: 14) from 5000 feet. However Friedmann and Williams had earlier (1968: 18) reported one from 8000 feet in the Impenetrable Forest, a record that was overlooked by Keith, although the paper is listed in his bibliography.

## FAMILY EURYLAEMIDAE

*Pseudocalyptomena graueri* Rothschild

Five specimens, 6800 to 7000 feet; Bwindi and Ruhizha areas; May 4 to June 1. These specimens have been discussed in detail elsewhere (Friedmann, 1970).

## FAMILY MOTACILLIDAE

*Anthus novaeseelandiae cinnamomeus* Ruppell

Two specimens, 6800 to 7500 feet; Ruhizha area; May 16 to 20. This pipit is, of course, not a forest bird but was taken in the adjacent open country.

## FAMILY TIMALIIDAE

*Turdoides jardinei emini* Neumann

Two specimens, 6800 to 7500 feet; Ruhizha area; May 22, June 4. This babbler is not a forest species, and must have been collected just outside the limits of the true woodlands.

## FAMILY MUSCICAPIDAE

*Muscicapa cassini* Heine

One specimen, 5200 feet; Ihihizu River; June 15. It is somewhat unexpected to find this flycatcher at this elevation, as it is otherwise known only as a lowland bird.

## FAMILY TURDIDAE

*Saxicola torquata axillaris* Shelley

Two specimens, 6800 to 7500 feet; Ruhizha area; May 12, June 4. Listed by Keith et al. (1969: 16) on sight records only, at 7000 feet. This

stonechat does not occur in the dense forest, but in the fairly dense bush country just outside it.

*Cossypha cyanocampter bartteloti* Shelley

Two specimens, 5300 feet; Itama area; June 27. A bird of the dense, second growth thickets rather than the deep forest, this robinchat probably does not occur much above the elevation of Itama.

FAMILY SYLVIIDAE

*Bradypterus graueri* Neumann

Nine specimens, 6750 to 6800 feet; Bwindi and Ruhizha areas; May 15 to 27. In the latter area the collectors noted that they found Grauer's warbler in a swamp that was not only very isolated but that was also extremely small in comparison to the one at Bwindi, where the species was collected in 1967 as well as in 1969. In their field notes they suggested that the birds probably locate these widely separated microhabitats by following the hidden streams, largely concealed by dense overhanging forest undergrowth, until they come to these small, more open, swampy areas. All of our specimens are adults; none show the darker, less white, underparts, recently described in the juvenile plumage of the subspecies *B. g. carpalis* by Britton (1970: 26-27).

*Bradypterus barratti barakae* Sharpe

Twelve specimens, 6750 to 7000 feet; Bwindi and Ruhizha areas; May 12 to June 11. A single example was collected in the 1967 survey (Friedmann and Williams, 1968: 29), which was the first actual specimen record from Uganda.

*Chloropeta natalensis massaica* Fischer and Reichenow

One specimen, 5300 feet; Itama area; June 16.

*Hemitesia neumanni* (Rothschild)

Seven additional specimens, 5300 to 6800 feet; Itama and Ruhizha areas; May 24 to July 4.

*Camaropectera chloronota toroensis* Jackson

One specimen, 5300 feet; Itama area; June 15.

*Graueria vittata* Hartert

Nine additional specimens, 6750 to 6800 feet; Bwindi and Ruhizha areas; May 10 to July 6.

*Cisticola carruthersi* Ogilvie-Grant

Four specimens, 6750 to 7000 feet; Bwindi swamp area; May 22 to 27. Inasmuch as all previous accounts of this grass warbler described it as inhabiting lower elevations (one record from as high as 6100 feet at Lake Mutanda) and as being a denizen of papyrus swamps, not of grass or reed growths, such as at Bwindi, these specimens were sent to Stuart Keith for comparison with the material in the American Museum of Natural History. He agreed with

our identification, but noted that the elevation and vegetational habitat were unusual. He also pointed out that one of the specimens was in the juvenile stage recently described by Britton (1970: 26-27) but even younger, as it has not grown its rectrices. Our present specimen has the chin, throat and breast pale buffy yellowish; the abdomen white tinged with pale tawny russet on the lower sides and flanks; the top of the head dull, fairly light brown without the rufous color present in the adult; the mantle and back similar with the dusky median portions of the feathers much smaller, narrower and paler, less blackish, more fuscous, than in the adults; bill horn-brown, becoming yellowish on the mandible and at the gape; iris dark brown; feet flesh-gray.

FAMILY LANIIDAE

*Lanius collaris capelli* (Bocage)

Two specimens, 6800 to 7000 feet; Ruhizha area; May 25 and June 4.

FAMILY PLOCEIDAE

*Ploceus xanthops* (Hartlaub)

Two specimens, 6800 to 7500 feet; Ruhizha area; May 11, June 4. This golden-headed weaver is a bird of the tree and bush dotted open grasslands outside the true forest. Chapin (1954: 348) noted it up to elevations of 6500 feet in the Kivu district, eastern Congo. Our specimens extend the range elevationally by another thousand feet.

*Euplectes capensis crassirostris* Ogilvie-Grant

Two specimens, 6800 to 7500 feet; Ruhizha area; May 18, June 4. Chapin (1954: 429) reported this species only up to 6000 feet in the Lendu plateau; our present examples extend the known range to 7500 feet.

FAMILY ESTRILDIDAE

*Euschistopiza cinereovinacea graueri* Rothschild

One specimen, 7500 feet; Ruhizha area; May 15. Listed by Keith et al. (1969: 21) from a specimen record at 6000 feet. The present example is mentioned here only because it is a species rarely collected. As pointed out by Chapin (1954: 479), J. C. Phillips collected two of these birds at Lake Chahafi, in the Kigezi District, near the Impenetrable Forest. This is a grassland, not a forest bird, the elevational range of which is now extended upwards by 1000 feet over Chapin's figure.

FAMILY FRINGILLIDAE

*Serinus citrinelloides frontalis* Reichenow

One specimen, 6800 feet; Ruhizha area; June 4. Listed by Keith et al. (1969: 40) in the hypothetical list of Impenetrable Forest birds. This is a bird of the open grasslands, not of the forest.

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# CONTRIBUTIONS IN SCIENCE

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FISH REMAINS, MOSTLY OTOLITHS AND TEETH, FROM  
THE PALOS VERDES SAND (LATE PLEISTOCENE) OF CALIFORNIA

By JOHN E. FITCH



LOS ANGELES COUNTY MUSEUM OF NATURAL HISTORY • EXPOSITION PARK  
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# FISH REMAINS, MOSTLY OTOLITHS AND TEETH, FROM THE PALOS VERDES SAND (LATE PLEISTOCENE) OF CALIFORNIA

By JOHN E. FITCH<sup>1</sup>

**ABSTRACT:** Eleven exposures of Palos Verdes Sand in southern California and an exposure in northern California believed to be equivalent to Palos Verdes Sand yielded nearly 2,000 otoliths, several hundred teeth and an assortment of other fish remains. These represented 18 kinds of sharks, skates and rays and 84 teleosts. In the southern Californian deposits, one shark and 10 teleosts were southern species, whereas the deposit in northern California contained remains of five teleosts that could be considered southern species at that latitude. Four of the 84 teleosts were mesopelagics but all of the others were typical inhabitants of the continental shelf, with most preferring non-rocky habitat and relatively shallow depths. Based upon the presence of six locally extinct southern species and an analysis of habitat and depth limitations of the 102 species comprising the "Palos Verdes Sand" fish fauna, these deposits were laid down during a lengthy period when ocean temperatures were considerably warmer than they are at present. Deposition occurred in sandy or sandy-mud bottom areas at depths no shallower than 10 fathoms nor deeper than 20.

The first report of fish remains from the Palos Verdes Sand is that of Arnold (1903) who noted two stings from "*Urolophus halleri*?" found in a deposit near San Pedro, California. Jordan and Hannibal (1923) quoted Arnold's record in their publication on fossil sharks and rays of the Pacific slope but did not add any others. In 1956, Kanakoff listed 28 species (13 kinds of sharks and rays plus 15 of bony fishes) from five southern Californian exposures of Palos Verdes Sand (Los Angeles County Museum, Invertebrate Paleontology sites [LACMIP] 59, 66-2, 68B, 77 and 131). He reported LACMIP 131 (in the 500 block, North Pacific Avenue, San Pedro) as being "Lower Pleistocene San Pedro sand" but the exposure at this locality is unquestionably Late Pleistocene Palos Verdes Sand.

Two publications by Fitch (1964, 1966) on a site at Playa del Rey (LACMIP 59) listed 62 species (14 elasmobranchs and 48 teleosts), and brought to 66 (17 elasmobranchs and 49 teleosts) the kinds of fishes known from the Palos Verdes Sand of southern California.

Subsequent to 1964, I have examined six additional exposures of Palos Verdes Sand in southern California (four near San Pedro and two on the mesa south of Upper Newport Bay), and one outcrop north of Arcata (Cranell Road) in northern California that appears to be an equivalent of Palos Verdes Sand. Two of the San Pedro localities and the Cranell Road deposit

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were sampled extensively in that several hundred pounds of fossiliferous matrix were collected, sieved under water and sorted from each, but only small quantities of material were examined from the other four sites. In all, these samples yielded nearly 2000 otoliths, several hundred teeth, and an assortment of vertebrae, caudal stings, fin spines, gill rakers, bucklers and miscellaneous bony fragments (Tables 1 and 2). A few additional fish remains, turned over to me by George P. Kanakoff, then curator of Invertebrate Paleontology, Los Angeles County Museum of Natural History, have been included in this account, and otoliths and teeth collected by Lloyd Barker and Roy Kohl at the Crannell Road site are mentioned in the species accounts. All of the material, except that in the Kohl and Barker collections, has been deposited at Los Angeles County Museum of Natural History.

Fanale and Schaeffer (1965), utilizing helium-uranium and ionium radiometric ratios and measurements, estimated the age of the youngest marine terrace at San Pedro (corresponding to Palos Verdes Sand) as 95,000 to 130,000 years before the present (B.P.). Valentine (1961) reported that the habitat, at the time and place of deposition, ranged from fine silty sand to coarse sand and gravel depending upon the locality and exposure to the open coast. Probable depth of deposition also varied depending upon locality, but none of the several deposits examined during my studies appears to have been laid down at depths greater than about 10 to 12 fathoms. Judged solely by the fish remains (Fitch 1964, 1966), deposits of Palos Verdes Sand represent a lengthy period when the ocean off southern California was considerably warmer than it has been at any time since temperature records were first kept (Fitch, 1969b). Many of the mollusks reported from these beds are locally extinct southern forms, and six of the fishes have not been seen much north of Magdalena Bay during modern times, while three others rarely have been reported from California even during several years of warmer than average ocean temperatures (Radovich, 1961).

#### SOUTHERN CALIFORNIA SITES

##### Playa del Rey Area

##### Lincoln Ave. (LACMIP 59)

Many tons of fossiliferous matrix from this site were examined by personnel from the Los Angeles County Museum of Natural History during a span of about three decades, and 1,409 otoliths, 276 teeth and numerous other fish remains were found in this material (Fitch, 1964, and Table 2). Because these items had been gleaned by an assortment of student volunteers who were looking primarily for mollusks, and since the work had been done without the aid of a microscope, I resampled the site in 1965 and removed a 200-pound field sample. Using microtechniques on the washed screenings from this field sample, I obtained an additional 1,174 identifiable teleost otoliths, and 58 teeth from 11 kinds of sharks, skates and rays (Fitch, 1966,

and Table 2). Unfortunately, three fish species in my earlier accounts of LACMIP 59 were misidentified. In my first report (Fitch, 1964), some of the otoliths I called *Phanerodon furcatus* should have been *Xenistius californiensis*, and others were *Trachurus symmetricus*; also, the sagitta listed as *Sebastes aurora* should have been *Prionotus stephanophrys*. In my later account (Fitch, 1966), *Occa verrucosa* should have been noted as *Synodus lucioceps*.

### San Pedro Area

#### Incinerator site

This locality was exposed when sand and gravel were excavated during and following construction of the Harbor Freeway to the northern limits of San Pedro. It is called the "Oyster Reef" by various college geology instructors who take field trips to the area. It covers about 100 acres, being bounded on four sides by the Union Oil Co. refinery (north), Harbor Freeway (east), the city incinerator (south), and Gaffey Street (west). A 50-pound field sample from this site yielded 36 otoliths from seven kinds of teleosts, and identifiable jaw teeth from five species of elasmobranchs and one teleost. In addition there were elasmobranch vertebrae (2) and dermal denticles (2), as well as teleost teeth (4), vertebrae (23) and fin spines (3). The 13 identified species, based upon otoliths (o), caudal stings (s) and teeth (t) from this site were:

<i>Citharichthys stigmaeus</i>	(8o)
<i>Cymatogaster aggregata</i>	(2o)
<i>Dasyatis dipterurus</i>	(1t)
<i>Galeorhinus zyopterus</i>	(1t)
<i>Genyonemus lineatus</i>	(7o)
<i>Lepidogobius lepidus</i>	(2o)
<i>Myliobatis californicus</i>	(1s, 7t)
<i>Pimelometopon pulchrum</i>	(1t)
<i>Porichthys myriaster</i>	(9o)
<i>Porichthys notatus</i>	(1o)
<i>Raja</i> spp.	(3t)
<i>Seriphus politus</i>	(7o)
<i>Squatina californica</i>	(2t)

#### Sun Lumber Co.

This exposure was excavated extensively during freeway construction and development of docking facilities throughout the Los Angeles-Long Beach harbor area. The site is bounded by the Union Oil Co. refinery (north), San Pedro-Wilmington Road (east and south) and the Harbor Freeway (west). It is about one-half mile east of the incinerator site, but fish remains have not been nearly so plentiful. Only two species were identified from four otoliths and a pharyngeal tooth found in a 50-pound field sample. One of the otoliths

was from *Porichthys notatus*, but the other three were too eroded to identify except as "embiotocids." The tooth was from *Rhacochilus vacca*, an embiotocid with massive, distinctive pharyngeal dentition. In addition, the 50-pound field sample contained 14 teleost vertebrae, one teleost fin spine and one rodent tooth.

Subsequent sampling in other exposures of this bed yielded otoliths of *Genyonemus lineatus* (4), *Lepophidium negropinna* (1) and *Seriphus politus* (1).

North Pacific Ave., 500 block (LACMIP 131)

Kanakoff (1956) listed three species of elasmobranchs and three of teleosts from this site, based upon teeth, stings and otoliths found while searching for mollusks over the several year period the outcrop was exposed. The only part of this bed remaining in 1969 was on private property and excavating was prohibited because of damage to the area by cave-ins. During the years the site could still be sampled, I removed several hundred pounds of fossiliferous matrix (mostly material that people had discarded while searching for mollusks) and processed this for fish remains. I found remains of the same three elasmobranchs that Kanakoff (1956) reported for this deposit (plus those of 10 others) and the three teleosts he noted. My sampling at this locality brought to 12 the number of identified sharks, skates and rays, and the list of teleosts now numbers 32 (Tables 1 and 2).

North Pacific Ave., 700 block [= V.T. Bridge site]

During construction of the western approach for the Vincent Thomas Bridge, the hill (terrace) on the east side of the street in the 700 block North Pacific Avenue was cut down and hauled away. For several days during these earth-moving activities, beds of shelly matrix were exposed and I removed about 500 pounds of this material to search for fish remains. Although these strata were only two short blocks (possibly 1,000 feet) north of LACMIP 131, the fish faunas at the two sites were not entirely complementary. In all, I recovered teeth and stings from 12 kinds of sharks, skates, and rays, and otoliths and teeth from 21 kinds of teleosts (Tables 1 and 2).

#### Newport Beach Area

Numerous outcrops near the top of the mesa that lies south of Upper Newport Bay were sampled by personnel from the Los Angeles County Museum of Natural History during two decades or more, and the fish remains from two of these were listed by Kanakoff in 1956. Subsequent to 1956, George Kanakoff sent additional fish remains to me that had been gleaned from exposures of Palos Verdes Sand in the Newport mesa, and I sampled several other outcrops that were uncovered during construction for housing projects and a shopping center. Fish remains were meager in all of these exposures, but since most of the fossiliferous Palos Verdes Sand in the Newport Beach area has been covered up, hauled away or otherwise rendered

TABLE 1  
Elasmobranch remains from the Palos Verdes Sand of California  
(all remains are teeth unless otherwise noted)

Species	Playa del Rey area		San Pedro area			Newport Beach area		Cranell Road
	Fitch, 1964	Fitch, 1966	500 blk.	700 blk.	others	All localities		
<i>Alopias vulpinus</i>	2	1	—	—	—	—	—	—
<i>Carcharhinus</i> spp.	26	7	4	3	—	69	—	—
<i>Carcharodon carcharias</i>	6 + 4v	—	—	1	—	3	—	—
<i>Cetorhinus maximus</i>	—	—	—	1r	—	1 + 1r	—	—
<i>Dasyatis dipterurus</i>	—	2	—	6	1	1 + 1s	—	—
<i>Galeorhinus zyopterus</i>	15	1	3	3	1	3	—	1*
<i>Heterodontus francisci</i>	—	1	2	3	—	2	—	—
<i>Isurus oxyrinchus</i>	2	2	2	—	—	13	—	—
<i>Lamna ditropis</i>	—	—	1	—	—	—	—	—
<i>Myliobatis californicus</i>	205	32	193	15	7 + 1s	1 + 1s	—	—
<i>Notorynchus maculatus</i>	4	—	—	1	—	—	—	—
<i>Prionace glauca</i>	—	—	1	—	—	1	—	—
<i>Raja</i> spp.	8v + 3d	4d	5 + 3d	5 + 2d	3	—	—	114 + 11d
<i>Rhizoprionodon longurio</i>	1	—	—	—	—	—	—	—
<i>Sphyrna</i> spp.	3 + 17v	6	2	2	—	1	—	—
<i>Squatina californica</i>	10 + 8v	6	3	2 + 1d	2	—	—	—
<i>Triakis semifasciata</i>	—	—	3	1	—	1	—	—
<i>Urolophus halleri</i>	164s	5s	22s	20s	—	36s	—	—
Unidentified elasmobranchs	3	15v	4v	6v	2v + 2d	—	—	1v

d = dermal denticlaes; r = gill rakers; s = caudal sting; v = vertebrae \* in Lloyd Barker collection

TABLE 2  
 Teleost remains from the Palos Verdes Sand of California (all remains are otoliths unless otherwise noted)

Species	Playa del Rey area		San Pedro area			Newport Beach area	Crannell Road
	Fitch, 1964	Fitch, 1966	500 blk.	700 blk.	others	All localities	
<i>Allosmerus elongatus</i>	—	—	—	—	—	—	7
<i>Ammodytes hexapterus</i>	—	—	—	—	—	—	4
<i>Amhistichus koelzi</i>	—	—	—	1	—	—	—
<i>Amphistichus rhodoterus</i>	—	—	—	—	—	—	1
<i>Anarrhichthys ocellatus</i>	—	—	—	—	—	—	1t
<i>Anchoa compressa</i>	—	4	—	—	—	—	—
<i>Anisotremus davidsonii</i>	1	—	—	—	—	—	—
<i>Argentina sialis</i>	—	1	—	—	—	—	—
<i>Atheresthes stomias</i>	—	—	—	—	—	—	1t
atherinids	—	10	1	—	—	—	—
<i>Atherinops affinis</i>	1	—	—	1	—	—	—
<i>Atherinopsis californiensis</i>	3	1	2	—	—	—	—
<i>Bairdiella icistia</i>	—	—	1	—	—	—	—
<i>Calamus brachysomus</i>	—	—	1t	—	—	—	—
<i>Chitonotus pugetensis</i>	1	7	4	—	—	—	—
<i>Citharichthys sordidus</i>	29	7	4	6	—	—	10
<i>Citharichthys stigmæus</i>	238	181	42	30	8	—	5
<i>Citharichthys xanthostigma</i>	—	—	4	—	—	—	—
<i>Citharichthys</i> spp.	23	47	9	—	—	—	—
<i>Clupea pallasi</i>	—	—	—	—	—	—	4



TABLE 2 (cont'd.)  
 Teleost remains from the Palos Verdes Sand of California (all remains are otoliths unless otherwise noted)

Species	Playa del Rey area		San Pedro area			Newport Beach area	Crannell Road
	Fitch, 1964	Fitch, 1966	500 blk.	700 blk.	others	All	
						localities	
<i>Menticirrhus undulatus</i>	1	5	1	—	—	—	—
<i>Merluccius productus</i>	24	11	1	—	—	—	5
<i>Microgadus proximus</i>	—	—	—	—	—	—	411
<i>Micropogon ectenes</i>	2	—	—	1	—	—	—
<i>Microstomus pacificus</i>	—	—	—	—	—	—	2
<i>Oncorhynchus tshawytscha</i>	—	—	—	—	—	—	1
<i>Ophiodon elongatus</i>	—	—	—	—	—	—	11t
<i>Ophioscion cf. scierus</i>	—	—	1	—	—	—	—
<i>Otophidium scrippsi</i>	140	49	60	20	—	6	—
<i>Otophidium taylori</i>	83	65	24	12	—	1	—
<i>Otophidium</i> spp.	—	—	3	—	—	—	—
<i>Paralabrax</i> spp.	—	3	—	—	—	—	—
<i>Paralichthys californicus</i>	1	5	3	1	—	—	—
<i>Parophrys vetulus</i>	1	3	—	—	—	1	14
<i>Phanerodon furcatus</i>	—	—	—	—	—	—	3
<i>Pimelometopon pulchrum</i>	7t	—	—	1t	1t	19t	—
<i>Platichthys stellatus</i>	—	—	—	—	—	—	1* + 3s
<i>Pleuronichthys ritteri</i>	1	—	—	—	—	—	—
<i>Porichthys myriaster</i>	15	3	14	2	9	2	—
<i>Porichthys notatus</i>	161	278	46	14	2	—	1

TABLE 2 (cont'd)

<i>Porichthys</i> spp.	—	—	—	—	—	—	9	—	—	—	—	—	—
<i>Prionotus ruscarius</i>	—	—	—	—	—	—	1	—	—	—	—	—	—
<i>Prionotus stephanophrys</i>	1	—	2	—	—	—	1	—	—	—	—	—	—
<i>Rhacochilus vacca</i>	—	—	—	—	—	—	2	—	—	1t	—	—	2t
<i>Roncador stearnsi</i>	19	—	—	—	—	—	3	—	—	—	—	—	—
<i>Sebastes diploproa</i>	1	—	—	—	—	—	—	—	—	—	—	—	—
<i>Sebastes jordani</i>	1	—	—	—	—	—	—	—	—	—	—	—	—
<i>Sebastes paucispinis</i>	6	—	—	—	—	—	—	—	—	—	—	—	—
<i>Sebastes rhodochloris</i>	1	—	—	—	—	—	—	—	—	—	—	—	—
<i>Sebastes serranoides</i>	—	—	—	—	—	—	—	—	—	—	—	—	1*
<i>Sebastes</i> spp.	13	8	—	—	—	—	4	—	—	—	—	—	14
<i>Seriphus politus</i>	275	116	—	—	—	—	73	34	7	—	—	—	1
<i>Sphyræna argentea</i>	1	—	—	—	—	—	—	—	—	—	—	—	—
<i>Spirinchnus starksi</i>	—	—	—	—	—	—	—	—	—	—	—	—	124
<i>Spirinchnus thaleichthys</i>	—	—	—	—	—	—	—	—	—	—	—	—	5
<i>Stenobranchius leucopsarus</i>	—	—	1	—	—	—	—	—	—	—	—	—	—
<i>Symbolophorus californiensis</i>	—	—	1	—	—	—	1	—	—	—	—	—	1
<i>Symphurus atricauda</i>	—	—	13	—	—	—	2	—	—	—	—	—	—
<i>Synodus lucioceps</i>	—	—	1	—	—	—	—	—	—	—	—	—	—
<i>Theragra chalcogramma</i>	—	—	—	—	—	—	—	1	—	—	—	—	—
<i>Trachurus symmetricus</i>	2	3	—	—	—	—	—	—	—	—	—	—	—
<i>Umbrina roncadore</i>	13	4	—	—	—	—	6	—	—	—	—	—	—
<i>Xenistius californiensis</i>	7	—	—	—	—	—	—	—	—	—	—	—	—
<i>Zanotolepis latipinnis</i>	—	—	1	—	—	—	—	—	—	—	—	—	—
Unidentified teleosts	33	8	—	—	—	—	1	—	—	—	—	—	1

c = opercular spine; j = teeth; s = scales

\* in Roy Kohl collection

\*\* in Humboldt State College collection

inaccessible for paleontological investigation, the fauna seems worthy of listing.

#### LACMIP 66

This site was first investigated by museum personnel in 1945. At that time, and for nearly two decades, there were numerous exposures of fossiliferous Palos Verdes Sand on both sides of a dry creek and in eight erosion gullies that drained into it. These gullies were listed successively as LACMIP 66-1, 66-2, 66-3, etc., and although each was sampled extensively for mollusks, few fish remains were found. A housing development now covers the entire mesa south of Newport back bay where LACMIP 66 yielded a rich assemblage of mollusks (Kanakoff and Emerson, 1959).

Fish remains (otoliths = o, teeth = t, caudal stings = s) gleaned from the main creek and its tributary gullies by museum personnel were identified as follows:

<i>Cynoscion nobilis</i> :	66 (1o)
<i>Dasyatis dipterurus</i> :	66 (1s)
embiotocid:	66 (1o, 6t)
<i>Genyonemus lineatus</i> :	66-2 (8o); 66-10 (3o)
<i>Heterodontus francisci</i> :	66-10 (1t)
<i>Leptocottus armatus</i> :	66-2 (1o)
<i>Otophidium scrippsi</i> :	66 (1o); 66-2 (2o)
<i>Otophidium taylori</i> :	66 (1o)
<i>Parophrys vetulus</i> :	66-1 (1o)
<i>Pimelometopon pulchrum</i> :	66 (17t)
<i>Sebastes</i> sp.:	66 (1o)
<i>Seriphus politus</i> :	66 (3o); 66-2 (2o); 66-10 (2o)

Kanakoff (1956) noted 11 kinds of sharks and rays from LACMIP 66-2 and five species of teleosts. Ten of the 11 elasmobranchs were different species from the two noted above (i.e., *Carcharhinus lamiella* [= *obscurus*]; *Carcharodon carcharias*, *Cetorhinus maximus*, *Isurus glaucus* [= *oxyrinchus*], *Lamna ditropis*, *Myliobatis californicus*, *Prionace glauca*, *Sphyrna zygaena*, *Triakis semifasciata* and *Urobatis* [= *Urolophus*] *halleri*).

#### LACMIP 68-B

This exposure was near the top of a cliff about 90 feet above the high tide line in Newport back bay. A housing development, across the bay from the one covering LACMIP 66, has destroyed this site. Kanakoff (1956) reported 12 teeth from *Carcharhinus lamiella* [= *obscurus*].

#### LACMIP 136

This 14- to 22-foot thick bed of Palos Verdes Sand was rich in mollusks but contained few fish remains. It was in the cliff near the top of the mesa that lies south of Newport back bay. The housing development that covers

LACMIP 66 also destroyed this locality. About 200 pounds of fossiliferous matrix yielded remains from the following six elasmobranchs and five teleosts ( $r$  = gill raker):

<i>Cetorhinus maximus</i> :	(1r)
<i>Dasyatis dipterurus</i> :	(1s)
<i>Galeorhinus zyopterus</i> :	(3t)
<i>Genyonemus lineatus</i> :	(5o)
<i>Heterodontus francisci</i> :	(1t)
<i>Leptocottus armatus</i> :	(1o)
<i>Myliobatis californicus</i> :	(1t)
<i>Otophidium scrippsi</i> :	(3o)
<i>Pimelometopon pulchrum</i> :	(2t)
<i>Porichthys myriaster</i> :	(skull with 2o)
<i>Urolophus halleri</i> :	(1s)

#### Newport-Corona del Mar Shopping Center

During construction of a vast shopping center east of Pacific Coast Highway and between Newport Beach and Corona del Mar, several beach deposits of Palos Verdes Sand were exposed. Badly eroded shells of the bean clam, *Donax gouldii*, comprised the bulk of the mollusk remains in these beds, but shells of Pismo clams, *Tivela stultorum*, moon snails, *Polinices* spp., whelks, *Nassarius* spp. and olives, *Olivella biplicata*, were also common. A 50-pound field sample from one of these beds yielded six badly eroded otoliths from *Genyonemus lineatus* and one from *Seriphus politus*. These strata are now under parking lots and an assortment of buildings.

#### NORTHERN CALIFORNIA SITE

##### Crannell Road

This locality was exposed during highway construction north of Arcata where Crannell Road intersects U.S. Highway 101. Excavation of the hill at the southeast corner of this road junction revealed a three foot thick, highly fossiliferous layer of relatively coarse sand beneath 150 feet of muddy silt containing numerous thin beds and lenses of marine fossils. All of the fish remains from this locality (Tables 1 and 2) were recovered from the sandy matrix at the base of the hill, at an elevation of approximately 20 feet (Crannell Quadrangle, Calif., 7.5' series, U.S.G.S. 1966).

Numerous students from Humboldt State College have sampled this site extensively and frequently, as have amateur and professional paleontologists. I have had access to the collections of three students, Lloyd Barker, Jack Hopkins and Roy Kohl, and two of the species I have included (*Platichthys stellatus* and *Sebastes serranoides*) are based upon otoliths in Roy Kohl's collection, while the soupfin shark (*Galeorhinus zyopterus*) record is based upon a tooth in Lloyd Barker's collection. The Pacific halibut (*Hippoglossus*

*stenolepis*) is represented by a mandible in a collection at Humboldt State College.

In all, the 700 to 800 pounds of matrix that I examined from this site yielded 724 otoliths and otolith fragments, 137 teeth including four species of teleosts not represented by otoliths, plus an assortment of vertebrae, skate bucklers and wing spines and miscellaneous bony fragmentia (Tables 1 and 2).

#### SPECIES ACCOUNTS

##### Elasmobranchs

*Alopias vulpinus* (Bonnaterre)—common thresher

Teeth of the common thresher were found only at Playa del Rey (Fitch 1964, 1966).

Total material: 3 teeth.

*Carcharhinus* spp.—requiem sharks

Although Kanakoff (1956) reported teeth of *C. lamiella* [= *obscurus*] from Playa del Rey and two Newport Beach localities, I prefer to list them simply as *Carcharhinus* spp. until *Carcharhinus* taxonomy is better understood than at present. *Carcharhinus* teeth were found at Playa del Rey (Fitch 1964, 1966), San Pedro, and Newport Beach (Table 1); at least two species are represented.

Total material: 109 teeth.

*Carcharodon carcharias* (Linnaeus)—white shark

*C. carcharias* has been reported previously from Playa del Rey (Kanakoff, 1956; Fitch, 1964) and Newport Beach (Kanakoff, 1956). A white shark tooth also was found at San Pedro (Table 1).

Total material: 10 teeth and 4 vertebrae.

*Cetorhinus maximus* (Gunnerus)—basking shark

Kanakoff (1956) reported a *Cetorhinus* tooth from LACMIP 66-2 at Newport Beach. Since then I have found single gill rakers in material from the 700 block North Pacific Ave., San Pedro, and from LACMIP 136 at Newport Beach (Table 1).

Total material: 1 tooth and 2 gill rakers.

*Dasyatis dipterurus* (Jordan and Gilbert)—diamond stingray

Kanakoff (1956) identified a caudal sting from LACMIP 77 at Wilmington, Calif., as being from this species, and Fitch (1966) reported two *D. dipterurus* teeth from Playa del Rey. Eight additional teeth and a sting have been found since then at San Pedro (700 block North Pacific and the Incinerator site) and at two Newport Beach localities, LACMIP 66 and 136 (Table 1).

Total material: 10 teeth and 2 caudal stings.

*Galeorhinus zyopterus* Jordan and Gilbert—soupfin shark

The eight teeth that Kanakoff (1956) identified as being from *Triakis semifasciata* proved to be from *Galeorhinus*. Fitch (1964, 1966) subsequently reported soupfin shark teeth from Playa del Rey, and included the seven that Kanakoff had misidentified. *Galeorhinus* teeth were later found in several San Pedro deposits, at Newport Beach and at Crannell Road (Table 1).

Total material: 27 teeth, including one in the Lloyd Barker collection.

*Heterodontus francisci* (Girard)—horn shark

Kanakoff (1956) reported finding four dorsal spines from *Heterodontus* at Newport Beach (LACMIP 66-2), and Fitch (1966) noted one tooth from LACMIP 59 at Playa del Rey. Seven additional teeth have been found at San Pedro and Newport Beach localities in recent years (Table 1).

Total material: 8 teeth and 4 dorsal spines.

*Isurus oxyrinchus* Rafinesque—mako

Kanakoff (1956) reported teeth from *I. glaucus* [= *oxyrinchus*] in deposits at Newport Beach (LACMIP 66-2) and San Pedro (LACMIP 131), and both Kanakoff (1956) and Fitch (1964, 1966) reported them from Playa del Rey (LACMIP 59). Only two additional mako teeth have been found in Palos Verdes Sand subsequent to these reports, and both of these were from the LACMIP 131 locality (Table 1).

Total material: 22 teeth.

*Lamna ditropis* Hubbs and Follett—salmon shark

Kanakoff (1956) noted five salmon shark teeth from the Palos Verdes Sand at Newport Beach (LACMIP 66-2), and reported that it is "strictly northern in distribution." Actually, *L. ditropis* inhabits oceanic waters both north and south of southern California, so Newport Beach can not be considered as being outside of its normal range, latitudinally. A salmon shark tooth found in Palos Verdes Sand at San Pedro (LACMIP 131) has not been reported previously.

Total material: 6 teeth.

*Myliobatis californicus* Gill—bat ray

Bat ray teeth are large and very distinctive, so they are easily seen in fossiliferous matrix. Their abundance in southern California Pliocene and Pleistocene deposits, especially Palos Verdes Sand (Table 1), reflects the ease with which they can be found. Kanakoff (1956) reported 160 *M. californicus* teeth from LACMIP 131 at San Pedro, and caudal stings from Playa del Rey and Newport Beach (LACMIP 66-2). I reported finding teeth of *M. californicus* at Playa del Rey (Fitch, 1964, 1966) and subsequently

have found them in fossiliferous Palos Verdes Sand at San Pedro and Newport Beach (Table 1).

Total material: 613 teeth and 8 stings.

*Notorynchus maculatus* Ayres—sevengill shark

*N. maculatus* previously was reported from Playa del Rey by Kanakoff (1956) and Fitch (1964) based upon 12 teeth. A single tooth found at San Pedro (700 block, North Pacific Ave.) has not been noted previously. The range of *N. maculatus* has generally been given as northern British Columbia to southern California, but there are now several records of capture from Baja California as far south as Pta. San Carlos.

Total material: 13 teeth.

*Prionace glauca* (Linnaeus)—blue shark

Blue shark teeth are rare in southern California fossil deposits, but Kanakoff (1956) reported finding eight at Playa del Rey and one at Newport Beach (LACMIP 66-2). In my sampling of the Palos Verdes Sand, I have found but a single tooth from *P. glauca* and that was in screenings from LACMIP 131 at San Pedro.

Total material: 10 teeth.

*Raja* spp.—unidentified skates

I previously reported *Raja* from Palos Verdes Sand based upon eight vertebrae and seven bucklers and “wing” spines (Fitch, 1964, 1966). Subsequent sampling at San Pedro has turned up five additional bucklers and 13 teeth, but *Raja* remains have not been found at Newport Beach. In northern California (Crannell Road), skate remains were abundant, and I was able to find 114 teeth and 11 wing spines and bucklers (dermal denticles) in the material I examined. Lloyd Barker's collection contains 16 teeth and five dermal denticles.

Total material: 143 teeth, 28 dermal denticles and 8 vertebrae.

*Rhizoprionodon longurio* (Jordan and Gilbert)—Pacific sharpnose shark

*R. longurio* was previously reported from Playa del Rey (as *Scoliodon longurio*) by Fitch (1964) who had a single tooth from there. No additional remains from this species have been found in any exposure of Palos Verdes Sand.

Total material: 1 tooth.

*Sphyrna* spp.—unidentified hammerheads

Kanakoff (1956) reported finding four teeth from *Sphyrna zygaena* at Playa del Rey and one at Newport Beach (LACMIP 66-2), but in my reports on the Playa del Rey fauna (Fitch 1964, 1966), I did not attempt to determine from what species of *Sphyrna* the nine teeth and 17 vertebrae came. Four

hammerhead teeth that I have obtained from deposits of Palos Verdes Sand at San Pedro (Table 1) appear to be from a single species, but I do not feel qualified to place a specific name on them. Gilbert (1967) reports only two species of *Sphyrna* from California during modern times, *S. tiburo* and *S. zygaena*.

Total material: 18 teeth and 17 vertebrae.

*Squatina californica* Ayres—Pacific angel shark

Teeth, vertebrae and dermal denticles of *S. californica* have turned up in Palos Verdes Sand at Playa del Rey (Fitch 1964, 1966) and San Pedro (Table 1), but no identifiable angel shark remains have been found at Newport Beach, as yet.

Total material: 23 teeth, 8 vertebrae, and 1 dermal denticle.

*Triakis semifasciata* Girard—leopard shark

Although Kanakoff (1956) reported finding eight teeth of *Triakis* at Playa del Rey and Newport Beach, a critical comparison of his material with teeth from living sharks revealed that they were actually from *Galeorhinus zyopterus*, a close relative. Deposits of Palos Verdes Sand at San Pedro and Newport Beach have yielded *Triakis* teeth, however (Table 1).

Total material: 5 teeth.

*Urolophus halleri* Cooper—round stingray

Several hundred caudal stingray fragments have been identified as being from round stingrays (Kanakoff, 1956; Fitch, 1964, 1966), and subsequent sampling of the Palos Verdes Sand has turned up additional stings (Table 1), but so far no other remains from *Urolophus* have been found. The jaws of an adult round stingray contain more than 1,000 teeth, but these are so small that they easily pass through a 20-mesh screen, and I have not examined very much residue that is finer than what is retained by 20-mesh screens.

Total material: 246 stings and fragments of stings.

Unidentified elasmobranchs

Most of the deposits of Palos Verdes Sand that I have examined have contained a few elasmobranch remains that are unidentifiable for one reason or another (Fitch, 1964, 1966; Table 1). Teeth sometimes are too fragmented or eroded to identify, and too little is known about vertebrae, wing spines and bucklers to assign reliable specific names.

Total material: 27 vertebrae, 3 teeth, and 2 bucklers.

Teleosts

*Allosmerus elongatus* (Ayres)—whitebait smelt

*Allosmerus elongatus* has been reported as ranging from the Strait of Juan de Fuca, Washington to San Pedro, but its occurrence south of Morro

Bay is subject to doubt. It seldom is taken in the surf zone or at depths greater than about 300 feet, but throughout much of this area, particularly north of San Francisco, whitebait smelt are extremely abundant during most years. The species is reported to attain a length of about nine inches, but of many thousands that I have seen over the past 20 years, none has exceeded six inches. The 9-inch fish probably was misidentified. Eleven otoliths from the Crannell Road deposit (four in the Lloyd Barker collection) constitute the only fossil record for the species. Sagittae of a large adult will exceed 3.5 mm in length.

Total material: 11 otoliths 2.7 to 3.6 mm (not figured).

*Ammodytes hexapterus* Pallas—Pacific sand lance

Pacific sand lance otoliths have been found in several Pliocene and Pleistocene deposits in California (Fitch, 1968, and unpublished data), but until now, they have not been reported from Palos Verdes Sand. If otoliths of this



FIGURE 1. Fish otoliths found in various deposits of "Palos Verdes Sand." Lengths (in mm) are given for each otolith; notations are made regarding its position in the skull (left or right); otolith condition is noted if imperfect; and locality of fossil deposit is given. All otoliths in this figure are sagittae, and all views are inner faces. a. *Spirinchus thaleichthys*, 2.7, l, Crannell Road; b. *Hypomesus pretiosus*, 3.0, r, Crannell Road; c. *Spirinchus starksi*, 3.5, r, Crannell Road; d. *Oncorhynchus tshawytscha*, 11.8, r, Crannell Road; e. *Anchoa compressa*, 1.9, r, Playa del Rey; f. *Engraulis mordax*, 4.0, l, V.T. Bridge; g. *Argentina sialis*, 3.0, r, Playa del Rey; h. *Synodus lucioceps*, 3.0, r, Playa del Rey; i. *Clupea pallasii*, 3.5, r, Crannell Road; j. *Stenobranchius leucopsarus*, 2.0, l, Playa del Rey; k. *Symbolophorus californiensis*, 4.4, r, Playa del Rey; l. *Electrona rissoi*, 3.6, r, LACMIP 131, badly eroded; m. *Diaphus theta*, 2.2, r, Crannell Road. Photographs by Jack W. Schott.

northern species had been found in southern California exposures of Palos Verdes Sand, it could be deemed "unexpected" to say the least, but their presence at the Crannell Road site is well within their normal present day range.

Total material: 4 otoliths (Fig. 6f).

*Amphistichus koelzi* (Hubbs)—calico surfperch

The calico surfperch ranges from Cape Flattery, Washington, to Santo Tomas Point, Baja California. It is a typical inhabitant of the sandy beach surf zone, but occasionally strays into depths of 60 to 75 feet. The species attains a length of about 10 inches and a pound in weight. Remains of *A. koelzi* have not been found in any other deposits. Sagittae of a large adult will exceed 7.0 mm in length.

Total material: 1 otolith 4.5 mm long (Fig. 5b).

*Amphistichus rhodoterus* (Agassiz)—redtail surfperch

The redtail surfperch ranges from Cape Flattery, Washington to Monterey Bay. It also is a typical surf zone inhabitant that occasionally strays into deeper water (to at least 60 feet). The species attains a length of 16 inches and nearly four pounds in weight. Remains of *A. rhodoterus* have not been found in any other deposit; the Crannell Road exposure lies well within their present-day range. The sagittae of a large adult will exceed 10.0 mm in length.

Total material: 1 partially digested otolith 6.6 mm long (Fig. 5d).

*Anarrhichthys ocellatus* Ayres—wolf-eel

The wolf-eel ranges from southeastern Alaska to Imperial Beach, California, but is rare south of Point Conception. It prefers the rocky subtidal and adjacent offshore shallow areas, but has been captured as deep as 400 feet. It is reported to attain eight feet, but the largest authentic record in recent years was six feet eight inches and 40 pounds. Otoliths of this species have not been found, but *A. ocellatus* has large, very distinctive teeth and two of these were recovered from the Crannell Road deposit.

Total material: 2 teeth, including one in the Lloyd Barker collection.

*Anchoa compressa* (Girard)—deepbody anchovy

Otoliths of *A. compressa* previously were reported from Playa del Rey (Fitch, 1966), and no additional remains have been found.

Total material: 4 otoliths (Fig. 1e).

*Anisotremus davidsonii* (Steindachner)—sargo

Fitch (1964) reported a sargo otolith from Playa del Rey that previously had been noted by Kanakoff (1956); no additional remains of *A. davidsonii* have been found.

Total material: 1 otolith (Fig. 4i).

*Argentina sialis* Gilbert—Pacific argentine

Fitch (1966) reported a Pacific argentine otolith from Playa del Rey; no additional remains have been found.

Total material: 1 otolith (Fig. 1g).

*Atheresthes stomias* (Jordan and Gilbert)—arrowtooth flounder

Otoliths of *A. stomias* have been found in Pliocene and Pleistocene deposits of southern California (Fitch, 1968; and unpublished data) but never in Palos Verdes Sand. Their teeth are large and have distinctive dart-shaped tips. Two jaw teeth of *A. stomias* were recovered from the Crannell Road deposit.

Total material: 2 teeth: one in the Lloyd Barker collection.

*Atherinops affinis* (Ayres)—topsmelt

The topsmelt previously was reported from Playa del Rey based upon a single otolith (Fitch, 1964); one additional topsmelt otolith has been found in a Palos Verdes Sand deposit in southern California (Table 2).

Total material: 2 otoliths (Fig. 4e).

*Atherinopsis californiensis* Girard—jacksmelt

Jacksmelt otoliths (4) previously were reported from Playa del Rey (Fitch, 1964, 1966). Subsequent sampling has yielded two additional otoliths from Palos Verdes Sand in the San Pedro area (Table 2).

Total material: 6 otoliths (Fig. 4f).

*Bairdiella icistia* (Jordan and Gilbert)—bairdiella

The bairdiella ranges from the head of the Gulf of California to southern Mexico, and it is one of the species that was successfully introduced into Salton Sea. It is an inhabitant of relatively shallow (to about 150 feet) near-shore waters in non-rocky habitat. The species seldom reaches a foot in length or a pound in weight. Sagittae of a large adult will exceed 11.0 mm in length. A single broken otolith was found in one of the San Pedro deposits (Table 2).

Total material: 1 otolith 3.7 mm long (Fig. 5g).

*Calamus brachysomus* (Lockington)—Pacific porgy

The pacific porgy has been recorded from Oceanside (twice) to 150 miles south of Lima, Peru, but it apparently does not spawn north of Sebastian Viscaino Bay, Baja California. Young fish are abundant in shallow water where the bottom is sandy or firm sandy mud whereas adults prefer somewhat deeper water in the same type of habitat. A large individual will exceed 20 inches in length and four pounds. Their flat-topped round molars

are easily recognized, and one of these was found in a Palos Verdes Sand deposit at San Pedro (Table 2).

Total material: 1 tooth.

*Chitonotus pugetensis* (Steindachner)—staghorn sculpin

Staghorn sculpin otoliths have been found in a number of Pliocene and Pleistocene deposits in southern California including Playa del Rey (Fitch, 1964; 1966). Aside from the Playa del Rey locality, the only other Palos Verdes Sand exposure to yield *C. pugetensis* otoliths was in the San Pedro area (Table 2).

Total material: 12 otoliths (Fig. 6l).

*Citharichthys sordidus* (Girard)—Pacific sanddab

Pacific sanddab otoliths have been found in many fossil deposits throughout California, often in great numbers, and their occurrence in Palos Verdes Sand has been reported at Playa del Rey (Fitch, 1964; 1966). Subsequent sampling of Palos Verdes Sand has yielded *C. sordidus* otoliths in all areas except Newport Beach (Table 2). Of 13 otoliths seen from the Crannell Road deposit, three are in the Lloyd Barker collection.

Total material: 59 otoliths (Fig. 3b).

*Citharichthys stigmaeus* Jordan and Gilbert—speckled sanddab

Speckled sanddab otoliths have been found in more deposits and more abundantly than those of *C. sordidus*. Previously they have been reported in Palos Verdes Sand at Playa del Rey (Fitch, 1964; 1966), but their occurrence in the San Pedro area and at Crannell Road (Table 2) has not been noted previously. They have not been found in the Newport Beach exposures of Palos Verdes Sand.

Total material: 504 otoliths (Fig. 3a).

*Citharichthys xanthostigma* Gilbert—longfin sanddab

Although longfin sanddab otoliths have been reported from the Pleistocene of southern California (Fitch, 1968), and have been found in many other Pliocene and Pleistocene deposits (unpublished data), only one exposure of Palos Verdes Sand contained some (Table 2).

Total material: 4 otoliths (Fig. 3c).

*Clupea pallasii* Valenciennes—Pacific herring

Pacific herring otoliths have been found in several Pliocene and Pleistocene deposits of southern California (Fitch, 1967, 1968; unpublished data), but five sagittae from Crannell Road (Table 2, plus one in the Lloyd Barker collection) represent the first record for the species from Palos Verdes Sand.

Total material: 5 otoliths (Fig. 1i).

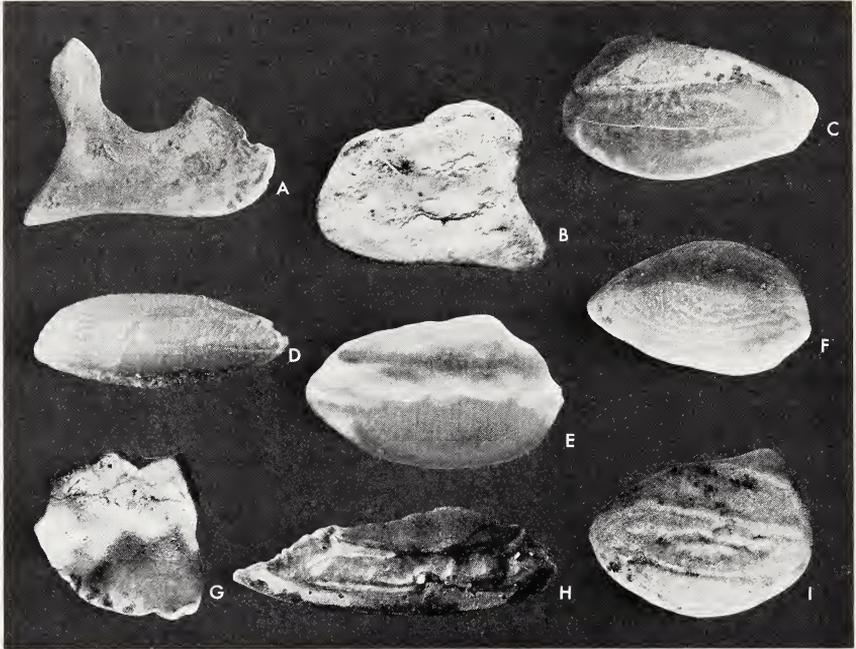


FIGURE 2. Fish otoliths found in various deposits of "Palos Verdes Sand." Lengths (in mm) are given for each otolith; notations are made regarding its position in the skull (left or right); otolith condition is noted if imperfect; and locality of fossil deposit is given. All otoliths in this figure are sagittae, and all views except *Theragra* are inner faces. a. *Porichthys myriaster*, 13.0, l, LACMIP 131; b. *Porichthys notatus*, 6.0, r, V.T. Bridge; c. *Lepophidium negropinna*, 10.2, r, V.T. Bridge; d. *Microgadus proximus*, 12.0, r, Crannell Road; e. *Coelorhynchus scaphopsis*, 7.9, l, Playa del Rey; f. *Otophidium taylori*, 7.9, l, V.T. Bridge; g. *Theragra chalcogramma*, 5.1, l, V.T. Bridge, badly eroded and posterior end missing; h. *Merluccius productus*, 19.6, l, Crannell Road; i. *Otophidium scrippsi*, 7.8, l, V.T. Bridge. Photographs by Jack W. Schott.

#### *Coelorhynchus scaphopsis* (Gilbert)—Gulf rattail

Otoliths of the Gulf rattail have been found only in Palos Verdes Sand. The species was previously reported by Fitch (1966) for Playa del Rey based upon a single otolith. A second otolith subsequently was found in a San Pedro exposure (Table 2).

Total material: 2 otoliths (Fig. 2e).

#### *Cymatogaster aggregata* Gibbons—shiner perch

Shiner perch otoliths previously have been reported from Palos Verdes Sand at Playa del Rey (Fitch, 1964, 1966). Subsequently they have been found at all San Pedro localities and Crannell Road, but not at Newport Beach

(Table 2). Lloyd Barker's collection contained 17 otoliths from *C. aggregata*.

Total material: 135 otoliths (Fig. 5i).

*Cynoscion nobilis* (Ayres)—white seabass

Five white seabass otoliths previously were reported from Palos Verdes Sand at Playa del Rey (Kanakoff, 1956; Fitch, 1964). A single otolith subsequently was found by museum personnel in one of the Newport Beach localities (LACMIP 66; Table 2).

Total material: 6 otoliths (Fig. 5p).

*Cynoscion reticulatus* (Günther)—striped corvina

Fossil remains of this southern species have been found only in Palos Verdes Sand. They have been reported from Playa del Rey based upon 5 otoliths (Fitch, 1964, 1966), and six additional otoliths were found in two deposits at San Pedro (Table 2).

Total material: 11 otoliths (Fig. 5r).

*Diaphus theta* Eigenmann and Eigenmann—California headlightfish

Otoliths of this mesopelagic lanternfish have been found in many Pliocene and Pleistocene deposits in southern California (Fitch, 1968, and unpublished data), but the single sagitta from the Crannell Road locality (Fitch, 1969a; Table 2) is the only record of *D. theta* from Palos Verdes Sand.

Total material: 1 otolith (Fig. 1m).

*Electrona rissoi* (Cocco)—chubby flashlightfish

Otoliths of *E. rissoi* have been found in Pliocene (Fitch and Reimer, 1967) and Pleistocene deposits (Fitch, 1968), including Palos Verdes Sand at San Pedro (Fitch, 1969a).

Total material: 1 otolith (Fig. 1l).

*Embiotoca* cf. *jacksoni* Agassiz—black perch

Otoliths of *E. jacksoni* have been found in a Pliocene deposit near San Diego (unpublished data), but the single badly worn otolith from Palos Verdes Sand at San Pedro (Table 2) represents the only record (a doubtful one) from Pleistocene.

Total material: 1 badly eroded otolith (Fig. 5f).

*Engraulis mordax* Girard—northern anchovy

Northern anchovy otoliths were abundant in Palos Verdes Sand at Playa del Rey (Fitch, 1964; 1966), and were present at two San Pedro localities and Crannell Road, but none has been found at Newport Beach (Table 2). The fossil record of *E. mordax* in California is unbroken over the 10 million year span since the beginning of the Pliocene, including the

most recent 7,000 years of the earth's history as divulged by investigating Indian middens (Fitch, 1969b).

Total material: 280 otoliths including one in the Lloyd Barker collection (Fig. 1f).

*Eopsetta jordani* (Lockington)—petrale sole

Otoliths of *E. jordani* have been found in several Pleistocene deposits (Fitch, 1967, and unpublished data), but they have not previously been reported from Palos Verdes Sand. A single sagitta was found in the Crannell Road deposit (Table 2), and three others are in the Lloyd Barker collection. Total material: 4 otoliths (Fig. 3g).

*Genyonemus lineatus* (Ayres)—white croaker

Otoliths of *G. lineatus* were among the five most abundant sagittae at Playa del Rey (Fitch, 1964, 1966), and have turned up at all other localities where Palos Verdes Sand has been sampled (Kanakoff, 1956; Table 2). Although white croakers have been reported as far north as Vancouver Island, their occurrence north of San Francisco is spotty (Miller and Gotshall, 1965) and depends a great deal upon warm oceanic temperatures. The sagittae in the Crannell Road deposit (including 2 in the Lloyd Barker collection) were from large adults.

Total material: 740 otoliths (Fig. 5l).

*Glyptocephalus zachirus* Lockington—rex sole

Rex sole remains have been found in an assortment of Pliocene and Pleistocene deposits in California (Fitch, 1967, 1968, and unpublished data) but not previously in Palos Verdes Sand. No otoliths of *G. zachirus* were found in any of the southern California localities (Table 2) but two (one in the Roy Kohl collection) were present in Crannell Road material examined. Total material: 2 otoliths (Fig. 3j).

*Hippoglossus stenolepis* Schmidt—Pacific halibut

The Pacific halibut ranges from the Bering Sea to Point Piedras Blancas, California, in depths of 60 to 3,600 feet. Males are known to reach a weight of 123 pounds, and females, 495. Otoliths of *H. stenolepis* have never been found in any fossil deposit, but in the Humboldt State College collection there is a lower jaw of a fairly large individual that came from the Crannell Road deposit.

Total material: 1 lower jaw in Humboldt State College collection.

*Hyperprosopon anale* Agassiz—spotfin surfperch

The spotfin surfperch is an inhabitant of the surf zone along sandy, outer coast beaches between Seal Rock, Oregon, and Blanca Bay, Baja California. Individuals occasionally are caught in depths of 60 feet or more

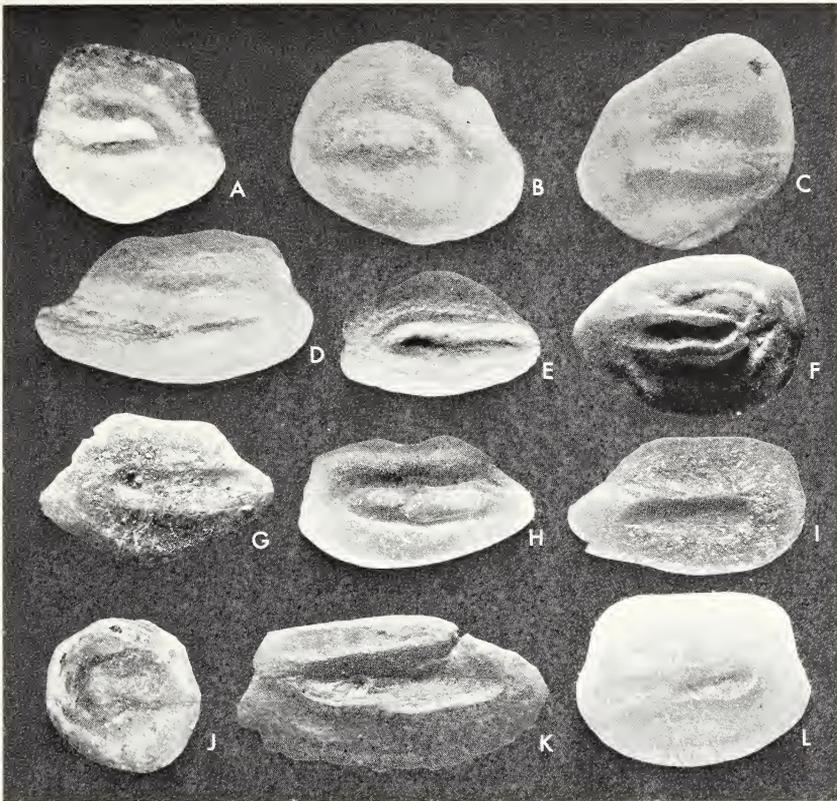


FIGURE 3. Fish otoliths found in various deposits of "Palos Verdes Sand." Lengths (in mm) are given for each otolith; notations are made regarding its position in the skull (left or right); otolith condition is noted if imperfect; and locality of fossil deposit is given. All otoliths in this figure are sagittae, and all views are inner faces. a. *Citharichthys stigmaeus*, 2.8, l, V.T. Bridge; b. *Citharichthys, sordidus*, 6.7, l, LACMIP 131; c. *Citharichthys xanthostigma*, 3.6, r, LACMIP 131; d. *Paralichthys californicus*, 8.2, r, LACMIP 131; e. *Pleuronichthys ritteri*, 3.2, l, Playa del Rey; f. *Lyopsetta exilis*, 3.5, r, Playa del Rey; g. *Eopsetta jordani*, 6.0, l, Crannell Road; h. *Parophrys vetulus*, 6.3, l, Crannell Road; i. *Microstomus pacificus*, 5.4, r, Crannell Road; j. *Glyptocephalus zachirus*, 2.0, l, Crannell Road, badly eroded; k. *Platichthys stellatus*, 9.5, l, Crannell Road; l. *Isopsetta isolepis*, 6.3, r, Crannell Road. Photographs by Jack W. Schott.

but they are not abundant at any depth. The largest fish reported was eight inches long and weighed just five ounces. Their otoliths have been found in several Pliocene and Pleistocene deposits (unpublished data), but only at Crannell Road have they turned up in Palos Verdes Sand. One of seven

otoliths from this site is in the Roy Kohl collection. Sagittae of a large adult will exceed 6.5 mm in length.

Total material: 7 otoliths from 2.5 to 5.2 mm long (Fig. 5g).

*Hyperprosopon ellipticum* (Gibbons)—silver surfperch

The silver surfperch ranges from Clallam County, Washington, to Point Dume, California. It prefers the surf zone along sandy, outer coast beaches, but also frequents rocky subtidal pools and occasionally strays into depths of 60 feet or more. They are known to attain a length of 10.5 inches and a weight of about one-quarter pound. The two otoliths from the Crannell Road deposit (Table 2) represent the only fossil record for this species. Sagittae of a large adult will exceed 6.0 mm in length.

Total material: 2 otoliths 3.9 to 4.5 mm long (Fig. 5e).

*Hypomesus pretiosus* (Girard)—surf smelt

The surf smelt ranges from Prince William Sound, Alaska, to Long Beach, California but it is rarely seen south of Morro Bay. It is an inhabitant of sandy beaches along the outer coast, where it spawns during daylight hours in the breaking surf and strays into depths of 60 feet or more when not spawning. The species is known to reach a length of 10 inches and a weight of about three ounces. Only one genus (*Mallotus*) in family Osmeridae has a fossil record according to McAllister (1963). *H. pretiosus* is but one of four osmerids from which otoliths were found in the Crannell Road deposit. In addition to the 18 that I found, there are three in the Lloyd Barker collection. Sagittae of a large adult will exceed 5.0 mm in length.

Total material: 21 otoliths 2.6 to 3.4 mm long (Fig. 1b).

*Icelinus quadriseriatus* (Lockington)—yellowchin sculpin

The yellowchin sculpin previously was reported from Palos Verdes Sand at Playa del Rey based upon 10 otoliths (Fitch, 1966). No additional otoliths have turned up since then.

Total material: 10 otoliths (Fig. 6k).

*Icelinus tenuis* Gilbert—spotfin sculpin

Otoliths of the spotfin sculpin have been found in a number of Pliocene and Pleistocene deposits in southern California (Fitch, 1967, 1968, and unpublished data), but they have not been reported previously from Palos Verdes Sand. Two otoliths from one of the San Pedro sites were identified as from this species (Table 2).

Total material: 2 otoliths (Fig. 6j).

*Isopsetta isolepis* (Lockington)—scaly-fin sole

The scaly-fin sole ranges from Alaska to southern California, but it is rare south of about Morro Bay. It inhabits areas where the bottom is sandy or sandy mud, and prefers depths shallower than about 150 feet although it

has been found deeper than 300. It is known to attain a length of 22 inches, but no weights are available for such large individuals. The Crannell Road site is the only locality where fossil remains of *I. isolepis* have been found. In addition to the 21 otoliths that I found, I have seen two in the Lloyd Barker collection and one in Roy Kohl's. Sagittae of a large adult will exceed 9.0 mm in length.

Total material: 24 otoliths 1.4 to 6.3 mm long (Fig. 3l).

*Lepidogobius lepidus* (Girard)—bay goby

The bay goby has been recorded from Palos Verdes Sand at Playa del Rey (Fitch, 1964, 1966), but the 28 otoliths obtained from San Pedro sites (Table 2) have not been noted previously. This species has not been found at Newport Beach or Crannell Road (Table 2).

Total material: 37 otoliths (Fig. 6g).

*Lepophidium negropinna* Hildebrand and Barton—giant cusk-eel

Remains of *L. negropinna*, a locally extinct southern species, have been found only in the Palos Verdes Sand of southern California. The two sagittae from Playa del Rey were reported by Fitch (1964), but the two from San Pedro sites (Table 2) have not been previously noted.

Total material: 4 otoliths (Fig. 2c).

*Leptocottus armatus* Girard—staghorn sculpin

Staghorn sculpin remains have been found in several southern California Pliocene and Pleistocene deposits (Fitch, 1967, 1968, and unpublished data), but until now, only an opercular spine had been reported from Palos Verdes Sand (Kanakoff, 1956). There were no otoliths of *L. armatus* at Playa del Rey and few at San Pedro and Newport Beach sites (Table 2), but the Crannell Road deposit yielded 13 otoliths and four opercular spines (plus four otoliths and three spines in the Lloyd Barker collection and five otoliths in Roy Kohl's).

Total material: 22 otoliths and 7 opercular spines (Fig. 6m).

*Lethops connectens* Hubbs—halfblind goby

Otoliths of this species have been found in two southern California Pleistocene deposits (Fitch, 1968, unpublished data), but not in Palos Verdes Sand south of Monterey, which is the present-day northern limit of their range. The Crannell Road site, several hundred miles north of their known range, yielded seven otoliths of *Lethops* (Table 2).

Total material: 7 otoliths (Fig. 6h).

*Leuresthes tenuis* (Ayres)—grunion

Fossil grunion otoliths have been found only at Playa del Rey whence they have been reported by Fitch (1964, 1966).

Total material: 10 otoliths (Fig. 4d).

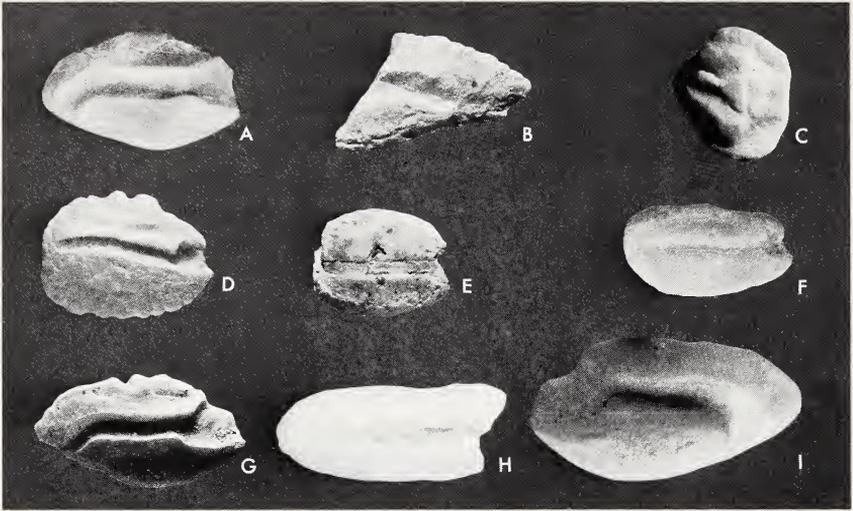


FIGURE 4. Fish otoliths found in various deposits of "Palos Verdes Sand." Lengths (in mm) are given for each otolith; notations are made regarding its position in the skull (left or right); otolith condition is noted if imperfect; and locality of fossil deposit is given. All otoliths in this figure are sagittae, and all views are inner faces: a. *Trachurus symmetricus*, 6.7, l, Playa del Rey, badly eroded and rostrum missing; b. *Paralabrax* sp. 7.8, r, Playa del Rey, anterior half missing; c. *Symphurus atricauda*, 2.5, r, Playa del Rey; d. *Leuresthes tenuis*, 2.9, l, Playa del Rey; e. *Atherinops affinis*, 3.1, l, V.T. Bridge, badly eroded and anterior tip missing; f. *Atherinopsis californiensis*, 5.8, l, LACMIP 131; g. *Xenistius californiensis*, 9.0, l, Playa del Rey, rostrum tip missing; h. *Sphyræna argentea*, 10.7, l, Playa del Rey, badly eroded and anterior end missing; i. *Anisotremus davidsonii*, 9.8, r, Playa del Rey, eroded and rostrum tip missing. Photographs by Jack W. Schott.

*Lycodopsis pacifica* (Collett)—blackbelly eelpout

Although sagittae of *L. pacifica* have been found in numerous Pliocene and Pleistocene deposits of California (Fitch, 1967, 1968, and unpublished data), only the Crannell Road site among the Palos Verdes Sand localities investigated (Table 2) contained an otolith.

Total material: 1 otolith (Fig. 6o).

*Lyopsetta exilis* (Jordan and Gilbert)—slender sole

Slender sole otoliths are abundant in many Pliocene and Pleistocene deposits, but the single otolith reported from Playa del Rey (Fitch, 1964) is the only evidence of the species in Palos Verdes Sand.

Total material: 1 otolith (Fig. 3f).

*Menticirrhus undulatus* (Girard)—California corbina

Aside from the six otoliths reported from Playa del Rey (Fitch, 1964,

1966), only one additional sagitta has been found in deposits of Palos Verdes Sand (Table 2).

Total material: 7 otoliths (Fig. 5k).

*Merluccius productus* (Ayres)—Pacific hake

Otoliths of Pacific hake (initially reported by Kanakoff, 1956) have been present in almost every Pliocene and Pleistocene deposit that I have investigated (Fitch, 1969b), but most have been from small fish. Except for the Crannell Road deposit, where all five hake otoliths (Table 2) were from large fish, the Palos Verdes Sand localities have yielded few large sagittae. Twenty otoliths from Crannell Road in the Lloyd Barker and Roy Kohl collections also are mostly from large fish.

Total material: 61 otoliths (Fig. 2h).

*Microgadus proximus* (Girard)—Pacific tomcod

Pacific tomcod otoliths have been found in numerous Pliocene and Pleistocene deposits of California (Fitch, 1967, 1968, and unpublished data; Fitch and Reimer, 1967), but only at the Crannell Road site are they abundant. This deposit, the only Palos Verdes Sand to contain them, yielded 411 sagittae to my efforts (Table 2), and 623 others to Lloyd Barker and Roy Kohl.

Total material: 1,034 otoliths (Fig. 2d).

*Micropogon ectenes* Jordan and Gilbert—berrugato

Fossil otoliths from this locally extinct southern species have been found only in Palos Verdes Sand: two at Playa del Rey (Fitch, 1964) and one at San Pedro (Table 2).

Total material: 3 otoliths (Fig. 5m).

*Microstomus pacificus* (Lockington)—Dover sole

Sagittae of *M. pacificus* have been rare in the Pliocene and Pleistocene deposits that I have examined. Prior to finding two at the Crannell Road locality (Table 2), only Timms Point Silt had yielded an otolith (Fitch, 1968). An additional Dover sole otolith was seen in the Lloyd Barker collection.

Total material: 3 otoliths (Fig. 3i).

*Oncorhynchus tshawytscha* (Walbaum)—King salmon

King salmon have been taken in the Pacific Ocean from San Diego to the Bering Sea and south, on the Asiatic side, to Japan. They are seldom seen or caught south of Morro Bay, however. They are known to attain lengths of at least five feet and a weight of 126.5 pounds, but a 50-pounder is rare enough to generate publicity when brought ashore. Aside from a very questionable record of *O. tshawytscha* from the Pleistocene of Oregon, based

upon fragments of jaws, teeth and vertebrae (Uyeno and Miller, 1963), the otolith from the Crannell Road locality (Table 2) represents the only fossil occurrence of this important anadromous fish. Sagittae from a large adult king salmon will exceed 15.0 mm in length.

Total material: 1 otolith 11.8 mm long (Fig. 1*d*).

*Ophiodon elongatus* Girard—lingcod

The lingcod ranges from northwestern Alaska to San Carlos anchorage, Baja California, but is not abundant south of Point Conception except on a few offshore banks. It appears to prefer rocky bottom areas and depths shallower than about 350 feet, but many are caught on sandy or sandy-mud bottoms, and to depths of 2,700 feet. Lingcod reportedly attain lengths exceeding five feet and weights over 70 pounds, but 40-pound fish are rare off California. The strong conical jaw teeth of large *O. elongatus* are distinctive among California's marine fishes, and 11 of the teleost teeth I found in the Crannell Road deposit had come from this species. An additional 12 lingcod teeth were seen in the Lloyd Barker collection.

Total material: 23 jaw teeth.

*Ophioscion* sp.—sciaenid

Several species of *Ophioscion*, smallish sciaenids that seldom attain a foot in length, are inhabitants of the tropical eastern Pacific. In this genus, two of the three pairs of otoliths (sagittae and lapilli) are almost identical in size. Except among ostariophysans, teleost lapilli from a given fish are almost invariably microscopic compared with sagittae from the same individual. Thus, the lapilli of *Ophioscion* are easily identified to genus by their size and configuration, but I have been unable to find characters among several species that will permit a specific determination. *O. scierus* has been noted at Magdalena Bay on the outer coast of Baja California during historic times, but this is not sufficient reason to name the lapillus found in Palos Verdes Sand at San Pedro.

Total material: 1 lapillus 6.6 mm long (Fig. 5*n*).

*Otophidium scrippsi* Hubbs—basketweave cusk-eel

Otoliths of *O. scrippsi* have been among the most abundant teleost remains in many southern California Pliocene and Pleistocene deposits (Fitch, 1964, 1966, and unpublished data; Fitch and Reimer, 1967; Kanakoff, 1956). They were found at all Palos Verdes Sand localities except Crannell Road (Table 2).

Total material: 275 otoliths (Fig. 2*i*).

*Otophidium taylori* (Girard)—spotted cusk-eel

Otoliths of *O. taylori*, an inhabitant of more northerly and deeper water than *O. scrippsi*, have been found in even more Pliocene and Pleistocene deposits than *O. scrippsi*, but were missing at Crannell Road (Table 2). The

first fossil occurrence of these was noted by Kanakoff (1956).

Total material: 185 otoliths (Fig. 2f).

*Paralabrax* spp.—sand or kelp bass

Three *Paralabrax* otoliths, reported from Palos Verdes Sand at Playa del Rey by Fitch (1966), are the only serranid remains found in the Pliocene or Pleistocene of southern California to date.

Total material: 3 otoliths (Fig. 4b).

*Paralichthys californicus* (Ayres)—California halibut

California halibut otoliths have been found only at Signal Hill (Fitch, 1967), Playa del Rey (Fitch, 1964, 1966) and two San Pedro sites (Table 2).

Total material: 10 otoliths (Fig. 3d).

*Parophrys vetulus* Girard—English sole

Otoliths of *P. vetulus* have been found in many Pliocene and Pleistocene deposits including Palos Verdes Sand (Fitch, 1964, 1966, 1968; Fitch and Reimer, 1967). None was found in Palos Verdes Sand at San Pedro, but one turned up at Newport Beach and 14 at Crannell Road (Table 2). An additional 12 were seen in the Lloyd Barker collection.

Total material: 31 otoliths (Fig. 3h).

*Phanerodon furcatus* Girard—white seaperch

Otoliths of *P. furcatus* have not been found often, nor have they been abundant (unpublished data). I have found only one in Palos Verdes Sand (Crannell Road, Table 2), although the Lloyd Barker and Roy Kohl collections also contain white seaperch otoliths (3) from Crannell Road. The nine otoliths from the Playa del Rey locality that I reported as *Phanerodon* (Fitch, 1964) were misidentified. A careful re-examination of these has revealed that seven of the nine were from *Xenistius californiensis* and the other two (small and badly eroded) from *Trachurus symmetricus*.

Total material: 13 otoliths (Fig. 5c).

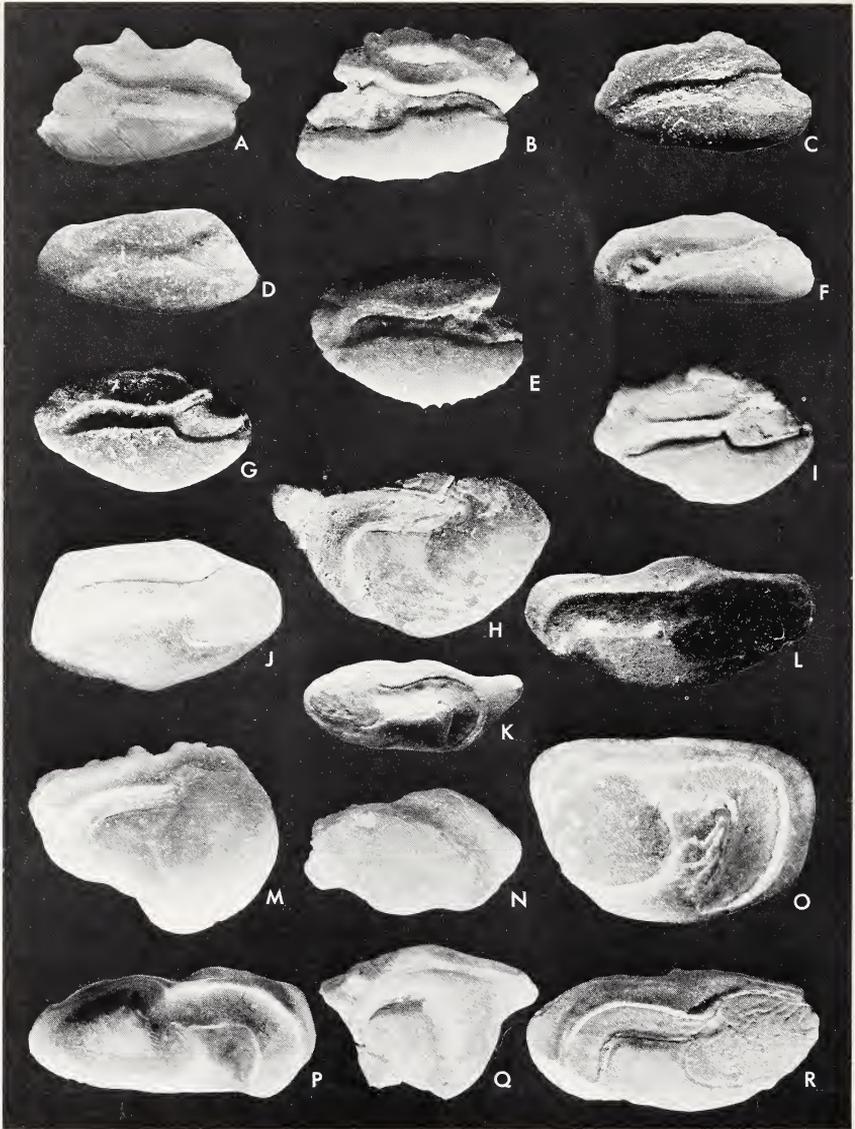
*Pimelometopon pulchrum* (Ayres)—California sheephead

The distinctive jaw and pharyngeal teeth of *P. pulchrum* have been found in many fossil deposits, but to date, no sheephead otoliths have turned up. Teeth previously were reported from Palos Verdes Sand at Newport Beach (Kanakoff, 1956), and Playa del Rey (Fitch, 1964), but those from San Pedro (Table 2) are being noted for the first time. None has been found at Crannell Road.

Total material: 28 teeth.

*Platichthys stellatus* (Pallas)—starry flounder

The starry flounder ranges throughout the north Pacific, having been recorded south to Santa Barbara in the eastern Pacific, but generally north



of Morro Bay. They prefer sandy or sandy mud bottoms and have been caught in fresh, brackish, and salt water. In the ocean, they are most abundant in depths shallower than 200 feet, but some individuals have been caught five times that deep. They are reported to reach a length of three feet and a weight of 20 pounds, but few are seen that exceed 15. A single otolith in the Roy Kohl collection, plus five stellate scales (two in Lloyd Barker's collection) are the

FIGURE 5. Surfperch and croaker otoliths found in various deposits of "Palos Verdes Sand." Lengths (in mm) are given for each otolith; notations are made regarding its position in the skull (left or right); otolith condition is noted if imperfect; and locality of fossil deposit is given. All otoliths in this figure except *Ophioscion* (a lapillus) are sagittae, and all views are inner faces. a. *Rhacochilus vacca*, 8.1, r, LACMIP 131, badly eroded and portions missing from both ends; b. *Amphistichus koelzi*, 4.5, r, V.T. Bridge, portions missing from rostrum and posterior end; c. *Phanerodon furcatus*, 8.6, l, Crannell Road; d. *Amphistichus rhodoterus*, 6.6, l, Crannell Road, badly eroded; e. *Hyperprosopon ellipticum*, 3.9, l, Crannell Road; f. *Embiotoca cf. jacksoni*, 6.0, l, V.T. Bridge, badly eroded; g. *Hyperprosopon anale*, 5.2, l, Crannell Road; h. *Roncador stearnsi*, 9.4, l, LACMIP 131, badly eroded; i. *Cymatogaster aggregata*, 6.0, l, V.T. Bridge; j. *Seriphus politus*, 7.9, l, V.T. Bridge; k. *Menticirrhus undulatus*, 5.1, r, Playa del Rey; l. *Genyonemus lineatus*, 11.5, l, Crannell Road; m. *Micropogon ectenes*, 7.8, l, V.T. Bridge; n. *Ophioscion* sp., 6.6, r, LACMIP 131; o. *Umbrina roncadorensis*, 10.9, r, LACMIP 131; p. *Cynoscion nobilis*, 21.5, r, Playa del Rey; q. *Bairdiella icistia*, 3.7, r, LACMIP 131, ventral margin missing; r. *Cynoscion reticulatus*, 8.7, l, V.T. Bridge. Photographs by Jack W. Schott.

only fossil record of this species. All of these remains are from the Crannell Road deposit. Sagittae of a large adult will exceed 12.0 mm in length.

Total material: 1 otolith 9.5 mm long (Fig. 3k) and 5 scales.

*Pleuronichthys ritteri* (Starks and Morris)—spotted turbot

The single otolith of *P. ritteri* that I reported from Playa del Rey (Fitch, 1964) is the only known fossil record of this species.

Total material: 1 otolith (Fig. 3e).

*Porichthys myriaster* Hubbs and Schultz—specklefin midshipman

Otoliths of *P. myriaster* have been found in every Palos Verdes Sand locality, except Crannell Road, and were present in several other Pliocene and Pleistocene exposures in southern California (Fitch and Reimer, 1967; Fitch, unpublished data). In addition to the otoliths listed here (Table 2), the Los Angeles County Museum collections contain a disarticulated, but nearly complete, skull including otoliths that came from a Newport Beach exposure of Palos Verdes Sand (LACMIP 136).

Total material: 47 otoliths (Fig. 2a) and a disarticulated skull.

*Porichthys notatus* Girard—plainfin midshipman

Otoliths of *P. notatus* are one of the five most abundant teleost remains in Palos Verdes Sand (Table 2) having been reported from Playa del Rey (Fitch, 1964, 1966), but not previously from San Pedro or Crannell Road. They are common to extremely abundant in numerous other Pliocene and Pleistocene exposures throughout California (Fitch, 1967, 1968, and unpublished data; Fitch and Reimer, 1967). Two of the three I have seen from Crannell Road are in Lloyd Barker's collection.

Total material: 504 otoliths (Fig. 2b).

*Prionotus ruscarius* Gilbert and Starks—shortfin searobin

*P. ruscarius* has never been caught north of Magdalena Bay, Baja California; it ranges from there south to Panama. It appears to prefer moderate depths, possibly 20 to 150 feet, in areas of sandy or sandy mud bottom. Shortfin searobins are reported to attain a foot in length and possibly a pound in weight. A single otolith in Palos Verdes Sand at San Pedro (Table 2) is the only known fossil record of this species. Sagittae of a large adult will exceed 7.5 mm in length.

Total material: 1 otolith 6.6 mm long (Fig. 6p).

*Prionotus stephanophrys* Lockington—lumptail searobin

In a previous report (Fitch, 1964), I erroneously identified an otolith *P. stephanophrys* as *Sebastes* [= *Sebastes*] *aurora*. Subsequently (Fitch, 1966), I noted two additional lumptail searobin otoliths from Playa del Rey, but the sagitta from San Pedro (Table 2) has not been reported until now. Fossil remains of *P. stephanophrys* are known only from Palos Verdes Sand.

Total material: 4 otoliths (Fig. 6n).

*Rhacochilus vacca* (Girard)—pile perch

Pile perch remains have been found in several Pliocene and Pleistocene deposits in southern California (Fitch, 1967, and unpublished data), but until now they have not been reported from Palos Verdes Sand. Their massive, straight sided pharyngeal teeth are very distinctive, and two of these were found at the Crannell Road site and one at San Pedro (Table 2). The only pile perch otolith in Palos Verdes Sand came from one of the San Pedro localities.

Total material: 1 otolith (Fig. 5a) and 3 pharyngeal teeth.

*Roncador stearnsi* (Steindachner)—spotfin croaker

Spotfin croaker otoliths have been found only in the Signal Hill Pliocene (Fitch and Reimer, 1967), and in Palos Verdes Sand (Fitch, 1964; Table 2).

Total material: 22 otoliths (Fig. 5h).

*Sebastes diploproa* (Gilbert)—splitnose rockcod

*Sebastes jordani* (Gilbert)—shortbelly rockcod

*Sebastes paucispinis* Ayres—bocaccio

*Sebastes rhodochloris* (Jordan and Gilbert)—swordspine rockcod

Otoliths from these four species of *Sebastes* have all been reported (as *Sebastes*) from Palos Verdes Sand at Playa del Rey (Fitch, 1964). All except *S. paucispinis* were represented by a single otolith (there were 6 of *paucispinis*), and all except *paucispinis* have been found in other Pliocene

and Pleistocene deposits of southern California (unpublished data), but not in other exposures of Palos Verdes Sand (Table 2).

Total material: 6 otoliths of *S. paucispinis* and 1 each of the other three species (Figs. 6b to 6e).

*Sebastes serranoides* (Eigenmann and Eigenmann)—olive rockcod

The olive rockcod ranges from Crescent City to Cape Colnett, Baja California, in depths to 480 feet, but it is rare north of San Francisco. The species is reported to attain a length of 24 inches and a weight of seven to eight pounds, but no fish of that size has been measured or weighed. A single otolith found by Roy Kohl at the Crannell Road deposit is the only known fossil record of this species. Sagittae of a large adult will exceed 20.0 mm in length.

Total material: 1 otolith 21.0 mm long (Fig. 6a).

*Seriphus politus* Ayres—queenfish

Queenfish otoliths have been abundant in many Pliocene and Pleistocene deposits throughout southern California (Fitch, 1967, 1968, and unpublished data; Fitch and Reimer, 1967) and were particularly common in Palos Verdes Sand at Playa del Rey (Fitch, 1964, 1966). Subsequently, otoliths of *S. politus* have been found in all other exposures of Palos Verdes Sand including Crannell Road (Table 2). The single otolith from the Crannell Road deposit was tiny and badly eroded, however.

Total material: 514 otoliths (Fig. 5j).

*Sphyræna argentea* Girard—California barracuda

Otoliths of *S. argentea* have been found in two Pliocene deposits of southern California (unpublished data), but the single badly eroded otolith from Palos Verdes Sand at Playa del Rey (Fitch, 1964) is the only record of the species in the Pleistocene.

Total material: 1 otolith (Fig. 4h).

*Spirinchus starksi* (Fisk)—night smelt

Otoliths of *S. starksi* have been found in several Pleistocene deposits of southern California (Fitch, 1967, and unpublished data), but until now, they have not been reported from Palos Verdes Sand. The material I examined from Crannell Road contained 124 night smelt otoliths and many others were seen in the Lloyd Barker and Roy Kohl collections.

Total material: 177 otoliths (Fig. 1c).

*Spirinchus thaleichthys* (Ayres)—longfin smelt

The longfin smelt ranges from Hinchinbrook Island, Prince William Sound, Alaska, to San Francisco. It spawns in fresh water, but when not spawning, it is found in shallow to moderate depths outside the surf zone along the open coast. It is known to attain a length of just over six inches, and

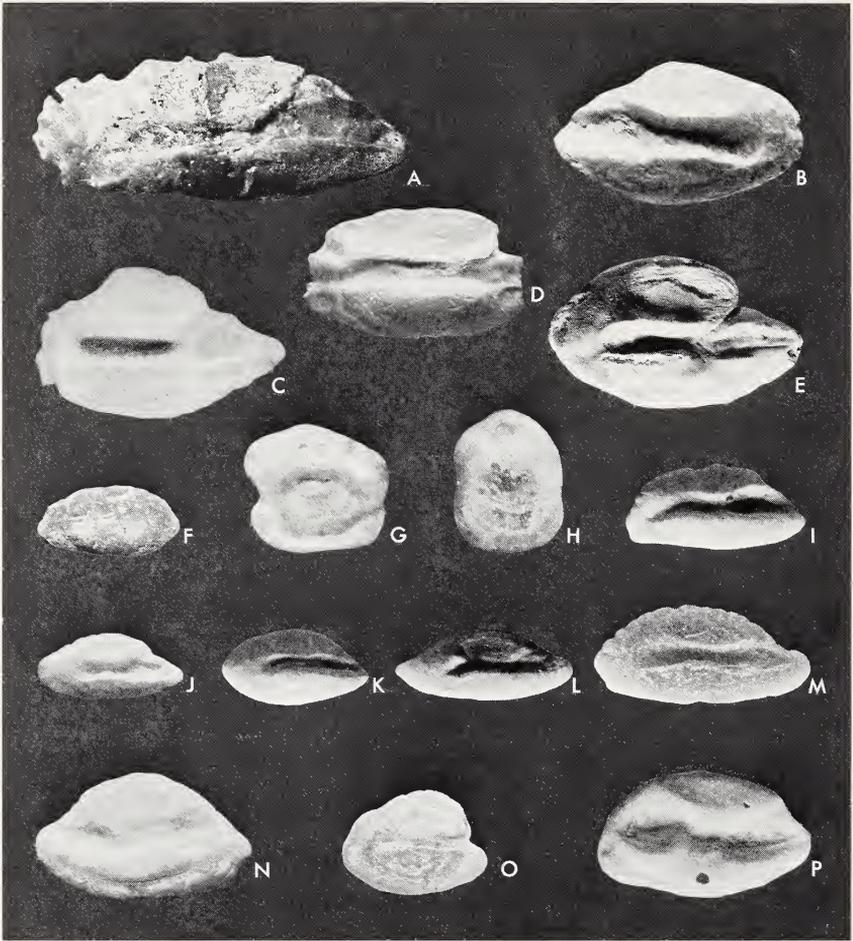


FIGURE 6. Fish otoliths found in various deposits of "Palos Verdes Sand." Lengths (in mm) are given for each otolith; notations are made regarding its position in the skull (left or right); otolith condition is noted if imperfect; and locality of fossil deposit is given. All otoliths in this figure are sagittae, and all views are inner faces. a. *Sebastes serranooides*, 21.0, l, Crannell Road; b. *Sebastes rhodochloris*, 7.0, r, Playa del Rey; c. *Sebastes diploproa*, 12.9, l, Playa del Rey; d. *Sebastes paucispinis*, 7.3, l, Playa del Rey, badly eroded and pieces missing from both ends; e. *Sebastes jordani*, 6.4, l, Playa del Rey; f. *Ammodytes hexapterus*, 3.0, r, Crannell Road; g. *Lepidogobius lepidus*, 2.3, l, V.T. Bridge; h. *Lethops connectens*, 1.4, l, Crannell Road; i. *Zaniolepis latipinnis*, 3.3, l, Playa del Rey, badly eroded; j. *Icelinus tenuis*, 3.8, l, V.T. Bridge; k. *Icelinus quadriseriatus*, 2.8, l, Playa del Rey, badly eroded; l. *Chitonotus pugetensis*, 4.6, l, Playa del Rey; m. *Leptocottus armatus*, 7.5, l, Crannell Road; n. *Prionotus stephanophrys*, 6.8, r, Playa del Rey; o. *Lycodopsis pacifica*, 3.2, l, Crannell Road; p. *Prionotus ruscarius*, 6.6, l, LACMIP, 131, badly eroded. Photographs by Jack W. Schott.

a weight of slightly more than one ounce. The five otoliths I found in the Crannell Road deposit constitute the only known fossil record for this species. Sagittae of a large adult will exceed 4.0 mm in length.

Total material: 5 otoliths 2.7 to 3.8 mm long (Fig. 1a).

*Stenobranchius leucopsarus* (Eigenmann and Eigenmann)—northern lampfish

The single otolith of *S. leucopsarus* from Playa del Rey (Fitch, 1966) is still the only record of this species from Palos Verdes Sand although its otoliths have been present in many other Pliocene and Pleistocene deposits and abundant in some (Fitch, 1967, 1968, and unpublished data).

Total material: 1 otolith (Fig. 1j).

*Symbolophorus californiensis* (Eigenmann and Eigenmann)—California lanternfish

Otoliths from *S. californiensis* have been found in several Pliocene and Pleistocene deposits in southern California including Palos Verdes Sand at Playa del Rey and Crannell Road (Fitch, 1964, 1969a). A single otolith also was found at one of the San Pedro sites (Fitch, 1969a; Table 2). The sagitta from Crannell Road is broken, and only the posterior half was found, but there is no question regarding its identification.

Total material: 3 otoliths (Fig. 1k).

*Symphurus atricauda* (Jordan and Gilbert)—California tonguefish

Two additional otoliths of *S. atricauda* have been found in Palos Verdes Sand at San Pedro (Table 2) since I first reported the species at Playa del Rey (Fitch, 1966). These 15 otoliths constitute the only fossil record of the species.

Total material: 15 otoliths (Fig. 4c).

*Synodus lucioceps* (Ayres)—California lizardfish

The California lizardfish has been recorded from San Francisco Bay to Cape San Lucas and throughout much of the Gulf of California. Larvae and young individuals up to about three inches live in the upper water layers, often over deep water many miles from shore. Adults live at or near the bottom in sandy areas, usually in depths of 60 to 150 feet but sometimes shallower or deeper. The largest individual known was 25 $\frac{1}{8}$  inches long and weighed just over four pounds. A single otolith from *S. lucioceps* was found at Playa del Rey; it was erroneously identified as *Occa verrucosa* in a previous report (Fitch, 1966). In *Occa* the cauda (posterior portion of the sulcus or groove on the inner face of the otolith) terminates farther forward than it does in *Synodus*, and this differentiating character sometimes is difficult to distinguish in eroded, worn, or broken otoliths. Sagittae of a large adult *S. lucioceps* will exceed 8.0 mm.

Total material: 1 otolith 3.0 mm long (Fig. 1k).

*Theragra chalcogramma* (Pallas)—walleye pollock

Four walleye pollock otoliths from Early Pleistocene in the cold-water Timms Point Silt (Fitch, 1968) and a badly eroded, broken fragment from the Palos Verdes Sand at San Pedro (Table 2) constitute the only fossil record for this northern species. The only reasonable explanation for its presence in a warm-water deposit would entail predation offshore in deep (cold) water, erosion by digestive action in the alimentary tract of the predator and excretion in shallow (warm) water several hours after ingestion. Otoliths of prey species often are broken while being eaten, and erosion of all exposed surfaces including concave areas can be accomplished only by digestive action.

Total material: 1 eroded otolith fragment (Fig. 2g).

*Trachurus symmetricus* (Ayres)—Pacific jack mackerel

The three otoliths reported from Playa del Rey (Fitch, 1966) and two that I misidentified as *Phanerodon furcatus* (Fitch, 1964) constitute the only record of *T. symmetricus* from Palos Verdes Sand although jack mackerel sagittae have been present in several other Pliocene and Pleistocene deposits (Fitch, 1967, 1968, and unpublished data).

Total material: 5 otoliths (Fig. 4a).

*Umbrina roncador* Jordan and Gilbert—yellowfin croaker

Remains of *U. roncador* have been found only in the San Diego Fm. (Pliocene) and in Palos Verdes Sand. The 17 otoliths from Playa del Rey (Table 2) have been reported (Fitch, 1964, 1966), but those from the San Pedro site have not been noted previously.

Total material: 23 otoliths (Fig. 5o).

*Xenistius californiensis* (Steindachner)—salema

The salema ranges from Monterey Bay to Peru, but it seldom is present off California except during warm water years and even then it usually is not abundant. It is an inhabitant of shallow water (to perhaps 60 feet) along the outer coast, but sometimes enters bays and lagoons. Salemas are reported to attain a length of 10 inches, but no weights are available for fish that size. Seven otoliths from Playa del Rey, erroneously identified as *Phanerodon furcatus* in my earliest report on that site (Fitch, 1964), constitute the only fossil record of this species. When in perfect condition, sagittae of adult *X. californiensis* differ from *P. furcatus* in many respects, but the two best characters on the worn fossils (i.e., posterior otolith taper and angle of downward flexure of the cauda) were overlooked in making my earlier determinations. Sagittae of a large adult will exceed 9.0 mm in length.

Total material: 7 otoliths 6.6 to 9.7 mm long (Fig. 4g).

*Zaniolepis latipinnis* Girard—longspine combfish

The single otolith of *Z. latipinnis* reported from Palos Verdes Sand at Playa del Rey (Fitch, 1966) is still the only fossil record of the species.

Total material: 1 otolith (Fig. 6i).

### Unidentified teleosts

Many otoliths are so badly broken or worn that they cannot be identified, even to family. Many others can be placed in a particular family but cannot be identified as to genus, and still others can be given generic, but not specific, names. Juvenile rockcod otoliths (*Sebastes* spp.) are almost impossible to assign to species, yet they are easy to distinguish from *Sebastolobus* and *Scorpaena*, the other two commonest genera in the family.

Forty-three otoliths found in various exposures of Palos Verdes Sand were too broken or worn to assign any taxon (Table 2). Twenty-three otoliths and nine teeth could be placed in three families (atherinids: 11 otoliths; cottids: 2 otoliths; and embiotocids: 10 otoliths and 9 teeth) but could not be assigned to genera within these families. Finally, 131 otoliths unquestionably belonged to four genera (*Citharichthys*, *Otophidium*, *Porichthys* and *Sebastes*) but could not be identified to species. For the first three named genera no additional species could have resulted, but if additional *Sebastes* otoliths could have been identified, it could have increased the faunal list for Palos Verdes Sand. As an example, at Crannell Road only one species of *Sebastes* could be named, but the 20 unnamed otoliths (six in Lloyd Barker's collection) were unquestionably from at least four additional species. Some, if not all of these, very likely were different from the four named species found in the Playa del Rey area (Table 2).

Total material: 197 otoliths and 9 teeth.

### DISCUSSION

Three of the 18 (at least) kinds of sharks, skates and rays reported from Palos Verdes Sand of southern California (Table 1) are "southern" species. *Rhizoprionodon* has been recorded only once north of Mexico, but *Carcharhinus* and *Sphyrna* are observed or caught in our coastal waters during most periods when ocean temperatures are considerably warmer than normal (Radovich, 1961). The other 15 kinds of elasmobranchs are year around residents of the ocean off California, but some of these are not present during all months and others are never abundant.

Since 10 of the 59 teleosts from the southern Californian deposits of Palos Verdes Sand are southern species and three are mesopelagics, one would not expect to capture these in routine netting operations or inside the 100-fathom curve. The 46 remaining species are year around residents, however, and all but three of these (*Pimelometopon*, *Sebastes rhodochloris* and *Theragra*) were components of beach seine and trawl catches made off southern California during recent years (Carlisle, Schott and Abramson, 1960; Carlisle, 1969; Table 3). Only *Theragra*, of the three not captured in these netting operations, is not normally taken south of Point Conception. *Pimelometopon* and *Sebastes rhodochloris* are common in offshore rocky habitat which is unsuitable for trawling.

Six of the 10 southern teleosts (*Bairdiella*, *Cynoscion reticulatus*, *Lepophidium*, *Micropogon*, *Ophioscion* and *Prionotus ruscarius*) have not been captured within several hundred miles of California during modern times (Table 4). Of the remaining four, *Xenistius* and *Prionotus stephanophrys* have been noted on many occasions, whereas, neither *Calamus* nor *Coelorrhynchus* has been reported north of Mexico more than two or three times.

TABLE 3

Teleosts reported from Palos Verdes Sand which comprised portions of beach seine and trawl catches

		Method and depth of capture	
Beach seine only <sup>1</sup> < 10 feet	Beach seine and trawl <sup>1, 2</sup> Maximum depth (in feet) noted		Trawl only <sup>2</sup> Minimum depth (in feet) noted
<i>Amphistichus koelzi</i>	<i>Citharichthys sordidus</i> 528		<i>Argentina sialis</i> 120
<i>Anchoa compressa</i>	<i>Citharichthys stigmaeus</i> 540		<i>Chitonotus</i> <i>pugetensis</i> 126
<i>Anisotremus</i> <i>davidsonii</i>	<i>Cymatogaster aggregata</i> 346		<i>Citharichthys</i> <i>xanthostigma</i> 60
<i>Atherinops affinis</i>	<i>Embiotoca jacksoni</i> 60		<i>Icelinus</i> <i>quadriseriatus</i> 60
<i>Atherinopsis</i> <i>californiensis</i>	<i>Engraulis mordax</i> 600		<i>Icelinus tenuis</i> 186
<i>Cynoscion nobilis</i>	<i>Genyonemus lineatus</i> 426		<i>Lyopsetta exilis</i> 60
<i>Leptocottus armatus</i>	<i>Lepidogobius lepidus</i> 300		<i>Merluccius</i> <i>productus</i> 360
<i>Leuresthes tenuis</i>	<i>Paralabrax</i> spp. 120		<i>Otophidium scrippsi</i> 60
<i>Menticirrhus</i> <i>undulatus</i>	<i>Paralichthys</i> <i>californicus</i> 436		<i>Otophidium taylori</i> 60
<i>Roncador stearnsi</i>	<i>Pleuronichthys ritteri</i> 285		<i>Parophrys vetulus</i> 60
<i>Sphyraena argentea</i>	<i>Porichthys myriaster</i> 387		<i>Porichthys notatus</i> 60
<i>Umbrina roncador</i>	<i>Rhacochilus vacca</i> 60		<i>Sebastes diploproa</i> 180
	<i>Seriphus politus</i> 126		<i>Sebastes jordani</i> 378
	<i>Symphurus atricauda</i> 563		<i>Sebastes paucispinis</i> 120
			<i>Synodus lucioceps</i> 60
	<i>Trachurus symmetricus</i> 600		<i>Zaniolepis latipinnis</i> 118

<sup>1</sup> from Carlisle, Schott and Abramson (1960)

<sup>2</sup> from Carlisle (1969)

TABLE 4

Fish species whose fossil record is exclusively in  
deposits of Palos Verdes Sand

Southern Californian exposures	Crannell Road (Northern California)
<i>Alopias vulpinus</i>	<i>Allosmerus elongatus</i>
<i>Dasyatis dipterurus</i>	<i>Amphistichus rhodoterus</i>
<i>Notorynchus maculatus</i>	<i>Anarrhichthys ocellatus</i>
<i>Rhizoprionodon longurio</i> *	<i>Hippoglossus stenolepis</i>
<i>Amphistichus koelzi</i>	<i>Hyperprosopon ellipticum</i>
<i>Anchoa compressa</i>	<i>Hypomesus pretiosus</i>
<i>Anisotremus davidsonii</i>	<i>Isopsetta isolepis</i>
<i>Argentina sialis</i>	<i>Onocorhynchus tshawytscha</i>
<i>Bairdiella icistia</i> *†	<i>Ophiodon elongatus</i>
<i>Calamus brachysomus</i> *	<i>Platichthys stellatus</i>
<i>Coelorhynchus scaphopsis</i> *	<i>Sebastes serranoides</i>
<i>Cynoscion reticulatus</i> *†	<i>Spirinchus thaleichthys</i>
<i>Lepophidium negropinna</i> *†	
<i>Leuresthes tenuis</i>	
<i>Menticirrhus undulatus</i>	
<i>Micropogon ectenes</i> *†	
<i>Ophioscion</i> sp.*†	
<i>Paralabrax</i> sp.	
<i>Pleuronichthys ritteri</i>	
<i>Prionotus ruscarius</i> *†	
<i>Prionotus stephanophrys</i> *	
<i>Symphurus atricauda</i>	
<i>Synodus lucioceps</i>	
<i>Xenistius californiensis</i> *	
<i>Zaniolepis latipinnis</i>	

\* southern species

† locally-extinct southern species

In our area, *Pionotus* and *Coelorhynchus* are found in depths exceeding 60 feet, but *Xenistius* and *Calamus* reside in relatively shallow near-shore waters.

Five of the 37 teleosts found in the northern California equivalent of Palos Verdes Sand (Crannell Road) are southern species for that latitude (i.e., *Genyonemus*, *Hyperprosopon anale*, *Lethops*, *Sebastes serranoides* and *Symbolophorus*), but only *Lethops* has not been reported that far north (by several hundred miles) during modern times. Except for the two mesopelagics (*Diaphus* and *Symbolophorus*), all of the fishes identified from the Crannell Road deposit can be captured at depths shallower than 120 feet. *Diaphus* has

been netted off northern California in 35 fms (210 feet), but *Symbolophorus* generally inhabits waters outside the continental shelf.

In my investigations of Plio-Pleistocene fishes of California I have identified the remains of 23 kinds (at least) of elasmobranchs and 150 species of teleosts. Some species (e.g., *Citharichthys*, *Genyonemus*, *Porichthys*, *Seriplus*, etc.) have turned up in almost every deposit I have examined, but others have been in only one stratum, or at one particular site to the exclusion of all others. Thirty-seven fishes, including four elasmobranchs, are found exclusively in Palos Verdes Sand, including the northern Californian equivalent (Table 4), but only the 11 southern forms could be considered indicator species for this period of the Pleistocene.

Critical examination of additional deposits of Palos Verdes Sand in northern California undoubtedly would lengthen the list of species (Table 4) exclusive to this stratum, but examination in northern California and Oregon of Pliocene and Pleistocene deposits representing other time periods would shorten the Crannell Road list of "exclusives" by possibly 50 percent.

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Jack W. Schott took the excellent otolith photographs, Larry Reynolds applied his photo processing skills on the otolith prints and Mrs. Loretta Proctor typed the final draft of the manuscript.

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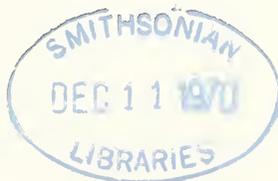
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NOVEMBER 13, 1970

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VIRGINIA D. MILLER  
*Editor*

A NEW SPECIES OF *BATRACHOSEPS*  
(SLENDER SALAMANDER)  
FROM THE DESERT OF SOUTHERN CALIFORNIA

By ARDEN H. BRAME, JR.<sup>1</sup>

ABSTRACT: A new species of *Batrachoseps* is described from the lower desert slopes of the Santa Rosa Mountains. This species occurs in a small canyon tributary of Deep Canyon beneath limestone sheeting where there is perennial water seepage and below talus on the canyon floor during the wetter months. The closest relative of this desert slender salamander is *Batrachoseps stebbinsi* with which it agrees by having large feet, low numbers of trunk vertebrae, and a reduced phalangeal formula of 0-2-3-2. The new species, a broadheaded salamander, is primitive, and probably is a fragment of a once widely distributed form. *Batrachoseps stebbinsi*, *B. pacificus* and *B. simatus* possibly represent other fragments of the same ancestral population.

In the most recent review of the genus, Brame and Murray (1968), described three new species of *Batrachoseps* and elevated *B. major* to a full species. In addition, they compared the morphology and ecology of each of the then known species. They indicated that *Batrachoseps wrighti* is the most primitive species and is restricted to derivatives of Arcto-Tertiary plant communities of north-central Oregon. They considered *Batrachoseps relictus* to be close to the ancestral form that gave rise to all of the species in California and northern Baja California, and showed it to occur in four disjunct regions: (1) the Santa Lucia Range of Monterey and San Luis Obispo counties, (2) 1,000 to 8,000 feet elevation on the western slopes of the Sierra Nevada, (3) Santa Cruz Island off Santa Barbara County, and (4) 6,000 to 8,000 feet elevation in the San Pedro Martir Range of Northern Baja California, Mexico. In each of these areas, *Batrachoseps relictus* occurs within derivatives of Arcto-Tertiary or Arcto-Tertiary-Madro-Tertiary ecotonal communities. Brame and Murray suggested that *Batrachoseps stebbinsi* of the Piute and Tehachapi mountains in Kern County, *Batrachoseps simatus* of the Kern River Canyon, Kern County, and *B. pacificus* of the Northern Channel Islands off Santa Barbara and Ventura counties, probably arose from a *relictus*-like ancestor at an early time and possibly represent fragments of a once continuous species inhabiting primarily Arcto-Tertiary communities. *Batrachoseps attenuatus*, ranging from southwestern Oregon to southwestern California and the lower elevations of the western slopes of the Sierra Nevada, and *B. major* of southwestern California and northwestern Baja California are considered more recently derived forms from *Batrachoseps relictus*. Both have been able

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to adapt to the drying trends of the Pleistocene and have successfully invaded the Madro-Tertiary floral communities. Brame and Murray discussed some dubious records for *Batrachoseps* from southwestern Alaska, the Nevada de Colima in Mexico, and the Cape region of southern Baja California, Mexico, the latter area being isolated by desert to the north and ocean or gulf on the other three sides. It is hoped that renewed interest in verifying these questionable records will now be stimulated based upon the unusual desert habitat for the new *Batrachoseps* species herein described.

Warden Russel W. Murphey of the California Department of Fish and Game, hiked down the steep east-facing desert slopes to a tributary of and above Deep Canyon, Riverside County, during the late summer of 1969, and found a moist water seepage area below the canyon cliffs. In order to create a small water hole for the native wildlife, he began pulling off the hard rock-like encrusted limestone overlying a moist sandy soil and granitic rock beneath and discovered, to his amazement, clusters of salamanders, the first desert record and the most eastern known salamander in California. Unfortunately these specimens died in captivity, but Warden Murphey, in the company of the author and James E. De Weese, returned to the locality early in 1970 and collected 8 additional specimens. The series of *Batrachoseps* proved to represent a new species, and due to the unusual arid environment for a salamander, I propose that it be known as:

*Batrachoseps aridus*, new species

Figures 1-5; Table 1

*Suggested common name.* Desert Slender Salamander.

*Holotype.* LACM 56271, an adult female from Hidden Palm Canyon, a tributary of Deep Canyon, elevation approximately 2500 feet, (10.5 miles by road S of the intersection of state Highways 111 and 74, town of Palm Desert), NW end of Santa Rosa Mountains, from slopes on western side of Coachella Valley, Riverside County, California; collected by Russel W. Murphey, James E. De Weese, and the author, February 27, 1970, (see map, Fig. 5, for locality and Figs. 1 and 2 of holotype).

*Paratypes.* LACM 56272-78 (7 specimens), collected with the holotype; and LACM 56570-80 (11 specimens), collected March 22, 1970, by Allan L. Reinholtz, Patricia L. Brame and the author.

*Diagnosis.* A moderately small species, 14 adults ranging from 30.3 to 48.4 mm (mean 37.4) in standard lengths; with short tails; and distinguished from all other species of *Batrachoseps* by its distinctive ventral coloration consisting of blackish maroon on belly and gular area, sharply contrasted with the flesh colored tail venter (see color pattern, Fig. 1); distinguished from all other species of *Batrachoseps* except *B. stebbinsi* by having an 0-2-3-2 hand and foot phalangeal formula (*B. attenuatus* rarely has an 0-2-3-2 formula); and distinguished from all other species of *Batrachoseps*, except *B. pacificus*, by having a proportionally broader head, standard lengths 5.7-7.4 (mean 6.5)

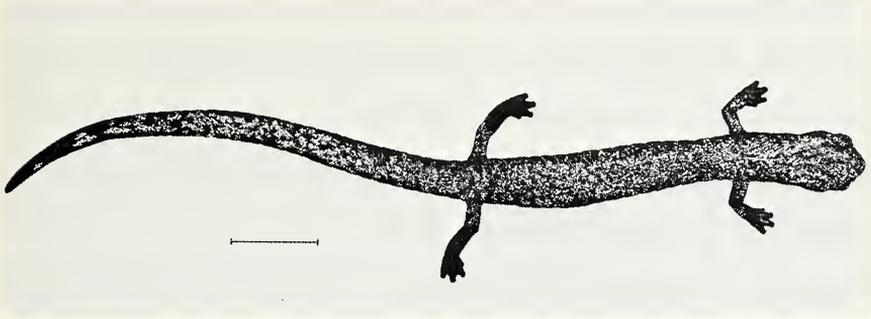


FIGURE 1. Holotype of *Batrachoseps aridus*, new species, LACM 56271, an adult female. Line equals 1 centimeter.

times head widths versus 7.0-8.1 (mean 7.4) in *pacificus* and greater than 7.5 for the other *Batrachoseps* species. See section on comparison for additional character differences between *Batrachoseps aridus* and the other seven species in the genus.

*Description of holotype.* An adult female, snout moderately short, somewhat pointed at tip; nostril moderately small, nasolabial groove well defined. Standard length 7.4 times head width; standard length 4.5 times snout-gular fold length. Eye large and protuberant. Well defined postorbital groove extends posteriorly from eye as shallow depression to three grooves that proceed sharply ventrally, for 2.2 mm to 1st groove which becomes the 1st nuchal groove ventrally, for 3.8 mm to the 2nd groove, which becomes the 2nd nuchal groove ventrally, and 5.7 mm to the 3rd groove which becomes the gular fold groove ventrally. The 1st nuchal groove is 2.8 mm and the 2nd nuchal groove is 1.8 mm anterior and parallel to the gular fold groove. Vomerine teeth 11 left, 12 right, extending diagonally in a posterior direction from the medial border of the internal nares, arranged in patches. Maxillary teeth 22 left, 23 right, extend about two-thirds through eye. Premaxillary teeth 10, not piercing lip. Intercostal grooves 18 per side. Tail short, 0.99 times standard length; dorsoventrally compressed at base but more rounded from middle to tip; not noticeably constricted at base. Postiliac gland not evident. Limbs very long, appressed limbs leave 6.5 intercostal folds uncovered; hind limb overlaps 5.5 intercostal folds; standard length 5.3 times right fore limb, 4.8 times right hind limb; coupling value 1.53 (axilla-groin length divided by combined hind and fore limb lengths). Webbing of hands and feet moderate, leaving 1 to 1.5 phalanges free of web. Fingers and toes with large subdigital pads except first digit, which has somewhat reduced pad; fingers in order of decreasing length: 3, 2, 4, 1; toes in order of decreasing length: 3, 2, 4, 1.

*Osteological characters from x-ray of holotype.* 20 trunk vertebrae; 2 caudal-sacral vertebrae; 19 ribs; phalangeal formula (both feet) 0-2-3-2,

(both hands) 0-2-3-2, terminal phalanges slightly expanded at tips; single premaxillary bone.

*Measurements (in mm).* Head width, 6.5; snout to gular fold (head length), 10.8; head depth at posterior angle of jaw, 2.7; eyelid length, 2.8; eyelid width, 2.0; anterior rim of orbit to snout, 2.2; horizontal orbital diameter, 2.0; interorbital distance, 1.2; distance between vomerine teeth and parasphenoid tooth patch, 1.0; snout to fore limb, 13.0; distance separating internal nares, 1.8; distance separating external nares, 1.8; snout projection beyond mandible, 0.8; snout to posterior angle of vent (standard length), 48.4; snout to anterior angle of vent, 45.8; axilla to groin length, 29.4; tail length, 47.8; tail width at base, 2.8; tail depth at base, 2.4; fore limb length, 9.2; hind limb length, 10.0; width of right hand, 2.6; width of right foot, 3.2.

*Color in life.* Dorsum blackish maroon, overlaid with an indistinct lighter dorsal band visible from the tip of the snout, top and sides of head; trunk dorsum, to four-fifths length of tail, composed of silver to brassy iridophores interspersed with some larger patches of metallic golden orange iridophores. Ventrally, the gular area and trunk are a darker blackish maroon, darker than dorsally, with numerous silver iridophores on the neck and some scattering on the gular surface. The tail venter is a pale pinkish brown (flesh colored) in marked contrast to the rest of the animal. The silver to brassy iridophores are also abundant on the upper arms and legs dorsally with a few scattered also on the fore arms. The iris is a deep blackish maroon with brassy iridophores.

*Variation.* There are no sexually dimorphic characters, other than the larger size of females and papillate vents of males. The holotype has the narrowest head (6.5 mm) at 48.4 mm standard length, and another female, LACM 56574, has the broadest head (6.4 mm), nearly the same head width at a much smaller size, 36.5 mm standard length. Aside from the somewhat striking variation in head widths, the series of *Batrachoseps aridus* is not too variable in other characters (see Table 1 for comparative measurements). All are quite similar in color to the holotype, except LACM 56571, a male, which is more of a uniform chocolate-brown in ground color with no iridophores present (see Fig. 1 for normal color pattern). The paratypes agree with the holotype in phalangeal formula, but 10 of the 18 paratypes have only 19 trunk vertebrae and 18 ribs, whereas 7 agree with the holotype in having 20 trunk vertebrae and 19 ribs. In six paratypes, tibial spurs can be seen (probably present in all *Batrachoseps aridus*, but difficult to see in x-rays). One paratype, LACM 56574, has multiple vertebrae fusions with four pairs of ribs extending from one fusion and three left, and two right from another fusion, so its vertebral count was not incorporated above.

*Comparison.* In addition to the characters discussed in the section on diagnosis, *Batrachoseps aridus* is distinguished from all other species of *Batrachoseps* by having proportionately longer heads, standard lengths 4.1-4.7 (mean 4.4) times snout-gular fold lengths (= head lengths); by having

proportionately longer limbs, standard lengths 4.0-4.8 (mean 4.4) times right hind limb lengths; costal folds left uncovered by appressed limbs (= limb interval) 3.5-6.5 (mean 5.0); coupling values (right hind limb length + right fore limb length divided into axilla-groin length) 1.08-1.53 (mean 1.31); by having proportionately larger feet, standard lengths 12.5-15.1 (mean 13.7) times right foot widths; costal grooves 16-19 (mean 17.8) per side (see Brame and Murray, 1968: 28-29, Table 5, for comparative data for the other seven species of *Batrachoseps*); and by its distinctive coloration of black to chocolate-maroon ground color dorsally with an indistinct band composed of hundreds of separated silver to brassy iridophores intermixed with orange-gold patches of iridophores on front part of head, trunk, first four-fifths of tail, sides of head, neck and shoulders, and silver iridophores scattered on gular surface and abundant on neck venter region; venter of trunk darker than dorsum and more of a darker maroon-black, tail flesh colored ventrally in marked contrast to trunk venter. Distinguished from its apparent closest relative, *Batrachoseps stebbinsi*, by its smaller size, 30.3-48.4 (mean 37.4 mm) standard lengths versus 50.8-60.4 (mean 55.2 mm); by its proportionately broader head, standard lengths 5.7-7.4 (mean 6.5) times head widths in contrast to 7.5-8.4 (mean 8.0) for 10 *B. stebbinsi*; by its proportionately longer head, standard lengths 4.1-4.7 (mean 4.4) times snout-gular fold lengths versus 4.5-5.4 (mean 5.1) for 10 *B. stebbinsi*; by its proportionately longer limbs, standard lengths 4.0-4.8 (mean 4.4) times right hind limb lengths compared to 4.5-5.1 (mean 4.8) for *B. stebbinsi*; coupling values for 18 *B. aridus* = 1.08-1.53 (mean 1.31) versus 1.38-1.62 (mean 1.51) for 10 *B. stebbinsi*; costal folds uncovered by appressed limbs 3.5-6.5 (mean 5.0) in contrast to 6-7 (mean 6.25) for 10 *B. stebbinsi*; by having proportionately broader feet, standard lengths 12.5-15.1 (mean 13.7) times right foot widths compared to 13.9-16.4 (mean 14.7) for 10 *B. stebbinsi*; by having usually one-half to one more costal grooves per side of trunk, costal grooves 16-19 (mean 17.8) per side versus 18-19 (mean 18.5) for 10 *B. stebbinsi* (trunk vertebrae 19-20 (mean 19.4) for *B. aridus* and 20 for *B. stebbinsi*); and by marked differences in coloration (see color pattern, Figs. 1 and 2, and Brame and Murray, 1968: 20); basic color differences are presence of distinct dorsal band (often beige), presence of distinct solid or broken dorsolateral black stripes, ground color of venter and tail black, white iridophores abundant ventrolaterally though mostly absent midventrally except on gular area, shoulders, and neck; iris light brown with brassy iridophores for *B. stebbinsi* in contrast to the coloration of *B. aridus* which has an indefinite dorsal band composed of hundreds of scattered silver to brassy iridophores and some gold-orange patches of iridophores on a dark black-maroon to chocolate-maroon ground color; dorsolateral stripes absent, ground color of venter blackish-maroon except for tail which is flesh color; silver iridophores absent both ventrolaterally and midventrally except on shoulders, neck and gular area, and iris very dark black-maroon with brassy iridophores. *Batrachoseps aridus* and

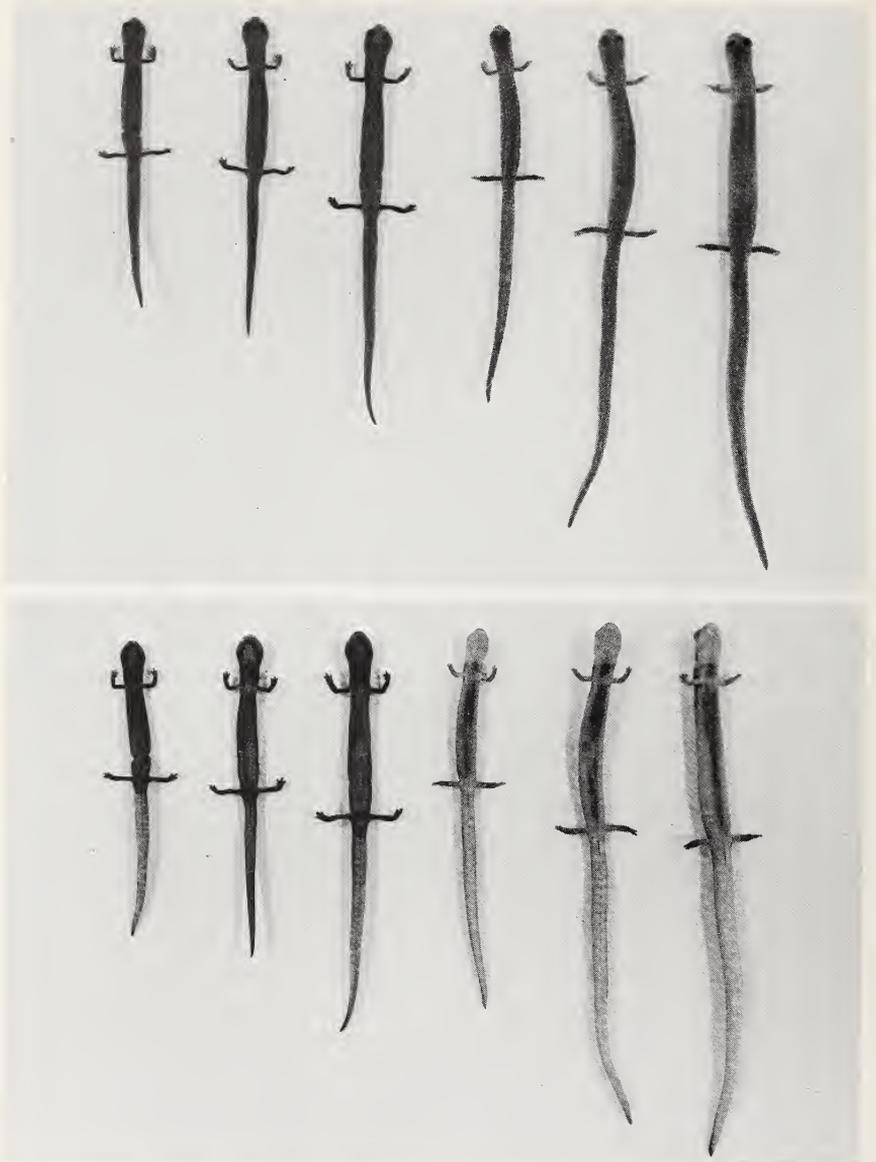


FIGURE 2. **Upper:** dorsal views of 3 *Batrachoseps aridus*, new species, at left, from left to right—LACM 56573, LACM 56272, and the holotype, LACM 56571, all from the type locality; and 3 *B. major* at right, from left to right—LACM 56283, LACM 56281, and LACM 56280, all from W. Exposition Blvd. between 5th and 10th Avenues, Los Angeles. **Lower:** ventral views of the same individuals in the same order.

*B. stebbinsi* are the only *Batrachoseps* to have a phalangeal formula of 0-2-3-2 for the feet although it occurs rarely in *B. attenuatus*. The normal phalangeal formula for the other six species (including *attenuatus*) is 1-2-3-2.

*Habitat.* The type locality is located on the lower eastern slope of Black Hill, about 500 feet elevation below State Highway 74 (= Pines to Palms Highway). The exposed slopes, both east and west above Hidden Palm Canyon, have a flora composed largely of cholla, agave, barrel cactus, prickly pear cactus, creosote, manzanita, juniper and mesquite. The canyon floor flora is dominated by sugar bush, willow, Washington palms, creosote, mesquite, and various grasses, and mosses, algae and maiden-hair fern on the perpetually shaded north and west facing cliff-like walls of the canyon. A continu-



FIGURE 3. View down the east facing slope with cholla and agave in the lower right corner of the picture; the canyon floor at the left center of the picture with the prominent Washington palms; the well shaded west facing slope in the background, composed of limestone deposits overlying sand and granitic rock beneath; the type locality of *Batrachoseps aridus*, new species, at the base of this slope and several yards up the canyon (hidden from view) to the right (south). This locality is Hidden Palm Canyon, about 2500 feet elevation. (See text for additional type locality description and data, and map, Fig. 5.)

ous water seepage occurs at various areas along these cliffs and is apparently much more widespread in wetter years judging from the extensive sheet-like calcium carbonate (limestone) deposits. Many of the *Batrachoseps aridus* were taken beneath sheets of limestone during the late summer of 1969<sup>1</sup>, but only a few were found there during February and March, 1970. Most of these were taken beneath rocks at the lower level of the cliffs or at the base of the north and west facing cliffs or in rock talus. The soil underneath the limestone sheets and talus rocks appears to be composed largely of coarse sand intermixed with small granitic rocks. Sugar bush is abundant at the base of the north and west facing cliffs (see habitat views, Figs. 3 and 4).

*Range.* Known only from the type locality (see map Fig. 5).

*Evolutionary relationships.* Morphologically, *Batrachoseps aridus* is closer to *B. stebbinsi* than to other species, and it possesses the proportionately broadest head, longest limbs and biggest feet of all species. It also has fewer



FIGURE 4. View of the type locality of *Batrachoseps aridus*, new species, the majority of the type series being taken from the talus slope at the lower right of the picture. A few were collected beneath the limestone sheeting at the left center. Water seepage occurs beneath the limestone and talus.

<sup>1</sup>On July 25, 1970, 10 additional specimens (LACM 61272-61281) were obtained from beneath and within moderately soft porous limestone at the type locality, thus confirming that this species is active in the summer months.

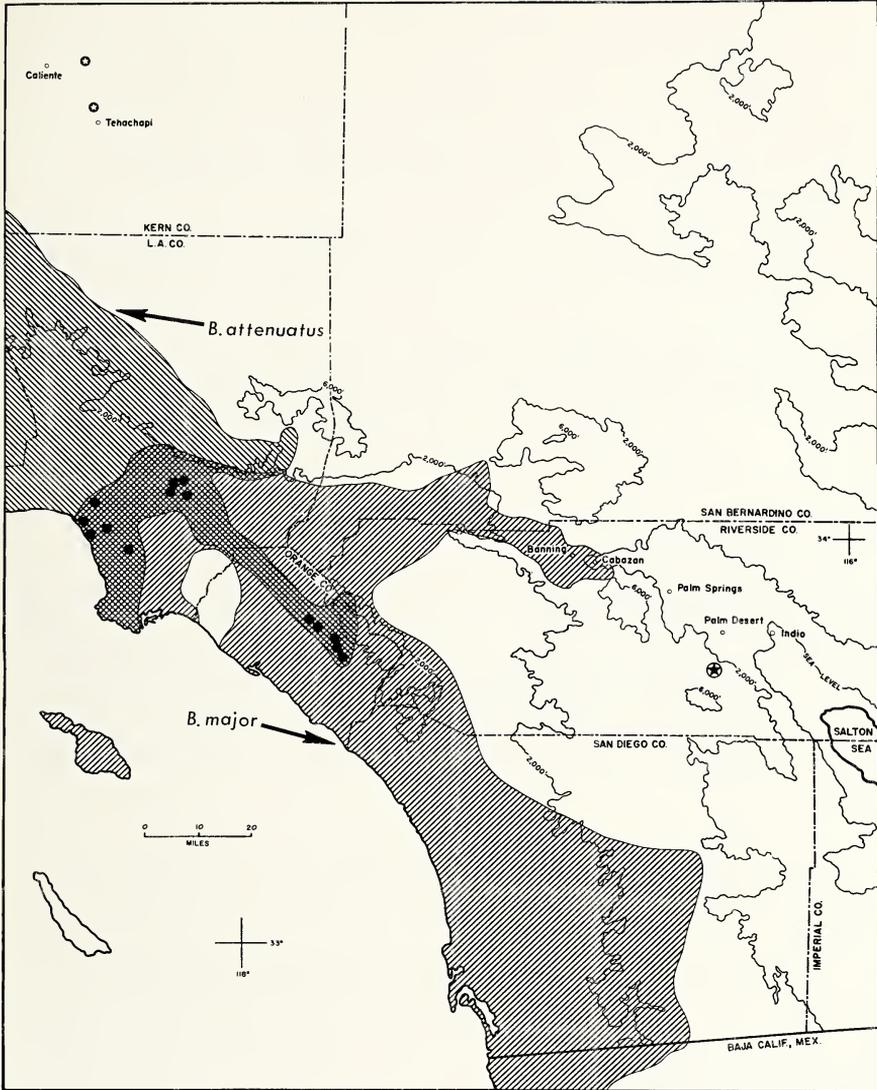


FIGURE 5. Map of southern California showing the type locality for *Batrachoseps aridus*, new species (solid star in open circle). The two localities for *Batrachoseps stebbinsi* are indicated by the open stars inside solid circles. The ranges of *B. major* in the southwest and *B. attenuatus* in the northwest are shown. Cross-hatching indicates the region of geographic overlap. Actual localities of sympatry between *B. major* and *B. attenuatus* are indicated by solid circles.

TABLE 1 Measurements and data for *Batrachoseps aridus*

	Sex	Standard Length	Axilla-Groin Length	Head Width	Hind Limb Length	Fore Limb Length	Intercostal Grooves	Limb Interval <sup>a</sup>	Coupling Value	Maxillary Teeth	Vomerine Teeth	Tail Length	Foot Width	Head Length
LACM 56271 <sup>b</sup>	♀	48.4	29.4	6.5	10.0	9.2	18	6.5	1.53	22-23	11-12	47.8	3.2	10.8
LACM 56272	♀	40.9	23.7	6.2	8.9	8.0	17.5	5.5	1.40	23-23	12-10	35.0	3.0	9.2
LACM 56570	♀	40.6	24.1	6.0	9.2	8.2	18	6	1.38	21-19	10-9	38.4	3.0	8.7
LACM 56573	♀	36.9	21.3	5.8	8.0	6.8	18	5.5	1.44	16-17	9-10	33.2	2.9	8.2
LACM 56574 <sup>c</sup>	♀	36.5	19.5	6.4	9.0	8.2	17 <sup>c</sup>	3.5 <sup>c</sup>	1.13 <sup>c</sup>	24-21	11-10	35.1	2.8	9.0
LACM 56576	♀	36.3	21.3	5.4	8.0	7.2	18.5	5	1.40	15-17	8-10	31.7	2.6	8.2
LACM 56575	♀	35.3	20.7	5.6	8.2	7.2	18	5.5	1.34	19-19	8-10	30.1	2.5	7.9
LACM 56275	♀	32.2	18.4	5.2	7.5	7.0	18	5	1.27	16-17	9-8	27.8	2.4	7.8
LACM 56577	♀	31.1	18.2	4.8	7.0	6.6	18	5.5	1.34	17-14	9-9	24.0	2.2	7.1
LACM 56273	♂	40.0	22.8	5.9	8.6	7.6	18	6	1.41	19-17	8-9	32.8	2.8	8.8
LACM 56571	♂	39.3	23.0	5.9	8.7	7.8	18	6	1.39	21-17	9-12	36.2	2.8	8.3
LACM 56572	♂	38.0	21.3	6.2	8.5	7.7	18	5	1.31	19-16	10-10	33.8	2.7	8.9
LACM 56274	♂	37.1	21.1	5.6	8.7	7.8	16.5	4	1.28	16-20	10-8	24.3 <sup>d</sup>	2.8	8.0
LACM 56276	♂	30.3	17.4	4.7	7.0	6.4	18	4.5	1.30	17-13	5-7	15.7 <sup>d</sup>	2.2	7.2
LACM 56578	juv.	29.8	16.8	4.8	6.9	6.7	18	4.5	1.24	15-18	7-8	22.8	2.2	7.0
LACM 56579	juv.	29.4	16.4	4.6	7.3	6.3	17	4.5	1.21	15-15	6-8	23.9	2.0	6.8
LACM 56277	juv.	28.5	16.2	4.3	6.8	6.2	18	4	1.08	17-16	7-8	20.3	2.1	6.7
LACM 56580	juv.	27.6	15.7	4.5	6.9	6.2	18	4	1.20	13-13	6-7	21.8	2.2	6.8

a = Number of intercostal folds left uncovered when the limbs are appressed to sides, b = Holotype.

c = Aberrant specimen with multiple vertebral fusions, d = Regenerated or broken tails.

trunk vertebrae, 19-20 (mean 19.4), and costal grooves, 16-19 (mean 17.8) except for some populations of *B. relictus* and all *B. wrighti* which have one to two less. These characters can all be classified as primitive and I believe *Batrachoseps aridus* evolved early, probably from a common ancestor of *B. stebbinsi*. Now it is apparently restricted to a spring-fed, protected canyon in an arid desert and possibly to other suitable relict "oases" and similar habitats in nearby regions, whereas *B. stebbinsi* is restricted to the two small area localities in the Piute and Tehachapi mountains of Kern County about 160 airline miles to the northeast in a pine-oak and riparian habitat (see map, Fig. 5). To a lesser extent, *Batrachoseps aridus* is related also to *B. pacificus* of the Northern Channel Islands and more remotely to *B. simatus* of the Kern River Canyon of Kern County. The four species, *B. aridus*, *B. stebbinsi*, *B. pacificus* and *B. simatus*, may represent fragmentations of a once widespread species. (See Brame and Murray, 1968: 27-34 for discussion of species relationships and evolution of the genus.)

#### REMARKS

Additional search should be made of well shaded desert canyons, especially in places where there are limestone deposits and perennial water seepage. Because of the limited extent of the habitat (the limestone sheets could easily be decimated) of *Batrachoseps aridus*, I strongly urge that it be placed on the official red book list of rare and endangered species (U.S.A. and International); steps should be taken to protect this unusual habitat and its interesting occupants. A similar action has already been taken with regard to *Batrachoseps stebbinsi*.

#### ACKNOWLEDGMENTS

My chief debt of gratitude is due Russel W. Murphey who discovered *Batrachoseps aridus* and who kindly led me to the locality. Further, I greatly appreciate the field aid of James E. De Weese of the University of Southern California, Allan L. Reinholtz and Patricia L. Brame. The latter prepared the illustration of the holotype. John W. Wright kindly reviewed the manuscript and made many useful suggestions. I am grateful to William Presch for x-raying the entire series.

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A NEW SALAMANDER (GENUS *OEDIPINA*)  
OF THE *UNIFORMIS* GROUP FROM WESTERN PANAMA

By ARDEN H. BRAME, JR. AND WILLIAM E. DUELLMAN



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VIRGINIA D. MILLER  
*Editor*

A NEW SALAMANDER (GENUS *OEDIPINA*)  
OF THE *UNIFORMIS* GROUP FROM WESTERN PANAMÁ

By ARDEN H. BRAME, JR.<sup>1</sup> AND WILLIAM E. DUELLMAN<sup>2</sup>

ABSTRACT: A new species of *Oedipina* from western Panamá is described from the montane cloud forest on the northern slopes of Cerro Pando. In many characters this long-bodied *Oedipina* falls in an intermediate position between the *uniformis* and *collaris* subgroups of the *uniformis* group and its closest relative appears to be *Oedipina cyclocauda*. Because it has similar coloration of a brown trunk dorsum and white to yellow or silvery lateral stripes as in *O. collaris*, *O. poelzi*, and *O. altura* (members of the *collaris* subgroup), it is placed within that subgroup.

An expedition conducted by Duellman, Charles W. Myers and Linda Trueb in May, 1966 to the north slopes of Cerro Pando resulted in the discovery of an extraordinarily rich salamander fauna including three undescribed species of *Bolitoglossa* plus *B. subpalmata* and *B. marmorea*. In addition, a large species of *Oedipina* was discovered; it represents the seventh species of the genus known to occur in Panamá, the other six being *Oedipina alfaroi*, *O. collaris*, *O. complex*, *O. cyclocauda*, *O. parvipes* and *O. uniformis* (see Brame, 1968 for a recent review). In allusion to its large size (only *O. collaris* attain a longer standard length) we propose that it be called:

*Oedipina grandis*, new species

Figures 1-3; Tables 1 and 2

*Holotype*. KU 116676, an adult male from the northern slopes of Cerro Pando, between 1810 and 1930 m elevation (5937-6330 feet), Provincia de Bocas del Toro, extreme western Panamá near the border with Costa Rica; obtained by Charles W. Myers, on May 14, 1966.

*Paratypes*. LACM 57055 and 57056, topoparatypes; KU 116673, 1930 m (6330 feet), KU 116674, 1950 m (6396 feet); KU 116678, 1920 m (6298 feet) and KU 116679, 1810 m (5904 feet); all from the northern slopes of Cerro Pando, Provincia de Bocas del Toro; collected by Charles W. Myers, William E. Duellman and Linda Trueb, May 11-30, 1966.

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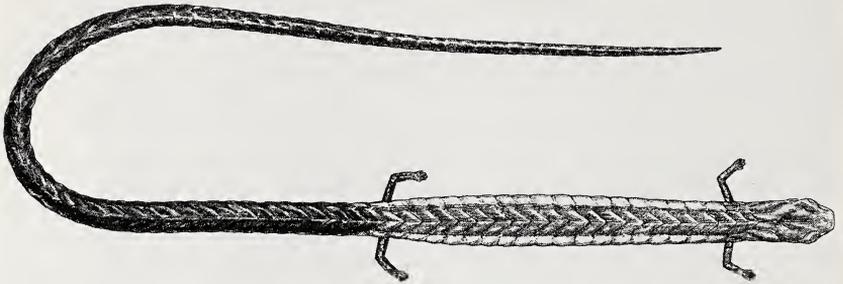


FIGURE 1. Dorsal view of *Oedipina grandis*, holotype, KU 116676, an adult male. Total length equals 214.9 mm.

*Diagnosis.* A member of the *Oedipina collaris* subgroup of the *uniformis* group but in some ways intermediate between the *collaris* and *uniformis* subgroups (see section on evolutionary relationships). The second largest species of *Oedipina*; standard lengths of 7 adults range from 55.1 to 71.4 (mean 65.1 mm). Distinguished from all members of the *collaris* subgroup (*O. collaris*, *O. poelzi*, *O. altura*, *O. pseudouniformis* and *O. cyclocauda*) by having proportionally narrower heads, shorter limbs and smaller feet. *Oedipina grandis* is similar to *O. poelzi*, some *O. collaris* and *O. altura* in having a color consisting of dark to medium brown back and head, trunk bordered by silvery to cream to yellow light dorsolateral stripes boldly demarcated from the deep black ventral coloration and black dorsum of tail (Figs. 1 and 2). (See section on comparison and Table 2 for proportional character differences between *Oedipina grandis* and the other members of the *collaris* subgroup plus *Oedipina stuarti* of the *uniformis* subgroup.)

*Description of holotype.* Adult male, snout short and gently rounded at tip; mental gland not evident externally, nostril small, labial protuberances small, canthus rostralis moderately arched. Standard length 11.1 times head width and 7.1 times snout-gular fold length (head length). Vomerine teeth 9 left, 9 right, extending to posterior lateral border of the internal nares. Maxillary teeth 24 left, 25 right, extending posteriorly to a point two-thirds distance through length of orbit. Two premaxillary teeth, both protruding through upper lip. Postorbital groove distinct, extending for 3.3 mm posteriorly from eye as moderate depression, abruptly proceeding ventrally and extending across gular area (as the nuchal groove) parallel to and 2.2 mm anterior to gular fold. Tail thick, nearly round at base but slightly compressed laterally for last half of length with constriction at base barely

evident; 2.21 times standard length. Postiliac glands large, round and prominent. Limbs moderately short, 12 costal folds remaining uncovered when limbs appressed to sides of trunk; standard length 9.1 times right fore limb, 8.4 times right hind limb, 34.5 times right foot width. Fingers and toes fairly thickened, inner and outer toes I and V fused to II and IV respectively; rest of toes extensively webbed with but the terminal one to one and one-half phalanges free. Fingers in order of decreasing length: 3, 2, 4, 1; toes in order of decreasing length: 3, 2, 4, 5, 1.

*Measurements (in mm).* Head width, 5.9; snout-gular fold (head length), 9.3; head depth at posterior angle of jaw, 3.1; eyelid length, 2.4; eyelid width, 1.5; anterior rim of orbit to snout, 2.9; anterior rim of orbit to external nares, 1.8; horizontal orbital diameter, 1.4; interorbital distance, 2.5; distance between vomerine teeth and parasphenoid tooth patches, 0.6; distance between vomerine teeth and premaxillary teeth, 2.2; internal choanae (nares) to premaxillary teeth, 2.0; distance separating external nares, 2.1; distance separating internal nares, 1.8; snout to fore limb, 15.6; snout projection beyond mandible, 0.8; snout to posterior angle of vent (standard length), 65.6; snout to anterior angle of vent, 61.8; axilla-groin length, 43.9; fore limb length, 7.2; hind limb length, 7.8; width of right hand, 1.6; width of right foot, 1.9; tail length, 145.3; tail depth at base, 3.9; tail width at base, 3.8.

*Color in life.* Dorsum dark brown with minute silver flecks, especially on head and limbs, and small irregular dark (black) marks on dorsum; chin pale brown with silver flecks; belly, lower flanks and ventral surfaces of tail black with or without silver flecks. Iris (under magnification) dark brown with small light brown flecks.

*Color (in 70% ETOH).* Color much faded from that of living specimen; dorsum of trunk brown bordered by silvery whitish dorsolateral stripes of uneven borders markedly set off from intense black venter and intense black tail color. Limbs with some brown spots on black background above; gular area gray and rest of ventral surfaces black.

*Variation.* Males have proportionally longer legs (standard length/hind leg length equals 8.1-8.7, mean 8.4, for males; 8.9-10.1, mean 9.3, for females) and proportionally larger feet (standard length/right hind foot equals 34.5-45.9, mean 39.3, for males; 38.3-47.0, mean 42.0, for females). Males, as usual for bolitoglossines, are smaller than females; males range from 55.1-67.6 (mean 62.8 mm), compared to 61.2-71.4 (mean 66.9 mm) for females. The holotype has a somewhat larger foot than the other specimens and KU 116674, another male, has the broadest head and longest legs proportionally (see Table 1). Other than the above mentioned differences and the usual sexually dimorphic characters (males with papillate vents and premaxillary teeth protruding through upper lip), the paratypes and type agree closely (see Table 1). The color is much the same for all specimens although the dorsolateral white-silverish to yellow stripes are broader and more distinct in most paratypes than for the holotype (see Figs. 1 and 2).

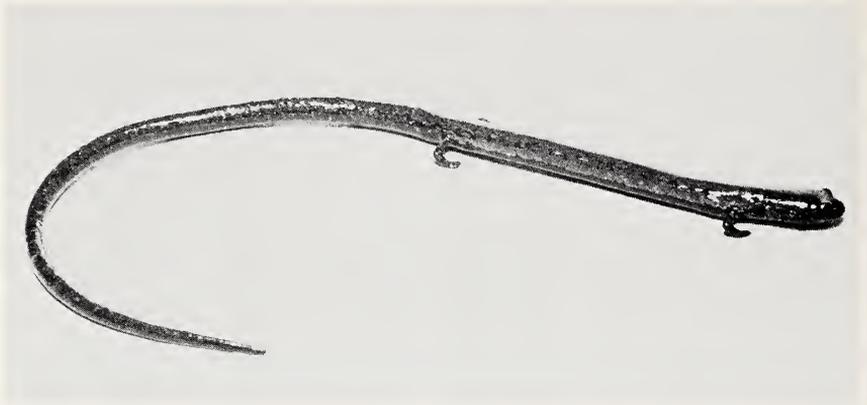


FIGURE 2. Dorsolateral view of *Oedipina grandis*, paratype, KU 116674, an adult male measuring 55.1 mm standard length and 154.1 mm total length. Photograph by Charles W. Myers.

*Comparison.* *Oedipina grandis* is the second largest species of the genus, 7 adults ranging from 55.1 to 71.4 (mean 65.1 mm); related to *poelzi*, *altura*, *pseudouniformis* and *cyclocauda* (these occurring in various parts of Honduras, Nicaragua, Costa Rica and Panamá [see Brame, 1968]). Distinguished from these four species by its larger size, 55.1-71.4 (mean 65.1 mm) standard lengths, compared to 45.1-63.6 (mean 55.6 mm) for 29 *poelzi*, 57.7 mm for one *altura*, 39.3-59.9 (mean 45.3 mm) for 23 *pseudouniformis*, and 36.4-44.1 (mean 41.5 mm) for 20 *cyclocauda*. Distinguished from *Oedipina poelzi* of Costa Rica by having a much narrower head, standard lengths 10.0-11.7 (mean 11.2) times head widths versus 5.1-6.7 (mean 6.1) for 29 *poelzi*; much smaller feet, standard lengths 34.5-47.0 (mean 40.9) times right foot widths in contrast to 25.0-28.9 (mean 26.5) for 5 *poelzi*; and fewer vomerine teeth, mean standard length 3.43 times mean vomerine tooth numbers versus 2.42 times in *poelzi*. Distinguished from *altura* of Costa Rica by having a short rounded snout, shorter legs, standard lengths 8.1-10.1 (mean 8.9) times right hind limb length compared to 8.2 in the single adult *altura*, smaller feet, standard lengths 34.5-47.0 (mean 40.9) times right hind foot widths versus 32.1 in *altura*, and larger numbers of maxillary teeth 38-60 (mean 49) in contrast to 27 in *altura*. Distinguished from *Oedipina pseudouniformis* of Nicaragua and Costa Rica by having a considerably narrower head, standard lengths 10.0-11.7 (mean 11.2) times head widths compared to 8.7-9.7 (mean 9.3) for 23 *pseudouniformis*, shorter limbs, standard lengths 8.1-10.1 (mean 8.9) times right hind limb lengths versus 6.5-8.1 (mean 7.4) for 23 *pseudouniformis*, smaller feet, standard lengths 34.5-47.0 (mean 40.9) times right foot widths in contrast to 30.2-32.1 (mean 31.4) for *pseudouniformis*, and fewer vomerine teeth, 16-23 (mean 19) compared to 17-34 (mean 25) for *pseudouniformis*, a smaller species, mean standard length times mean vomerine teeth

for *grandis* 3.43, for *pseudouniformis* 1.81. Distinguished from the small sized *Oedipina cyclocauda* of Honduras, Nicaragua, Costa Rica and Panamá by having proportionally narrower heads, standard lengths 10.0-11.7 (mean 11.2) times head width in contrast to 9.1-11.3 (mean 9.9) for 20 *cyclocauda*, shorter legs, standard lengths 8.1-10.1 (mean 8.9) times right hind limb versus 7.2-9.0 (mean 8.2) in 20 *cyclocauda*, by having smaller feet, standard lengths 34.5-47.0 (mean 40.9) times right hind foot widths in contrast to 29.0-36.7 for *cyclocauda*, and similar numbers of vomerine teeth 16-23 (mean 19) in *grandis* compared to 16-23 (mean 18) in *cyclocauda*, a much smaller species, mean standard length times mean vomerine teeth for *grandis* 3.43 versus 2.31 for *cyclocauda*.

The similarities in body proportions between *grandis* and *stuarti* (from Honduras) are probably due to convergence; proportions of limb length and numbers of maxillary teeth and vomerine teeth are similar (Table 2) but comparisons of head width, [standard lengths 10.7-11.7 (mean 11.2) times head widths versus 11.1-12.3 (mean 11.7)] reveal that *grandis* has a proportionately broader head, and comparisons of the feet [standard lengths 34.5-47.0 (mean 40.9) times right foot widths in contrast to 30.6-30.8 for *stuarti*] show that *grandis* has smaller feet. In addition, *stuarti* is uniform lead-black on all surfaces in sharp contrast to *grandis*, which has a brown back, white or silver to yellow sides and deep black venter.

*Habitat.* All specimens were obtained in undisturbed montane cloud forest (see Myers, 1969, for detailed description). The area between 1800 and 1950 meters on the northern slope of Cerro Pando is characterized by a broad-leafed evergreen forest with a canopy about 20 meters above the ground. The relatively open forest supports an understory of palms and tree ferns. Thick growths of mosses occur on trees and logs. The leaf litter is thick and, at least throughout May, 1966, continuously wet (see Fig. 3).

Five specimens were found beneath decaying logs on the forest floor and one was beneath rotting thatch from a former shelter. One individual was found as it was crawling on the ground in the camp clearing at night.

*Range.* Known only from the type locality and vicinity from between 1810 to 1950 meters (5937-6396 feet) elevation, on the northern slopes of Cerro Pando, Provincia de Bocas del Toro, extreme western Panamá, near the border with Costa Rica.

*Evolutionary relationships.* In many characters *Oedipina grandis* is intermediate between the *uniformis* subgroup (*uniformis*, *paucidentata*, *stuarti*, *ignea*, *alfaroi* and *taylori*) and the *collaris* subgroup (*collaris*, *poelzi*, *altura*, *pseudouniformis* and *cyclocauda*). These two subgroups compose the *uniformis* group. In head width and hind limb length, *Oedipina grandis* is intermediate between the bulk of the species in the two subgroups. Except for having tiny feet as in *uniformis*, *grandis* seems to be more closely related to the lowland *Oedipina cyclocauda* of the Caribbean slopes of Honduras, Nicaragua, Costa Rica and northwestern Panamá than to any other species.



FIGURE 3. Montane cloud forest habitat of *Oedipina grandis*, northern slope of Cerro Pando, 1950 meters (6396 feet) elevation, Provincia de Bocas del Toro, Panamá. Paratype, KU 116674, of *Oedipina grandis* was found under the log with hat on it in lower right. Photograph by Charles W. Myers, May 12, 1966.

*Oedipina grandis* should be placed on the dendogram (Brame, 1968: 58, Fig. 29) towards *cyclocauda* in an intermediate position between the two subgroups. Its dorsal and dorsolateral coloration is remarkably similar to *poelzi*, *altura* and some *collaris*, which have brown backs bordered by white-silverish to yellow dorsolateral stripes set off from the deep black ventral coloration, an additional reason for aligning *grandis* with the *collaris* subgroup. Thus, *grandis* is the most specialized member of this subgroup; it has a proportionately larger head and limbs but smaller feet, thereby approaching members of the *uniformis* subgroup. Therefore, it seems that *grandis* might be better adapted to a fossorial existence than other members of the *collaris* subgroup. The slight tendency in reduction in number of maxillary teeth and moderate tendency in reduction in number of vomerine teeth are indications of trends in specializations similar to those in *altura*, *stuarti*, *paucidentata*, *igneae*, *taylori* and *alfaroi*; possibly reduction in number of teeth is associated with a different diet from that of the multidentate species, a factor probably further influenced by their more fossorial habits. This description increases the total to 12 species inhabiting the region of suspected origin for the genus *Oedipina* in Costa Rica and western Panamá (Brame, 1968: 56), and increases the total number of known species of *Oedipina* to 16.

TABLE 1. Meristic data for specimens of *Oedipina grandis*

Museum Number	Sex	Snout-Vent Length	Axilla-Groin Length	Head Width	Hind Limb Length	Fore Limb Length	Costal Folds between Appressed Limbs	Right Foot Widths	Maxillary Teeth	Vomerine Teeth	Tail Length	Snout-Gular Fold Length
KU 116673	♂	67.6	47.3	5.8	7.8	7.3	13	1.8	58	22	---	10.2
KU 116676*	♂	65.6	43.9	5.9	7.8	7.2	12	1.9	49	18	145.3	9.3
KU 116674	♂	55.1	37.2	5.5	6.8	5.8	12½	1.2	41	17	99.0	8.9
LACM 57056	♀	71.4	50.2	6.3	7.1	7.1	13	1.8	52	23	122.3	9.8
KU 116679	♀	70.5	49.8	6.2	7.8	7.2	13	1.5	60	18	94.1**	9.8
KU 116678	♀	64.5	44.2	5.6	7.0	6.1	12½	1.5	46	22	121.7	8.5
LACM 57055	♀	61.2	43.3	5.5	6.9	6.2	13	1.6	38	16	130.8	8.1

\* = Holotype

\*\* = Regenerated tails

TABLE 2. Proportional measurements and data for *Oedipina grandis* and its relatives

Species	Standard Length	Standard Length		Standard Length	Standard Length		Standard Length	Standard Length	Standard Length	Standard Length	Standard Length	Standard Length
		Head Width	Hind Limb Length		Hind Limb Length	Foot Width						
<i>O. grandis</i>	7	55.1-71.4 (65.1)	7	10.0-11.7 (11.2)	7	8.1-10.1 (8.9)	7	34.5-47.0 (40.9)				
<i>O. poelzi</i>	29	45.1-63.6 (55.6)	29	5.1-6.7 (6.1)	29	6.7-10.0 (8.4)	5	25.0-28.9 (26.5)				
<i>O. pseudouniformis</i>	23	39.3-59.9 (45.3)	23	8.7-9.7 (9.3)	23	6.4-8.1 (7.4)	4	30.2-32.1 (31.4)				
<i>O. altura</i>	1	57.7	1	10.7	1	8.2	1	32.1				
<i>O. cyclocauda</i>	20	36.4-44.1 (41.5)	20	9.1-11.3 (9.9)	20	7.2-9.0 (8.2)	3	29.0-36.7				
<i>O. stuarti</i>	3	54.1-61.1 (57.9)	3	11.1-12.3 (11.7)	3	8.7-9.5 (9.1)	3	30.6-30.8 (30.7)				
Species	Maxillary Teeth	Vomerine Teeth	Intercostal Folds Covered by Appressed Limbs	Standard Length	Standard Length	Standard Length	Standard Length	Standard Length				
<i>O. grandis</i>	7	16-23 (19)	7	12-13 (12.7)	7	12-13 (12.7)	7	12-13 (12.7)				
<i>O. poelzi</i>	29	42-70 (53)	33	14-34 (23)	33	9-11.5 (10.1)	33	9-11.5 (10.1)				
<i>O. pseudouniformis</i>	23	36-57 (45)	22	17-34 (25)	23	9-12.5 (11.3)	23	9-12.5 (11.3)				
<i>O. altura</i>	1	27	1	17	1	13	1	13				
<i>O. cyclocauda</i>	20	28-47 (36)	20	16-23 (18)	20	11-12.5 (11.7)	20	11-12.5 (11.7)				
<i>O. stuarti</i>	3	43-44 (43)	2	17-18 (18)	3	12.5-13 (12.7)	3	12.5-13 (12.7)				

Boldface numbers = number of specimens

Numbers in parentheses = means

## ACKNOWLEDGMENTS

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## RESUMEN

Una especie nueva de *Oedipina* de la región occidental de Panamá se describe del bosque nublado montaño en la ladera norte de Cerro Pando. Debido a muchas de sus características esta *Oedipina* de cuerpo largo ocupa una posición intermedia entre los subgrupos *uniformis* y *collaris* en el grupo *uniformis* y parece estar muy relacionada a *Oedipina cyclocauda*. Por su coloración similar morena en el dorsum del tronco y blanca, amarilla o plateada en las bandas laterales como en *O. collaris*, *O. poelzi* y *O. altura* (miembros del subgrupo *collaris*), esta especie es incluida en ese subgrupo.

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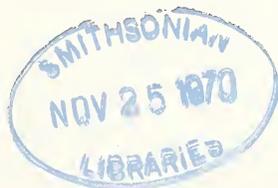
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THE ETHOLOGY OF THE WASP, *PSEUDOMASARIS EDWARDSII* (CRESSON),  
AND A DESCRIPTION OF ITS IMMATURE FORMS  
(HYMENOPTERA: VESPOIDEA, MASARIDAE)

By PHILIP F. TORCHIO



LOS ANGELES COUNTY MUSEUM OF NATURAL HISTORY • EXPOSITION PARK  
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VIRGINIA D. MILLER  
*Editor*

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THE ETHOLOGY OF THE WASP, *PSEUDOMASARIS*  
*EDWARDSII* (CRESSON), AND A DESCRIPTION  
OF ITS IMMATURE FORMS  
(HYMENOPTERA: VESPOIDEA, MASARIDAE)<sup>1</sup>

By PHILIP F. TORCHIO<sup>2</sup>

ABSTRACT: In a greenhouse, each nest of *Pseudomasaris edwardsii* (Cresson) was constructed of nectar-moistened soil, was solitary and was placed in open but concealed niches attached to a variety of substrates. The wasp anchored her egg by its posterior tip to the bottom of the cell, deposited a jellylike cylindrical provision composed of *Phacelia* pollen and nectar and constructed a cell cap. Soil carried to the nest was attached to the postgenal surfaces of the female's head, and the pollen and nectar were transported in her honey stomach. Cells were clustered and attached to each other and to the substrate along their lateral margins. Most nests were covered with separate layers of soil (surface ornamented in various ways) that camouflaged the nest against natural enemies and protected it against extreme temperatures.

The larva, after consuming its provision, spun a cocoon which closely adhered to the inner surface of the cell, and then voided its feces across the bottom of the cell. The post-defecated larva subsequently migrated to the anterior limit of the cell where it firmly appressed against the cocoon as it assumed a strongly decurved, overwintering, prepupal position. Rearings in the laboratory indicated that the species is univoltine and non-proterandrous.

The immature forms of *P. edwardsii* and *Euparagia scutellaris* Cresson are described and represent the first descriptions of the immatures within the family Masaridae. Relationship of these immatures is discussed and both are compared with the immature forms of other known vespoids.

INTRODUCTION

*Pseudomasaris* is one of 19 genera comprising the vespoid family Masaridae. Except for the predatory genus *Euparagia*, all masarid genera thus far studied provision their nests with pollen and nectar. This behavior is similar to the provisioning habits of bees, but it is not found in other wasp families and has, as a consequence, attracted attention from biologists and systematists alike.

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The family Masaridae is also distinctive morphologically. All its members possess clavate antennae, and, unlike other vespids, their wings (except in the *Quartinia* group) are not folded longitudinally when they are at rest. In 1962, O. W. Richards published a world revision of masarid wasps in which he summarized the literature pertaining to the nesting habits of 4 species of *Pseudomasaris*: *vespoides* (Cresson) (as reported by Ashmead, 1902, Davidson, 1913, Cockerell, 1913, and Hicks, 1927, 1929, 1931); *edwardsii* (Cresson) (by Hicks, 1931); *occidentalis* (Cresson) (by Hungerford, 1937); and *texanus* (Cresson) (by Bequaert, 1940). Richards (1963) published a revision of the genus *Pseudomasaris* in which he added biological notes on a fifth species, *P. coquilletti* Rohwer. Parker (1967) published notes on the nests of 3 additional species: *P. maculifrons* (Fox), *P. phaseliae* Rohwer and *P. zonalis* (Cresson). Thus, there is now at least limited published information about the biology of 8 of the 15 species recognized by Richards' revision.

Although Richards firmly established the systematics of the Masaridae and revised the genus *Pseudomasaris*, the biology of the genus remains imperfectly known because the species have limited distribution and the nests are difficult to locate. The literature does, however, indicate that the biology of *Pseudomasaris* is nearly as uniform as it is unique. All species construct nests of mud attached to open but partially concealed niches, provision their cells with pollen and nectar, attach one egg to the bottom of each cell before provisioning, and attach cells to the substrate or to each other along the long axis of each cell.

In late May, 1966, a large population of *P. edwardsii* associated with bloom of *Phacelia leucophylla* Torr. was discovered on a grassy hillside 7 miles south of Logan, Cache County, Utah, at an elevation of 1,525 meters. I transferred 25 females to a greenhouse provided with *Phacelia tanacetifolia* Benth. to determine whether they would nest in confinement. Three survived and nested, but only two cells were provisioned and capped. In one cell, the egg died before the larva hatched; in the second cell, the larva developed to the prepupal stage. Then, in early June, 1967, 70 freshly emerged *P. edwardsii* were captured from the same hillside and introduced into the same greenhouse. All the wasps died within 96 hours of their introduction. Later, it was discovered that inadequate ventilation along the greenhouse "ridgepole" allowed the temperatures at the upper levels to rise well above the survival tolerance of most flying Hymenoptera. This condition was corrected, and in late May, 1968, 54 female and 15 male *P. edwardsii* were introduced into the greenhouse. By the end of the nesting season in late August, 41 nests were found. The observations of the nesting wasps, their nests and the developing progeny are reported here.

#### NEST STRUCTURE

The soil nest of *P. edwardsii* is normally attached to a flat surface in an open but somewhat concealed niche, and each nest is composed of one

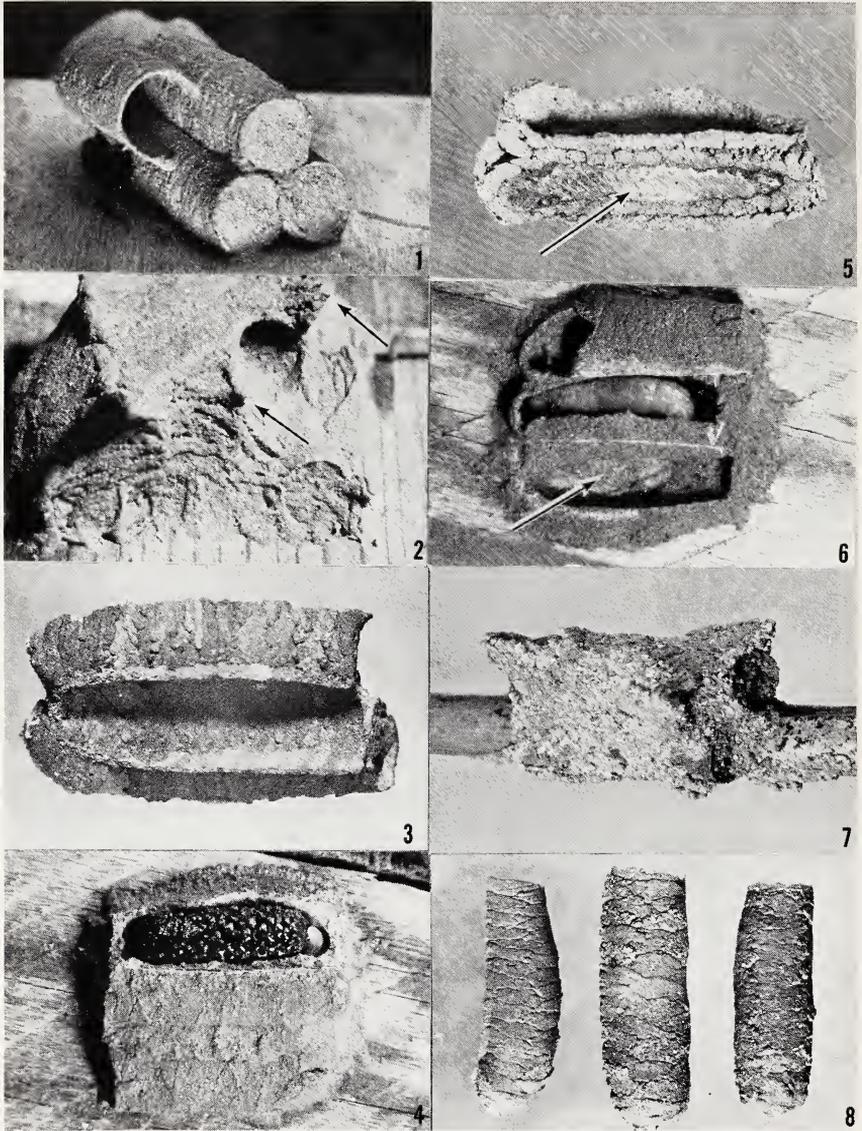
or more elongate, parallel-sided cells joined to the substrate or to other cells along the lateral margin. However, cells attached to the substrate are incomplete in that a small area of the substrate surface is not covered with soil but is used as part of the cell (figs. 5, 6). After the cells are constructed, additional soil is often placed over them as a complete covering. Orientation of the nests with respect to gravity appears to be random.

The examination of over 40 nests of *P. edwardsii* revealed that details of the nest architecture were highly variable although certain features remained constant. The major variations included the number of cells and their arrangement and the presence and degree of development of nest covering. The architectural features that remained constant were: (1) the shape and form of each cell; (2) the manner in which the cells were attached to each other and/or to the substrate; (3) the use of soil for all components of the nest; and (4) the fact that cells made up the greatest volume of each nest.

After the first cell was constructed, the wasp normally initiated construction of a second cell which she attached to the first. However, a few wasps did not construct more than one cell per nest, and of these, some did not provide nest covers, but others constructed complete covers of various shapes. Most nests were composed of two or more cells, and all but one of these nests contained cells joined to each other along the lateral margin. When many cells were constructed within a nest, they were clustered and attached strongly to each other and/or to the substrate (fig. 1). However, in one nest, the cells were placed in a long narrow groove, arranged in a linear series, and separated from each other. Most nests (including those arranged in linear-series) were each covered by an additional layer of soil. However, several multicelled nests were abandoned immediately after the last cell was capped and others were only partially covered in various ways before they were abandoned. Some covers possessed spinelike projections and roughened surfaces (figs. 2, 7) which probably served to protect and camouflage the cells. Those nests that were provided with hemispherically shaped, smooth covers (fig. 17) were always exposed to the heat of the afternoon sun. All nests were fastened to one side of the substrate (figs. 2, 7), even if the substrate was slender and cylindrical, as a stem or a bamboo stake (fig. 7).

#### CELL DESCRIPTION

The most diagnostic feature in the nest architecture of *Pseudomasaris* is the soil cell. It is a parallel-sided structure whose outer dimensions range between 14 and 21 mm in length and 5 to 6 mm in width. The variation in cell wall thickness is between 0.25 and 1.0 mm; however, the wall thickness of any particular cell is constant. The inner surface is smooth, unlined and nonreflective. The cell cap is a plug of soil with a flat, unlined inner surface that usually possesses two concentric rings (fig. 16). Its outer surface is normally flat, smooth and flush with the anterior margin of the cell (fig. 1). The thickness of the cell cap varies between 0.75 and 1.80 mm.



FIGURES 1-8. *Pseudomasaris edwardsii*. Fig. 1. Cluster of cells. Fig. 2. Completed nest with spinelike projections produced from soil covering. Fig. 3. Nest cover represented as a ridge of soil deposited across the surface of each cell. Fig. 4. Nest with cells parallel and nest cover a continuous, smooth surface. Fig. 5. Cocoon visible where cell was attached to substrate. Fig. 6. Nest with lower cell dissected to expose area of cell attachment not covered with soil or a cocoon. The upper cell contains a last-stage larva consuming its provision. Fig. 7. Completed nest attached to bamboo stake. Nest covering produced into spinelike projections. Fig. 8. Outer surface of cells with scars demarking each soil deposition.

Figures 1 and 7 demonstrate how the cells are attached to each other and to the substrate. Those attached to each other are complete and cylindrical in cross section. Those cells attached to the substrate are incomplete and asymmetrical in cross section because the area of attachment is not coated with soil (figs. 5, 6).

A total of 87 completed cells were constructed in the 41 nests examined; the number of cells found in each nest ranged from 1 to 7, or a mean of 2.46 cells per nest. Twenty-four cells contained dead immature forms: 16 had collapsed eggs; 2 had growing larvae; 2 had prepupae; 2 had pupae; 1 had an egg destroyed by dermestid beetles; and 1 prepupa was parasitized by the chalcid wasp, *Monodontomerus obscurus* Westwood. Of the 41 nests examined, 4 were attached to bamboo stakes, 7 were fastened to flat-surfaced lumber and 30 were found on metal.

## NESTING

### *Preliminary activities*

The first three days after wasps were introduced in the greenhouse were utilized to complete orientation, mating, selection of nest sites and selection of soil collecting sites. Each wasp was fastidious in its selection of soil. All but two individuals which nested in the greenhouse selected one soil type (high in silt-particle size) from a wide variety of soils available. Apparently, only soils with proper texture, particle size and wetting capacity were selected. Each wasp, however, usually restricted its collecting to a small portion of the total area where the proper soil type was found. The wasps were gregarious in their collection of soil, but each wasp invariably returned to the same microniche of the soil site for additional soil loads. Some used one microniche throughout their nesting activities; others established new soil-collecting sites for each cell constructed; and a few used two soil sites during the construction of a single cell. However, competition for any particular soil collection site was never observed.

Nest sites were always established in open but concealed niches available throughout the greenhouse. As a result, the nests were solitary and widely dispersed.

### *Cell construction*

Cell construction was initiated after the wasp selected a nesting site and a soil-collecting site. The manner of attaching the first layer of mud as a cornerstone of the first cell was characteristic. First, she attached a small quantity of soil to each side of the postgenal surface of her head and carried it to the nesting niche. There, she tried unsuccessfully to apply the soil directly to the substrate by dragging the underside of her head across the site. After several attempts, she returned to the soil-collecting site and added more soil to the original deposit. She then returned to the nesting site where she again

dragged the underside of her head across the surface. She sometimes made as many as 12 trips of this type before she acquired a load large enough to deposit on the nesting surface. This behavior may help the female establish a strong orientation between the nesting site and the soil-collecting site.

*P. edwardsii* used only one method of collecting and carrying soil. Each time a wasp returned to her soil site, she hovered 10 to 60 cm above it while she intermittently bobbed up and down a maximum distance of 3.75 cm in either direction. This hovering activity continued for 8 to 49 seconds, whereupon the wasp landed and immediately proceeded to collect soil. Little variation was expressed in the method of soil collecting; the female first moved her mouthparts forward 20 to 40° from their normal perpendicular position, embedded the tips of the mandibles nearly a millimeter into the loose-textured, slightly damp or dry soil surface and then began to spread and close her mandibles while flexing her head downward and toward her thoracic venter. As the wasp repeatedly scraped the soil surface with her mandibles, she periodically kicked soil from beneath her head region with rapid, flicking motions of her front legs. These activities made it possible for her to scrape up particles of soil with her mandibles that were subsequently pulled in the direction of her postgenal area by a combination of events initiated with the flexing of her head. This flexing caused her mandibles to scoop into the soil until her head reached its normal perpendicular position. As her head continued to flex, her mandibles were pulled posterodorsally until the collected soil particles were deposited under her head. She continued to carve into the same excavation until a mound of soil eventually appressed against her mouthparts which, when folded, lay well below the postgenal surfaces. At this juncture, her front legs periodically excavated the central area of the mound to clear the area directly below her mouthparts. This activity divided the mound into two portions, and each was sufficiently large to appress against the stipites and postgenal surfaces of the head capsule. Nectar (method by which this liquid was determined to be nectar will be discussed in section on foraging) was then exuded through her folded mouthparts where it was rapidly absorbed into the soil mounds until the surface of each mound was moistened and adhered to the postgenal surfaces of her head. Additional nectar was exuded periodically as the size of the mound increased. Eventually, the complete load of soil was represented by two large, moist, nearly spherical balls that filled a space delimited by the wasp's stipites and the mesepisternal and postgenal surfaces.

After the wasp gathered a load of soil, she flew back to her nest where she quickly fashioned each load into the particular structure she was building. During cell construction, the returning wasp landed on the brim of the cell and curved her body until the posterior two or three abdominal sterna touched the outer surface of the cell immediately below the brim. At the same time, she thrust her head into the cell cavity until her mandibles, which appressed against the inner cell surface, were opposite the posterior abdominal sterna.

She then pulled her mandibles apart as soil flowed from her postgenal areas, across the dorsal faces of her mandibles and onto the cell brim. As soil was deposited, she moved her mandibles to shape the deposit while she simultaneously tamped the outer surface of the fresh deposit vigorously with her posterior abdominal sterna. During each deposition of soil, she periodically jerked her front legs across both faces of her postgenal areas, presumably to clear them of soil. She also moved her large labial palpi across the load in an oarlike fashion to aid in the deposition.

During the latter phases of cell construction (prior to provisioning and following cell cap construction) the wasp periodically added soil to areas of the outer surface of the cell. Apparently, these additional deposits reinforced the structure. The method by which she transferred this soil from her head to the substrate was similar to the second method described. However, she first examined the surface by rapidly pacing about and tapping the substrate continuously with her apical antennal segments. Then she applied one or more soil deposits from one load by using her mandibles and labrum to smear the material over a relatively large area. This method of deposition was also practiced during the construction of the nest cover.

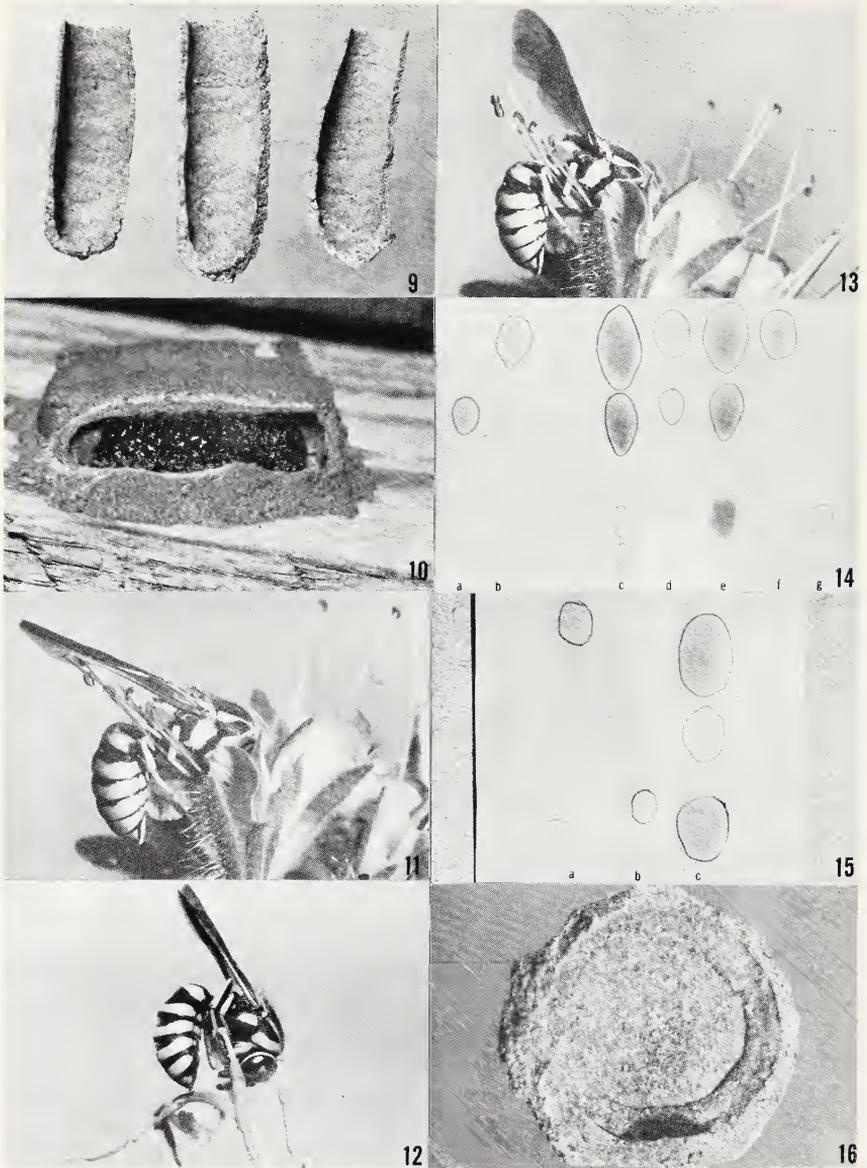
Each deposit added to the cell during its construction left an outline scar (fig. 8) which roughened the inner and outer surfaces of the cell wall. As construction neared completion, the wasp deposited the last few loads of soil within the cell (fig. 25) and smeared it as evenly as possible to smooth the inner surface (fig. 9). The smoothing was accomplished as follows: the returning wasp landed in front of the cell opening, crawled head first into the cell until only her posterior abdominal segments were visible above the cell, and then began to crawl backward and forward within the cell as she deposited and smeared the moistened soil over the surface. Deposition of the final load of soil therefore required a lengthy period (9 minutes, 30 seconds) as the wasp slowly rotated within her cell.

The method of soil deposition practiced during the construction of the cell cap is described in that section.

#### *Egg deposition*

Although actual oviposition was not observed, one wasp was watched during the period of egg laying (fig. 25). This wasp, after depositing and smearing her last load of soil across the inner face of the cell, backed out, turned, and backed into the cell until her head was 1 mm below the cell orifice. Then she remained motionless for 3 minutes, 30 seconds while her egg was deposited, whereupon she crawled out of the cell head first, turned, and re-entered it head first to deposit the first load of the provision. Subsequently, this particular cell, as well as other capped cells, was dissected to study details of the egg and its placement.

Each egg examined was white, 2.1 to 2.8 mm long, 0.955 to 1.0 mm wide medially, and slightly curved; the surface was minutely reticulated. Normally, it was anchored by its narrowed (0.15 mm wide) posterior tip to



FIGURES 9-16. *Pseudomasaris edwardsii*. Fig. 9. Inner surface of cells with a layer of soil coated over scars. Fig. 10. Position of egg and provision within cell. Fig. 11. Sleeping position of female on a *Phacelia* flower. Fig. 12. Sleeping position of female on *Brassica*. Fig. 13. Female awakened from sleep (wings raised). Fig. 14. Paper chromatograph of glucose (A), fructose (B), water solution of pollen from cell (C), water solution of cell walls (D), contents from honey stomachs (E), fructose (F), and sucrose (G). Fig. 15. Paper chromatograph of fructose (A), sucrose (B), and nectar of *Phacelia tanacetifolia* flowers (C). Fig. 16. Inner face of cell cap.

the cell wall near its base. The curvature of the egg closely paralleled the convex posterior face of the provision (see description of provisioning), and its unattached anterior tip (0.31 mm wide) faced the cell cap and terminated less than a millimeter below the provision (fig. 10). As the egg matured, its posterior area gradually cleared. The first stage larva emerged 46 hours after egg deposition.

In some cells, the egg was found attached to the provision rather than to the cell, and its ventral surface was appressed against the inner face of the provision medially with both unattached tips facing the cell walls. Since the egg was always deposited before the cell was provisioned, this aberrant position probably resulted when the wasp pressed her first load of pollen and nectar against the ventral surface of the egg. Subsequently, the strong surface tension of the provision pulled the egg from its attachment to the cell wall and straightened it until only the tips of the egg remained detached from the provision.

### *Provisioning*

The provision of *P. edwardsii* is a tacky, homogeneous mass of *Phacelia* pollen bound with *Phacelia* nectar (fig. 10), shaped into a solid cylinder, 12.5 to 12.7 mm long and 3.5 mm in diameter. The anterior and posterior surfaces are normally smooth and slightly convex, while the remaining lateral surface is covered with numerous tightly appressed, cone-shaped, papillalike projections (fig. 10). Each projection is broad basally, as much as 0.75 mm wide, and narrows apically for nearly 0.75 mm until the diameter approaches 0.10 mm. The remainder of the projection is composed of a parallel-sided, spine-like, apical extension which varies in length from 0.20 to 0.75 mm; the terminus is either blunted or pointed. The longer projections touch the inner face of the cell wall while those which are shorter remain free apically. The posterior surface of the provision normally lies 2.5 to 3.0 mm above the base of the cell, and the anterior surface is positioned 2.0 to 2.5 mm below the cell cap. The provision, therefore, touches the cell walls only by the apical tips of its longer projections.

Notes on provisioning habits were taken from 7 cells, but the observations were so similar that the following description of the only complete provisioning observed could serve as a general description (fig. 25). However, the time spent gathering pollen and nectar was obviously affected by the abundance, proximity and species of *Phacelia* bloom available.

The wasp provisioned her cell in 4 hours, 25 minutes; 24 minutes was spent within the cell depositing the provision, and the remaining time was spent foraging. Eight pollen and nectar trips ranging from 21 to 34 minutes (a mean of 30 minutes) were made to complete provisioning of one cell. The minimum time required to deposit one load was 1 minute, 30 seconds, and the maximum period was 5 minutes, 40 seconds (a mean of 2 minutes, 55 seconds). The vertical distance in the cell displaced by each consecutive load of pollen was 2.45, 2.23, 0.77, 1.40, 0.95, 1.90, 1.50 and 1.50 mm.

On the last foraging trip prior to egg deposition, the wasp collected her first load of pollen and nectar, stored it in her honey stomach, and then collected a load of soil. As noted, once she deposited the soil on the inner walls of the cell and deposited her egg near the bottom of the cell, the wasp crawled from the cell, turned, and re-entered it head first until only the tip of her abdomen was visible above the cell orifice. The provision was deposited immediately above the egg as the abdomen pulsed rapidly while the body rotated intermittently within the cell (clockwise 180°, clockwise 90°, counterclockwise 360°, clockwise 45°, and counterclockwise 280°). Thus, in one trip, the wasp collected a load of pollen, a load of soil, deposited the soil, laid its egg and deposited the first load of pollen. Periodic examination of the cell during the period of provisioning revealed that each deposit of pollen, including the first, was a moist mass spanning the inner diameter of the cell. The anterior surface of each deposit remained smooth and strongly convex. The papillalike projections covering the outer wall of the provision were molded during the deposition of each load of pollen and nectar.

The wasp scarcely deviated in her method of depositing the eight loads of pollen. However, during the third and subsequent deposits the wasp rotated her body intermittently counterclockwise through at least one revolution, and during the deposition of the last two loads she made four and five complete revolutions respectively. The method by which she added pollen could be observed only during the final deposition when the surface of the provision was immediately below the cell orifice. This elevated position prevented her from inserting and concealing her head within the cell. As she touched her mouthparts to the provision, she regurgitated the mixture of pollen and nectar from her honey stomach for a short period and then slowly lifted her head above the provision for a maximum distance of 2 mm. When her head was fully lifted, she stopped depositing pollen, rotated a short distance clockwise within the cell, and repeated the procedure of laying down the provision and adding the papillalike projections to its surface. She often used her front legs to complete transfer of pollen from her mouth to the provision as follows: the front legs were pulled together with the femora paralleling the underside of the head while the tibiae were held perpendicular to her head. Then, with these legs held rigidly in this position, she jerked them rapidly forward and backward. These leg movements not only increased the rapidity of pollen transfer but also aided in the compaction of pollen into the provision. Each time that the wasp stopped rotating to deposit pollen, she turned the tip of her abdomen ventrally until it touched the outer cell surface, whereupon, she began to pulsate it rapidly and vigorously.

### *Sleeping*

The female wasp slept within its nearly completed cell, within a corolla tube of a host plant flower, *Phacelia* spp. (fig. 11), or attached to a non-flowering structure of mustard, *Brassica* spp. (fig. 12). The sleeping position differed for each niche. When a wasp slept in her cell, she crawled

into it head first 1 to 2 hours before sunset, crossed her wings, and remained motionless until 9:00-9:30 AM (M.D.T.) the following day. She always slept with her sterna facing in the direction of the cell attachment, regardless of its relation to gravity.

*Phacelia* bloom provided a favorite sleeping station. In late afternoon, the wasp entered the corolla tube head first, pressed her thoracic sterna against the style, and positioned her propodeum above the stigma. She subsequently clasped the pistil firmly between her mandibles while using her front legs to encompass some anther filaments. Her flexed midlegs, which were pressed against the thoracic pleura, also clasped a few filaments at the tibiotarsal joint. Her partially flexed hind legs did not normally encompass filaments, but rather grasped the margin of a lower petal with the hind tarsal claws. Her wings were held flat and partially crossed apically, and her metasoma was bent ventrally 90° where the posterior segment normally touched a petal (fig. 11). She normally slept with her head, front legs and the anterior area of her thorax embedded within the corolla tube.

Although a number of males were introduced into the greenhouse, none was observed in the sleeping position.

All wasps sleeping on mustard were found clinging to green seed pods in a completely exposed environment. Their sleeping position was assumed in late afternoon when each wasp grasped a seed pod with her mandibles and the tarsal claws of her flexed midlegs and hind legs (fig. 12). The thoracic sterna were pressed against the seed pod which terminated apically under her propodeum. The antennae were positioned downward in front of the mandibles and the metasoma was turned ventrally 90° or more until it touched the opposite face of the seed pod. The wings were held flat and partially crossed apically and the front legs were folded and held against the postgenal surfaces.

Termination of sleep was apparently dependent on rising temperatures. Each morning as 21°C was approached, the wasp began to palpitate her abdomen at a rate that was slowly increased until it reached 150 palpitations per minute. She then lifted and spread her wings above her body (fig. 13), released her grasp of the plant and straightened her abdomen. After a short preening period, she flew directly to a host plant and began to collect nectar.

*Pseudomasaris edwardsii*, unlike many aculeate Hymenoptera, is solitary in both its nesting and sleeping behavior. It never clusters or is attracted to other wasps during the search for a sleeping station, nor does it sleep night after night at a particular station. The species, however, is highly adaptable, as demonstrated by almost every facet of its biology including its sleeping habits. Therefore, it was not surprising to learn that each female could and did sleep in most niches and assumed every position of sleep described at least once during her nesting life.

### *Foraging*

In the greenhouse, *Pseudomasaris edwardsii* practiced two methods of collecting *Phacelia* pollen: (1) A wasp would land on the sexual organs of

the flower, grasp a few stamens and the style with her midlegs and hind legs, and then remove the pollen from each anther with her mandibles while her prothoracic legs clasped the supporting filament; or, (2) after hovering above a flower for 2 to 8 seconds, the wasp would drop closer to the flower until her extended legs bounced on the anthers once or twice. Then, still hovering, she would remove pollen from the anthers with her mouthparts while using her forelegs, and sometimes her midlegs, to grasp and steady each filament.

Both methods of collecting pollen were used during any one foraging trip. However, the first method was observed more frequently within the first hour of flight activity or whenever the greenhouse became cooler. The second method was observed more frequently during cell provisioning or when bloom was in poor condition. Females collected pollen periodically whenever they were foraging, but the rate of pollen consumption increased markedly during cell provisioning.

The wasp collected *Phacelia* nectar during each foraging trip throughout her adult life by using techniques much like those she used to collect pollen. During the morning, she usually landed on the inner face of the corolla or on the sexual organs and extended her proboscis to the base of the corolla tube where she imbibed nectar. In the afternoon, she normally hovered immediately above a flower with her legs sometimes grasping the anthers and/or filaments while she extended her proboscis to reach the layer of nectar at the base of the corolla. However, both methods of collecting nectar were used on any one foraging trip throughout each day's activities.

Extensive observations of foraging indicated that the methods by which the wasp collected *Phacelia* pollen and nectar were influenced by: (1) the quantity and condition of available bloom (when either or both were reduced, the hovering method was used more often); (2) the response to light and temperature (if either or both were reduced, the landing technique was employed more frequently); and (3) the particular phase of nest construction (the hovering technique was generally used during cell provisioning).

Cooper (1952) reviewed the flower records of masarid wasps and discussed the oligolectic tendencies expressed within the genus *Pseudomasaris*. He concluded that *Pseudomasaris* collects pollen and nectar primarily from 3 host genera: *Phacelia*, *Eriodictyon* (Hydrophyllaceae) and *Penstemon* (Scrophulariaceae). Some wasps, such as *P. vespoidea*, are monolectic on *Penstemon*, but most of the smaller wasp species such as *P. phaceliae*, *zonalis* and *maculifrons* have a predilection for *Phacelia* and less often for *Eriodictyon*. One species, *P. wheeleri* Bequaert, is found on both *Eriodictyon* and *Penstemon*. Interestingly, none of the 15 species of *Pseudomasaris* collects from both *Penstemon* and *Phacelia*, but several species utilize *Eriodictyon* and either *Phacelia* (*P. edwardsii*) or *Penstemon* (*P. wheeleri*). Apparently, *Eriodictyon* represents a host whose size of flower falls between the size offered by *Phacelia* and *Penstemon* and is, therefore, periodically used by either *Phacelia* or *Penstemon*-collecting *Pseudomasaris* species. It would be

interesting to compare the tongue length of *Pseudomasaris* species with the length of the corolla tubes of their respective host plants.

The greenhouse studies therefore tended to support Cooper's conclusions regarding the oligolectic tendencies expressed by *Pseudomasaris*. Both sexes of *P. edwardsii* collected only from flowers of *Phacelia leucophylla* in the field, and when they were introduced to a variety of flowers in the greenhouse (*Melilotus* spp., *Baileya multiradiata* Harv. and Gray, *Cosmos* sp., *Borago* sp., *Medicago* spp., *Brassica* spp., *Clarkia unguiculata* (Lindl.), *Phacelia tanacetifolia*, *Lycopersicon* spp. and *Helianthus* sp.), only *Phacelia tanacetifolia* was visited. When the supply of *P. tanacetifolia* dwindled, bouquets of *P. leucophylla* were introduced into the greenhouse from the field, and the wasps freely collected pollen and nectar from both *Phacelia* species during any foraging trip.

The supplying of bloom to *P. edwardsii* in the greenhouse revealed several interesting aspects of the wasp's biology that normally would have been overlooked. First, the collection of pollen and nectar is apparently characteristic at the generic rather than the specific level because this habit is not peculiar to *P. edwardsii* and is widespread in the genus. Secondly, there was a direct correlation between time required to construct and provision a nest of *P. edwardsii* in the greenhouse and the quality and quantity of available bloom. Figure 25 outlines the time required to construct and provision a cell when bloom was in excellent condition and its quantity was sufficient to support the wasp population. Third, wasps nesting in the greenhouse lived nearly twice as long as individual wasps in the field population from which they were collected. Apparently, the continual addition of *Phacelia* bloom in the greenhouse allowed the wasps to express their life potential more fully. Conversely, the field population quickly pollinated its *Phacelia* host plant and then disappeared as the bloom turned to seed.

A number of wasps were observed throughout the entire periods of cell and nest construction and cell provisioning. At no time did they gather liquids other than nectar, but they always added liquids to soil collected for cell building. Indeed, it was only during the cell construction period that the honey stomach was full. Also, when samples taken from the honey stomachs of cell building and provisioning wasps were compared (by using a paper chromatography method) with samples of (1) a solution derived from an unprovisioned cell; (2) nectar from *Phacelia* blossoms; (3) cell provisions; and (4) known concentrations of glucose, fructose and sucrose in water (figs. 14, 15), it was apparent that the liquid added to the soil and the liquid added to the cell provisions was regurgitated *Phacelia* nectar stored in the honey stomach where it had been subjected to minimum enzymatic action. The large quantities of *Phacelia* pollen found in the midgut and hindgut of all dissected wasps indicated that they always consumed enough pollen to satisfy their nutritional needs.

### *Cell capping*

The cell cap was composed of a soil plug, 4.5 mm in diameter, 0.75 to 1.8 mm thick centrally, and 1.3 to 2.0 mm thick laterally. The inner face (fig. 16) was divided into a thickened, peripheral ring 0.7 mm wide and 1.3 to 2.0 mm thick which surrounded a flattened inner surface (inner cell cap) 3.0 mm in diameter and 0.25 to 1.0 mm thick. In some cells, the inner cell cap was also divided into a peripheral soil ring surrounding a central core of soil 1.0 mm in diameter. The outer surface of the cell cap was normally flat, devoid of annulations and did not extend above the anterior edge of the cell wall. Sometimes, however, the cell walls were extended for several millimeters above the cell caps during construction of the nest cover so that some cell caps looked as if they were placed well below the anterior margin of the cells.

Construction of cell caps was observed on three occasions each of which occurred immediately after cell provisioning. The soil-laden wasp returned to the cell, placed her head into the cell orifice, and applied soil to the inner face of the cell immediately below its anterior edge as the rapid pushing motion of her front legs transferred soil from her postgenal areas to her mandibles. She slowly circled the lip of the cell as the soil was deposited until a complete peripheral cell cap ring was formed (fig. 16). In one of the three cells observed, one load of soil was required to complete construction of the ring; in the other two cells two loads were required for each. One or 2 additional loads of soil were deposited to complete closure of the cell cap. During the deposition of these loads of soil, the wasp moved clockwise and counter-clockwise as she filled the lateral edges of the inner cap with a thin layer of soil until only a small, circular area at the center of the cap remained uncovered. She then rotated in one direction while she plugged this central area of the inner cell cap. This operation required 30 to 40 seconds. At this juncture, she began to spread the moist soil by brushing the dorsal face of her clubbed flagellum across the freshly deposited material (the flagellum was lifted upward and outward on each brush stroke). The brushing continued for 15 to 23 seconds until the central soil was smooth and thoroughly incorporated into the dry surrounding soil of the inner cell cap. Whenever a wasp failed to brush the lateral edges of the central deposit thoroughly, the inner cell cap appeared subdivided into a peripheral ring (first deposit) and a central core (second deposit).

Additional loads of soil, which varied in number, were added to the outer surface of the cell cap until it was flush with the anterior edge of the cell walls. Each of these loads was deposited as a single mound that was thoroughly tamped into the cell cap. The wasp used her labrum and the apical tips of her antennae to tamp as she jerked her head up and down very rapidly for short periods.

### *Nest covering*

Figures 2, 3, 4 and 17 show the variability of the nest coverings. Structural similarities include: (1) each covering was attached to the cells (figs. 3,

4); (2) each layer of the nest cover was 1 mm or less thick (figs. 3, 5); (3) in nests where cells were not completely covered, soil was laid down as a thin perpendicular layer on the long axis of each cell (fig. 3); (4) in nests where cells were completely covered, the layers were deposited horizontally on top of the cells (fig. 4); (5) the nest covering extended well beyond both the anterior and posterior margins of the cells (fig. 18); (6) air spaces were present between the covering and the anterior-posterior margins of the cells (fig. 18); (7) the cell walls of each cell were extended beyond the cell cap and reached the nest covering (fig. 18).

Nests devoid of soil coverings generally had one partially constructed cell attached to one or more completed cells (fig. 1). In others, the area between the attached cells was filled or partially filled with soil. One nest was composed of a single, naked cell, while in another nest the single cell was completely covered. These features indicate that some females apparently died or abandoned their nests before or during construction of the nest covering. Conversely, I was not able to ascertain if all completed nests possessed soil coverings.

#### LARVAL DEVELOPMENT

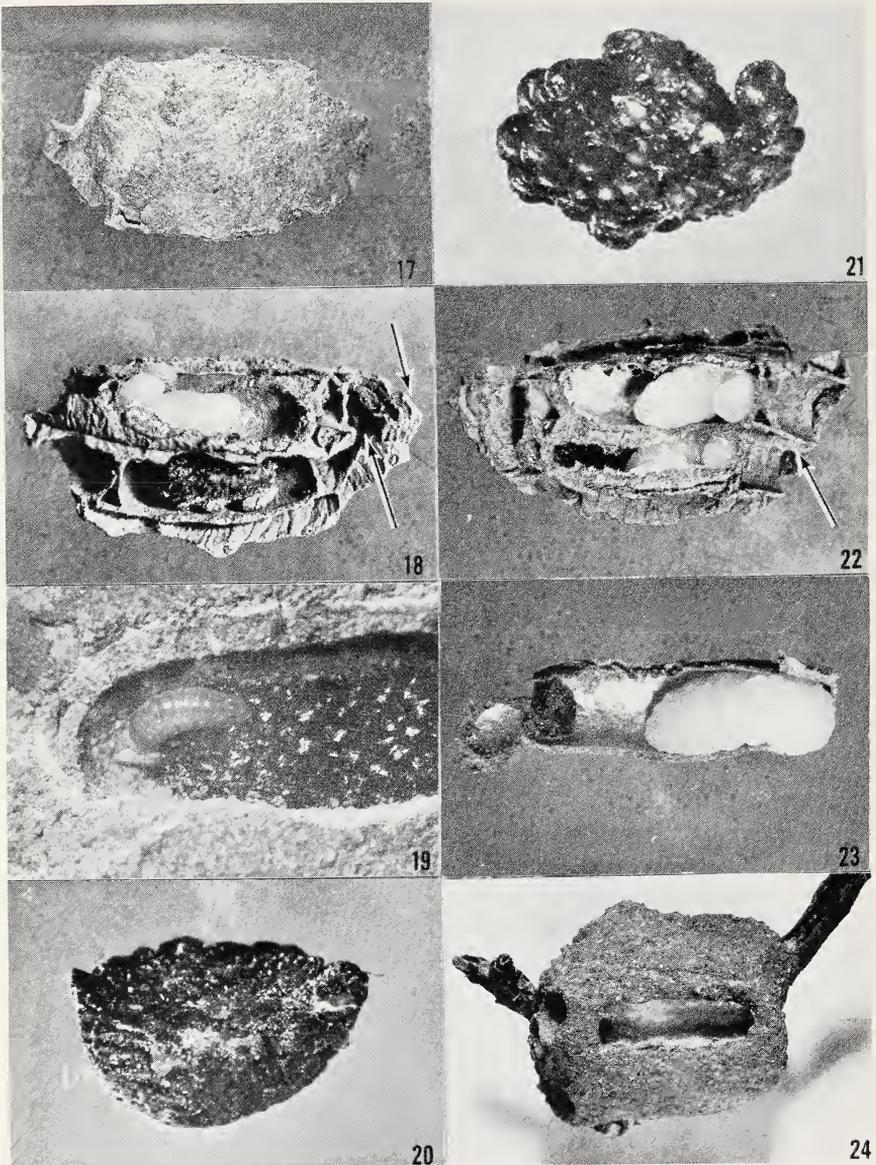
##### *Feeding*

The first-stage larva began to feed after freeing itself from the anterior tip of the egg and crawling onto the basolateral surface of the provision. Eventually, only its posterior abdominal sterna rested on the anterodorsal area of the collapsed egg chorion (fig. 19). The second-stage larva completely abandoned the egg chorion which remained attached to the cell wall by its posterior tip. As the larva migrated anteriorly, it either began to drill a central core through the provision or to consume the surface of the provision, including the papillalike projections. The "drillers" were usually found in cells oriented perpendicular to gravity. The "nondrillers" were found in cells attached to horizontal surfaces. After the larva had cut a core through the provision, it began feeding on its periphery until it was consumed.

Regardless of whether the cells were placed on the top surface or the under surface of horizontal structures, the larvae always placed themselves so their sterna faced gravity as they fed. Invariably, each larva rested its sternum on a thin layer of the provision, which was consumed last.

The feeding larva normally buried its head capsule completely in the provision. Then, as the mandibles were pulled apart, the head was retracted slightly, and conversely, as the mandibles were closed, the head was protracted slightly. In this way the mandibles procured a quantity of pollen that was forced into the mouth by rapid protractions and retractions of the labium.

The postfeeding, precocoon spinning larva was active, turgid and always oriented to face the cell cap. It was long and narrow (2.75 mm in diameter); its posterior abdominal segment rested on the bottom of the cell and its head nearly reached the cell cap. The cuticle, though highly reflective, was sufficiently translucent where the gut and the major tracheae were visible through it.



FIGURES 17-24. *Pseudomasaris edwardsii*. Fig. 17. Smooth-surfaced nest covering. Fig. 18. Dissected nest exposing air spaces, and extensions of the nest cover. Fig. 19. First instar larva crawling onto provision. Fig. 20. A normal fecal cake. Fig. 21. A fecal mass consisting of appressed fecal pellets. Fig. 22. Dissected nest exposing extensions of cell walls beyond the cell caps, and the position and shape of overwintering larvae. Fig. 23. A dissected cell containing the fecal cake, cocoon, and overwintering larva. Fig. 24. *Pseudomasaris vespoides*. Nest attached to limb with a cell dissected to expose the cocoon lining.

MINUTES

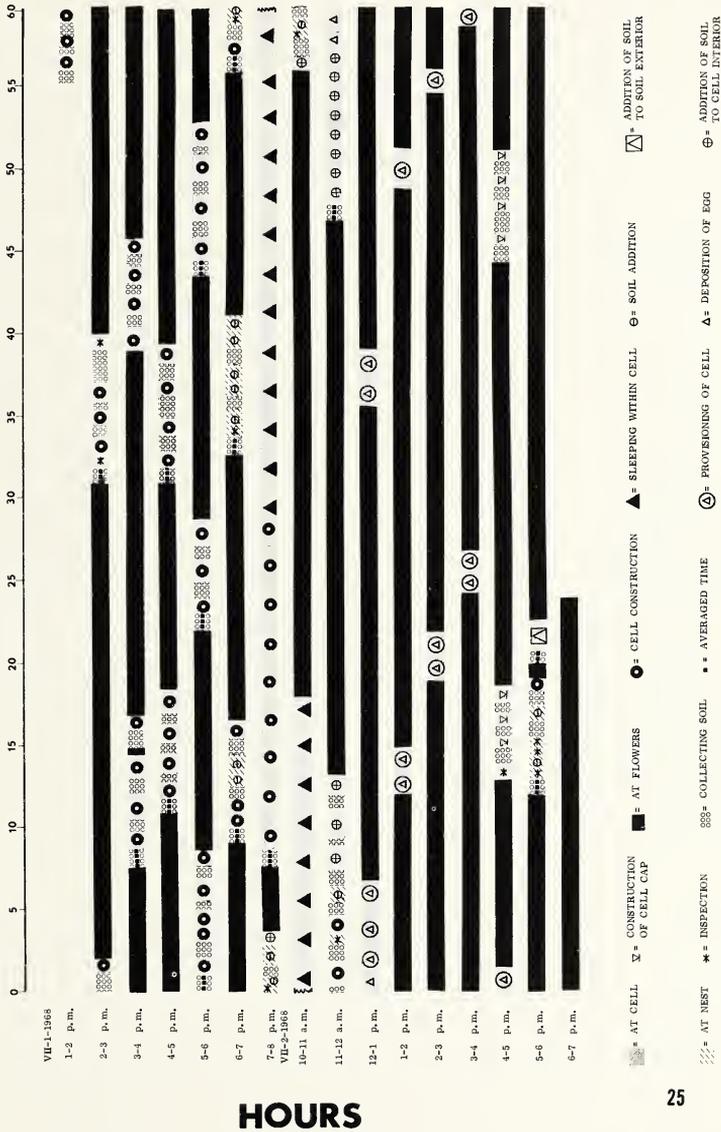


FIGURE 25. *Pseudomasaris edwardsii*. Activities of a single female throughout the period of constructing one cell.

### *Cocoon construction*

The cocoon was a single-layered structure closely adhering to the inner soil surface of the cell wall and cap. It was pliable, less than 0.01 mm thick and composed of salivary secretion laid down as a translucent matrix interspersed with numerous silk strands.

The larva started to spin its cocoon almost as soon as it had consumed its provision. It laid down two forms of salivary secretion (strands and matrix) intermittently. When depositing the matrix, the larva pressed the apical area of its prementum firmly against the cell wall and secreted a quantity of salivary material that it spread across the surface of the cell wall with its transverse salivary lips. During the few minutes that the matrix remained moist, it was incorporated slightly into the cell wall, thereby attaching the two surfaces firmly together. Each silk strand was formed when the larva attached a spot of salivary material to the cell surface through its salivary lips. When it pulled its head away from this point of attachment, a strand of salivary material was drawn through the salivarium. Invariably, the larva dragged its salivary lips across the surface of the cell as each strand was emitted, thus guaranteeing complete attachment of each strand to the cell surface. At times, deposition of these strands appeared organized; the larva deposited 20 to 30 subequal lengths closely parallel to each other and less than 0.06 mm apart. Then, for no apparent reason, it would abruptly change position and deposit strands more randomly. As each strand was deposited, the transverse salivary lips and mandibles opened and closed, and the labium palpitated rapidly. Sometimes, the movement of the mouthparts caused the strands to be emitted at varying speeds, which resulted in strands of unequal thickness.

Cocoon spinning was usually completed within three days. During this time, the larva frequently interrupted its spinning for various periods, straightened its body, and moved its anterior segments in random directions. Cocoon spinning continued after the larva completely encased itself, but the additional spinning was restricted to attachment of silk to the inner cocoon surface near its anterior margin. Thus, the larva always terminated cocoon spinning activities before a second cocoon layer was formed.

### *Defecation*

After the larva completed construction of the cocoon, it straightened its body until its head nearly touched the cap. If the free surface of the cell faced gravity, the larva positioned itself with its terga touching that side of the cell facing gravity and then began to slowly protrude and retract its head slightly. These movements initiated a persistalsis which continued for nearly an hour. The larva then assumed a C-shaped position, with its head touching or nearly touching its 4th to 6th abdominal sterna and maintained this position for variable periods (4 minutes, 3 seconds to 18 minutes, 52 seconds). Within the first minute, while it remained motionless, a fecal particle was extruded that remained attached to the anus by a thin strand of translucent, rapidly

drying, anal secretion. During the remaining time it maintained the C-shaped position, the larva periodically, but rapidly, moved its mouthparts, except its mandibles, and pulsated its body slowly. Eventually the larva uncurled and moved its terminal body segments in circles and figure eights for nearly 2 minutes, 30 seconds. Then it again assumed the C-shaped position and deposited another fecal particle. This behavioral pattern was repeated with little variation until defecation was completed (54 to 76 hours).

Before defecation, the larval body was distended, fat bodies were visible beneath the cuticle and the cuticular surface was highly reflective. As defecation neared completion, the cuticle turned opaque white, and the body became semiflaccid.

The fecal cake was deposited on top of the inner surface of the cocoon at the bottom of the cell. It was a compressed, flat-surfaced, brittle, dark purple cake about half as deep as wide and molded to (but not attached to) the cocoon (fig. 20). The surface of the cake was always perpendicular to the side walls of the cell regardless of the orientation of the cell to gravity. The surface sometimes contained discolored areas which probably represented malpighian excretion deposited after defecation.

Although the feces were deposited as individual pellets, the resultant fecal cake did not normally contain discernible pellets; it usually consisted of a uniform mass of pollen exines (attached to each other by a rectal secretion) which was formed after each pellet was smeared across the base of the cell by the terminal segments of the twisting and turning larva. However, in some cells each fecal cake was composed of dorsoventrally compressed pellets of various sizes that were strongly attached to each other (fig. 21).

When larvae were placed in a petri dish, the feces were observed to be extruded as moist, subcylindrical, brown pellets normally narrowed at both tips. They were 0.2 mm wide centrally and 0.1 mm wide at their narrowed tips and their lengths varied from 1.2 to 1.8 mm. When not disturbed, these pellets remained attached to each other by a thin, translucent strand of anal secretion. When a freshly extruded fecal particle was slowly teased away from its anal attachment, a long strand of clear anal secretion, 0.2 to 0.5 cm long attached to the posterior tip of the fecal particle, was emitted through the anus. Possibly, then, the anal strand was a continuous secretion that traversed the long axis of all the fecal particles rather than a discontinuous secretion that merely attached the fecal pellets to the anus.

As each fecal particle dried in the petri dish, its color changed from medium brown to nearly black and its shape changed from nearly straight to slightly arched. Most, but not all, fecal pellets extruded from any particular larva possessed a lateral groove that traversed the length of each side of each particle and measured 0.025 mm deep and 0.05 mm wide. In addition, the surface of a few pellets in each fecal cake appeared to be covered with a smooth, thin varnish, which possibly represented secretions of the peritrophic membrane.

During the relatively long defecation period, an average of 2.04 pellets per hour were extruded. If they had been deposited loosely in the cell, they would have nearly filled it. Obviously, compression of the pellets into a solid cake was necessary to conserve space.

#### *Postdefecation activities*

The larva moved to the area of the cell cap immediately after depositing the last fecal particle and curved the anterior area of its body posteroventrally. Eventually, the slightly retracted head and the anterior margin of the prothoracic segment were appressed against the first two abdominal sterna, and the metathoracic tergum and abdominal terga I (or I and II) were pressed against the cell cap and the anterior margin of the cell wall. The slightly protuberant ventrolateral tubercles of the mid- and posterior body segments and the ventral area of the last two abdominal segments also touched the cocoon. Although the larva became flaccid as it established this decurved position, it continued to remain firmly appressed against the anterior area of the cell. This position separated it from its fecal cake by approximately a third of the cell's length (figs. 18, 22, 23).

Four prepupae were placed in a cool room (constant 10°C) on July 30, 1968. By January 6, 1969, these larvae straightened and became semiturgid. They remained motionless until they transformed into pupae (10 males, 3 females) between January 11 and 12, 1969. The pupae were active and cream white when they were first formed and pigmentation of the adult cuticle developed gradually. The eyes darkened within 60 hours after pupation, well before others parts of the body began to darken. Subsequently, the head, and then the thorax, gradually became pigmented. The abdomen, legs and antennae were the last to darken. Adults emerged on January 25 and 26, 14 to 15 days after they entered the pupal stage. When 8 additional larvae were subsequently reared together, 3 male and 5 female pupae transformed into the adult forms within a 36-hour period. These data indicate that the species does not practice proterandry in the greenhouse.

#### ASSOCIATES

Hicks (1929) reported three parasites attacking *P. edwardsii*: a mutillid, *Photopsis* sp., a chrysidid, cited as *Chrysura densa* (Cresson) (= *Chrysis densa* Cresson, and an unidentified chalcid wasp (considered as possibly a hyperparasite). In the same paper, Hicks reported *C. densa* and a new species (near *Chrysura tota* Aaron) attacking *P. vespoides*. Parker (1967) reported *C. densa* as a parasite of *P. zonalis* and Hungerford (1937) reported it on *Pseudomasaris occidentalis*. Some chrysidids parasitize megachilid bees, and others are parasites mostly of wasps. The parasitism of *Chrysura densa* on *Pseudomasaris* may result from the similarity of provisions between megachilids and *Pseudomasaris*.

In the present study, one *P. edwardsii* cell was attacked by *Monodontomerus obscurus* Westwood (family Torymidae). Inasmuch as *M. obscurus*

was already established in the greenhouse as a parasite of *Megachile rotundata* (Fab.) and other osmiine bees, its association with *Pseudomasaris* is not clear, especially when only one cell was parasitized.

#### NESTS OF OTHER MASARID WASPS

In addition to *P. edwardsii*, cells of *P. vespoides*, *P. phaceliae*, and *Euparagia scutellaris* were examined. They are described and compared with cells of *P. edwardsii*.

##### Nest of *Pseudomasaris vespoides*

The one nest of *P. vespoides* examined (fig. 24) was collected in an orchard in Box Elder County, Utah. It consisted of a cluster of nine parallel cells attached to a twig of a peach tree. The cluster was covered laterally and ventrally by the same soil mixture used to construct the cells. The smooth nest covering was attached directly to the cells and filled the areas between them which caused the nest to be nearly spherical. The area of the nest anterior of the cell caps was not covered so that each cell cap was exposed. However, extensions of the cell walls were sometimes constructed above the cell caps and their lengths varied between 3 and 9 mm.

The large parallel-sided cell measured 20 to 23 mm long and 7 mm wide at its widest point centrally. A single-layered cocoon covered the entire inner surface of the cell and it was tightly pressed against the unlined inner cell wall and cap. Its composition of a clear matrix interspersed with many silk strands was very similar to the cocoon of *P. edwardsii* although it was thicker and shinier. Also, the cell cap of *P. vespoides*, even though thicker (4.5 mm) than those of other *Pseudomasaris* species examined, was very similar to that of *P. edwardsii* in shape and in form. In addition, the shape, color, form and placement of the feces was nearly identical with *P. edwardsii*. The provision of *P. vespoides*, as well as the position of the prepupa as described by Hicks (1927), were nearly identical to those of *P. edwardsii*.

##### Cell of *Pseudomasaris phaceliae*

One broken cell of *P. phaceliae* and its dried provision were examined. The cell differed from those of *P. edwardsii* and *P. vespoides* in only that it was more delicately constructed and the inner face of the cell cap was not differentiated into a distinguishable sequence of rings. The provision was similar to that of *P. edwardsii* except that the anterior surface possessed a central spine of pollen, 0.675 mm long, 0.450 mm wide basally and 0.100 mm wide apically.

##### Cells of *Euparagia scutellaris*

The 4 cells of *E. scutellaris* were examined and compared with cells of *Pseudomasaris* spp. Several distinct similarities were noted: (1) cells of both taxa were constructed of soil; (2) cells were nearly identical in shape and form; and (3) the inner faces of the cell walls were unlined. The shape of the overwintering larvae of the two taxa were also similar. However, the larvae of

TABLE I.

A comparison of *Pseudomasaris* and *Euparagia* immature forms with other vespoïd immature forms as figured and described by Reid (1942) but utilizing characters exclusive of those used by Reid

Characteristics	<i>Pseudomasaris edwardsii</i>	<i>Euparagia scutellaris</i>	Eumeninae	Polistinae	Polybiinae	Vespoïnae
1. Cleavage line complete	-	-	-	±	-	-
2. Salivary opening a transverse slit surrounded by sclerotized lips	+	+	+	+	+	±
3. Mandibles with three teeth	-	+	+	-	-	+
4. Mandibles broadened	-	+	+	-	-	+
5. Antennae positioned low on head	-	+	+	-	-	±
6. Spiracular atria with spines	-	-	-	-	-	+
7. Mandibles crossed apically	+	-	-	-	-	±
8. Labrum emarginate medially	+	+	±	+	+	+
9. Labrum spinulate	-	+	+	±	+	±
10. Vertex strongly indented	+	-	-	±	±	±
11. Antennae with sensilla apically	+	+	+	±	+	+

*Euparagia* were much less flaccid and were positioned at the base of the cell with their ventrolateral tubercles not appressed against the lateral walls of the cell. Because *Euparagia* and *Pseudomasaris* are members of different subfamilies and, since *Euparagia* represents the only known predatory masarid, it is not surprising that their cocoons and fecal cakes have many differences.

The cocoon of *Euparagia* was a brownish, paper-textured structure that lined the inner walls of the cell. It was opaque and pressed against the cell wall but not strongly attached to it. Also, it was very thin (less than 0.01 mm thick) and composed of a homogeneous matrix lightly interspersed with silk strands. The outer surface was dull brown, and the inner surface was highly reflective. The anterior covering was perfectly flat, traversed the cell at least 2 mm below the position of the cell cap (cells examined were without cell caps) and was composed of two complete layers separated by as much as 0.75 mm. The area between the layers was filled with a mixture of soil, feces and a few sclerites of the weevil prey. The cell walls between the flattened anterior end of the cocoon and the cell cap were lined with cocoon silk. Most of the weevil prey, represented by unconsumed head capsules and other structures, were deposited at the base of the cell and appressed between the cocoon and the cell wall. Some feces were intermixed with these weevil parts but most fecal particles were deposited on the inner surface of the cocoon over most of the lower fifth of the cell. The fecal cake was dark grey, brittle, 0.1 mm thick and strongly attached to the cocoon surface.

#### DESCRIPTION OF IMMATURE FORMS

##### *Pseudomasaris edwardsii* (prepupa)

*Head*: Integument sclerotized; with mandibular apices, anterior tentorial pits, apices of maxillae including palpi and galeae, hypopharynx, labial palpi, salivary lips and hypostomal area darkened; few setae scattered on head capsule; numerous sensoria on head capsule; epicranial suture narrow, incomplete, terminating above clypeus; epicranial area limited dorsally by large indentation of vertex and terminating ventrally above the anterior tentorial pits; antennae represented by large circular convexities, each with three sensoria; parietal bands distinct, narrow, but moderately long; posterior thickening of head capsule well developed laterally and moderately developed dorsally; hypostomal thickening well developed; pleurostomal thickening broad, well developed; anterior tentorial pits distinct, at lateral margin of clypeus; epistomal suture strong laterally, distinct centrally; clypeus moderately protuberant; labroclypeal suture slightly emarginate, distinct; labrum with distal margin emarginate centrally, tuberculate laterally; lateral margin of labrum curved; labral tubercles moderately protuberant; mandibles elongate, bidentate, narrowed and pigmented apically; outer tooth larger, inner tooth ending subapically, more sharply tapered; teeth minutely serrate on inner edges; inner apical surface with concavity traversing length of pigmented area; concavity surrounded by carinalike lateral edges of mandibular teeth;

maxillae with scattered sensoria; larger than postmentum from which it is separated; hypopharynx flattened anteriorly, with flattened area strongly rugose; salivarium surrounded by transverse salivary lips positioned apically on prementum; salivary lips serrate apically, transverse width of prementum, and extend well above its surface; labial palpi subapical, broader than long, with two apical sensoria; labial palpi less developed than maxillary palpi; prementum plicate dorsally.

*Body:* Overwintering form strongly decurved; head hidden; strongly appressed against abdominal sterna; body subcylindrical, semiflaccid; integument with sensoria; intersegmental lines complete; dorsolateral and ventrolateral tubercles absent; spiracle not elevated above cuticle; peritreme flat, atrium slightly sclerotized, grapefruit-shaped, with walls smooth, lacking spines or denticles, 0.033 mm in diameter; primary tracheal opening with collar, without spines; subatrium convoluted; anus a transverse apical slit on terminal segment.

*Pupa:* The pupa, except for its color and delicacy, is very similar to the adult form. It is, therefore, necessary to describe only those structures and positions of structures peculiar to this stage; clypeus with tubercle on apical margin positioned medially; abdominal terga spinulate, spinulae not in a band but positioned randomly; male with antennae having tubercle on inner margin of flagellar segments 2 and 3; club normal; antennae bent posteroventrally; first flagellar segments rest on tarsi of front legs and antennal clubs rest on tarsi of middle legs; mouthparts extended posteriorly with glossa resting on antennal clubs where clubs touch along innerapical margins; *female* with antennal clubs resting on basitarsi of front legs; glossa free.

*Euparagia scutellaris* (prepupa)

*Head:* Integument sclerotized with mandibular apices and articulation, maxillary and labial palpi, salivary lips, and anterior tentorial pits heavily pigmented, antennae lightly pigmented; pleurostomal and hypostomal thickenings, and posterior thickening of head capsule pigmented; head capsule, clypeus, labrum and labium with few small setae, maxillae with few long hairs; clypeus spinulate apically; labrum heavily spinulate along apical edge; epicranial suture strong, incomplete, represented by a deep narrow furrow ending at frons; vertex of the head capsule round, not indented; frons represented as a flattened, triangular, indistinct area limited anteriorly by the epicranial suture and laterally by the anterior tentorial pit; pair of large shallow indentations on frons above epistomal ridge; small deep pit superimposed on each large indentation basally; epistomal ridge very broad and sinuate dorso-medially; epistomal suture distinct; parietal bands distinct, narrow, slightly produced, straight but converge dorsally; antennae slightly produced, positioned low on head capsule, each with three sensoria; a pair of circular, deep pits located above antennae and adjacent to frons; clypeus produced; labroclypeal suture distinct, tuberculate; labrum large, truncate apically with narrow central area deeply emarginate; posterior thickening of head capsule

narrow but well developed and equally developed around head; dorsal margin of posterior head capsule thickening positioned below vertex of the head; hypostomal thickening strongly developed; pleurostomal thickening well developed, but not as well developed as hypostomal thickening; tentorial pits distinct; mandibles robust, sclerotized, nearly truncate apically, apical margin interrupted by three short teeth, inner apical surface concave and limited basally by transverse carina; abductor and adductor apodemes shorter than mandible, mandibular apex and area surrounding concavity deeply pigmented; maxillae distinct with galea and palpus positioned subapically, palpus with three sensoria; labium produced, prementum and postmentum distinct; salivary opening a transverse slit surrounded by sclerotized lips which project very little above prementum; labial palpi subapical, large, but not strongly produced, each with three sensoria.

*Body:* Postdefecating form strongly decurved with head touching second abdominal sternum; body not flaccid; intersegmental lines complete; intrasegmental lines indistinct; dorsolateral and ventrolateral tubercles developed, without sensoria; cuticle plicate; spiracle not elevated above cuticle; peritreme flat; atrium 0.066 mm in diameter, "donut"-shaped, with walls lightly sclerotized, reticulated; primary tracheal opening without spines and without developed collar; subatrium with walls smooth, expanded, diameter greater than atrium, posteriorly narrowed into primary trachea; surface of subatrium and trachea without denticles; anus a transverse slit positioned subapically on terminal segment.

#### DISCUSSION

##### *Nest architecture and biology*

The family Masaridae, with 19 genera and 228 species, is a relatively large taxon, but the biology of most of its species and the morphology of the immature forms of almost all of them are unknown (see appendix). Therefore, a discussion of the phylogeny of the family based on a biological comparison between *Pseudomasaris* and other masarid genera is premature at this time. Conversely, particular aspects in the biology of *Pseudomasaris* should be compared and discussed for a number of reasons: (1) the degree of ethological variability expressed within the genus can be demonstrated; (2) some questions proposed in the literature can now be answered; and (3) some of the earlier literature included faulty observations and unwarranted assumptions and conclusions that require correction.

During the course of this study numerous nests of *P. edwardsii* were examined and compared with those of two other *Pseudomasaris* species and with nests figured and described in the literature. These comparisons indicate that little variation in nest construction is shown among individuals of the same species (*P. edwardsii*) and not a great deal more variation is expressed between species. In the section on nest structure, there is a list of nest architectural features that are similar in all nests of *P. edwardsii*. Most of these are

also features in nests of other *Pseudomasaris* species studied. Additional nest similarities between species studied include: nests constructed in open but concealed niches; nest covers, when present, attached to cells; and cell walls with inner surfaces not lined.

Other ethological patterns discernible in the nests of *Pseudomasaris* also have relative constancy within the genus (cocoon, fecal deposits, and position of the overwintering larvae). The vespid characteristic of depositing the egg before provisioning the cell is retained in *Pseudomasaris*, but an exception to this habit within the superfamily Vespoidea is apparently practiced by *Euparagia*. According to Clement and Grissell (1968), *E. scutellaris* provisions its cell with weevil larvae before depositing its egg.

Descriptions of the provisions of four *Pseudomasaris* species [*P. maculifrons* and *P. phaceliae* (Parker, 1967), *P. vespoides* (Hicks, 1927), and *P. edwardsii* (Hicks, 1929, and the present paper)] indicate that only the size of the provision and the shape of the surface projections vary interspecifically. Hicks (1931) believed that each projection on the provision represented one load of pollen, whereas the present study demonstrates that a few papilla-like projections were constructed during each deposit of pollen and nectar. Because *Pseudomasaris* retains the vespid characteristic of laying its egg before provisioning its cell, the shape and form of the provision may represent the method by which the wasp has resolved the problems of airing the egg and larva, maintaining a constant humidity in the cell, protecting the provision and larva against temporary but excessive heat, and reducing the surface area of the provision in contact with the moisture-absorbing cell wall. If the genus has, in fact, evolved in this direction, it should not be surprising that little variation is found in the provisions of those species studied.

Richards (1962) pointed out that the labrum of the Masarini is sclerotized and suggested that this feature is in some way related to the extension and retraction ability of the glossa. In my studies, the labrum was used extensively for tamping and spreading wet soil during nest construction, and the sclerotized labrum aided the wasp in this use of the structure for tamping.

Richards (1962) also reported that one female specimen of *P. occidentalis* collected from Texas had a large lump of clay stored beneath the head and supported on the tips of the labial palpi. Two similar observations were made for *P. edwardsii* during two soil collections, but in the majority of cases, two separate balls of soil were found on the postgenal surfaces. On three different occasions, I observed a different individual carrying a single, dry, soil particle between its mandibles as it returned to its nest. Evans (1966), in quoting Bequaert (1940), mentioned that *Pseudomasaris* also carried pollen pellets between the mandibles. However, Bequaert states, "... the female wasp merely gathers with the mandibles and carries in pellets in the mouth." *P. zonalis* was studied in the greenhouse during 1969, and this species carried soil between its mandibles in pellet form. Possibly, the method of soil carriage is interspecifically variable in *Pseudomasaris*.

The question of whether the female consumes pollen that will be deposited in the cell was posed by Richards (1963). Direct observations of pollen and nectar collections by *P. edwardsii*, dissections and paper chromatographic analyses proved that the pollen and nectar collected for provisions are stored in the honey stomach. Further, little if any enzymatic action takes place in the nectar or pollen during this short period. The nectar serves a multiple function since it is also used as a wetting agent for soil collected during nest construction. When this soil dries, the incorporated nectar acts as a hardening agent.

#### *Immature forms*

Reid (1942) treated the vespoid immatures taxonomically and demonstrated that the subfamilies Eumeninae, Vespinae, Polistinae and Polybiinae, established on the basis of adult characters, could also be distinguished on the basis of larval characters. He also discussed the relationships of these subfamilies from the evidence of the larval characters. Accordingly, he separated Eumeninae and Vespinae from Polistinae and Polybiinae on a characteristic of the clypeus: Eumeninae and Vespinae have the entire lower margin of the clypeus ventral to a line drawn between the insertion of the mandibles; Polistinae and Polybiinae have all or most of the lower clypeal margin above this line. He distinguished Eumeninae from Vespinae on the basis of two characters: in Eumeninae, the width of the labrum is as great as, or greater than, the width of the clypeus where the two join, and the distance from the antenna to the nearest mandible is less than the distance from the midpoint on the anterior margin of the labrum to a line drawn between the dorsal mandibular articulations; in Vespinae, the width of the labrum is less than the width of its clypeus, and comparisons of the measurements are opposite the typical measurements for Eumeninae. The Polistinae and Polybiinae were separated by a single characteristic: in Polistinae, several sensory bristles were found behind each labial palpus; only one sensory bristle was found in Polybiinae. Reid also examined one species of *Zethus* and concluded that *Zethinae* was closely related to Eumeninae. Thus, Reid's classification of vespoid immatures nearly paralleled Richards' 1962 classification of the adults.

Because of the differences in food habits and the morphological diversity expressed by adults, it was not surprising that the immature forms of *Pseudomasaris edwardsii* and *Euparagia scutellaris* did not demonstrate a close relationship (figs. 26-33). It was, however, surprising to learn that these two masarids did not demonstrate a closer affinity to each other by Reid's system of classification. In *Pseudomasaris*, the clypeus lies above a line drawn between the mandibular insertion to the head capsule. By Reid's classification, this character should lead *Pseudomasaris* directly to the Polistinae-Polybiinae complex. Conversely, the apical margin of the clypeus in *Euparagia* lies well below the area of mandibular insertion, a character that should relate this genus to the Eumeninae-Vespinae complex. In Reid's separation of Eumeninae from Ves-

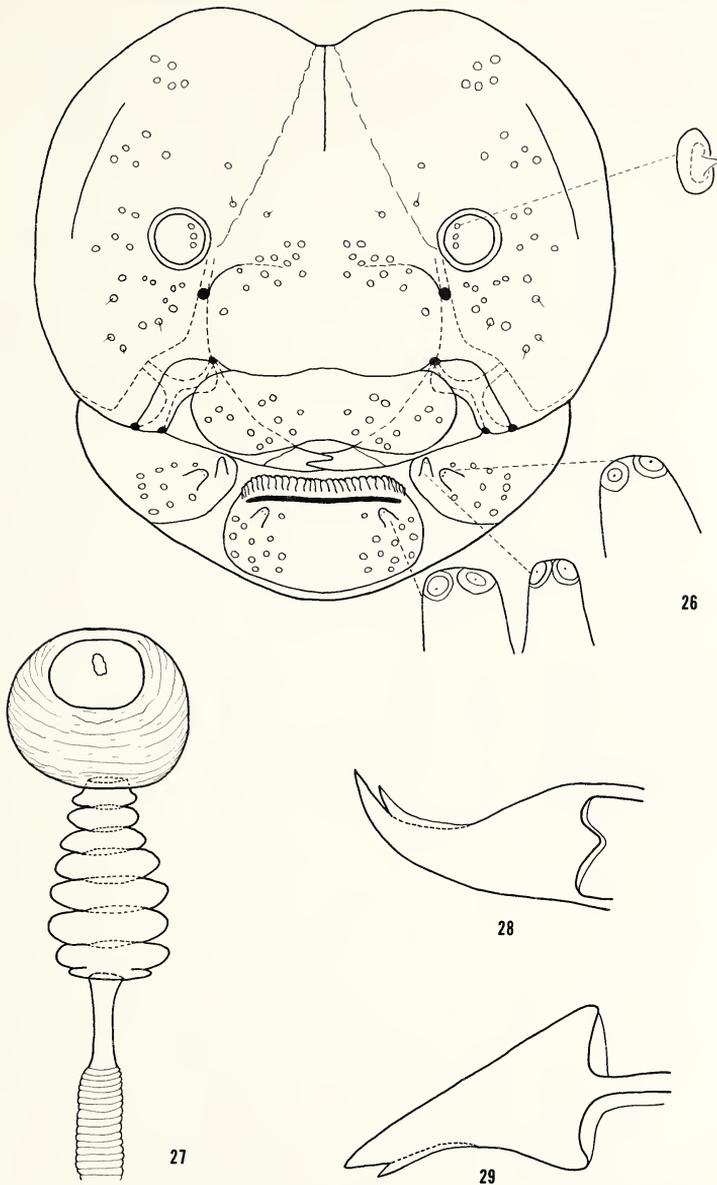
pinæ, several characteristics were compared, and, in each case, *Euparagia* associated better with Eumeninæ. Conversely, it was impossible to compare *Pseudomasaris* by Reid's separation of Polistinæ and Polybiinæ because this masarid lacks the only character he found to distinguish the two taxa, the sensory bristles behind the labial palpi.

When I compared larvae of *P. edwardsii* and *E. scutellaris* with Reid's description and figures of Eumeninæ, Vespinae, Polistinæ and Polybiinæ by using characters exclusive of those applied by Reid but important in the discrimination of bee larvae, I observed the results presented in table I. This table indicates an affinity between *Euparagia* and Eumeninæ, and between *Pseudomasaris* and the Polistinæ-Polybiinæ complex. It also demonstrates that the Vespinae do not fit neatly into the characters. Thus, the results gained from the study of additional characters are similar to those procured when both masarid groups are studied by Reid's classification.

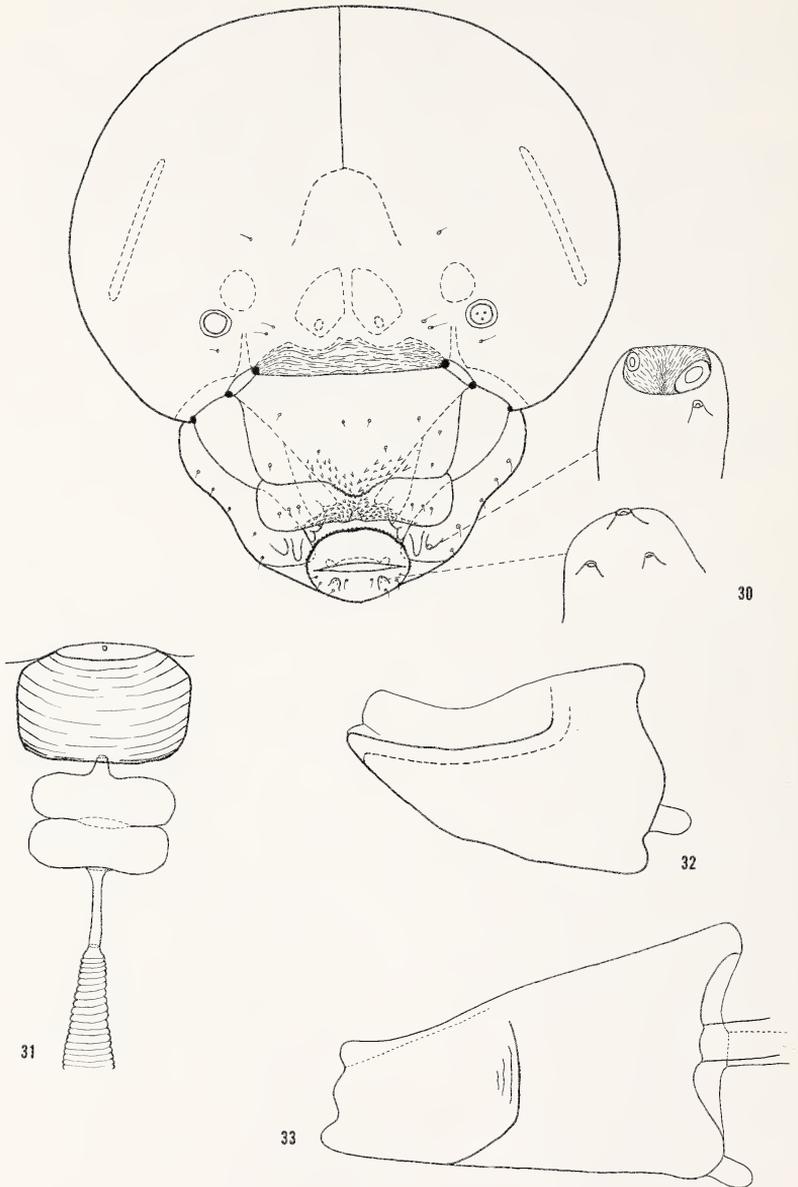
It is apparent that a second revision of vespид immatures is required. However, before another attempt is made, much more material should be collected and described.

#### ACKNOWLEDGMENTS

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FIGURES 26-29. *Pseudomasaris edwardsii* (prepupa). Fig. 26. Frontal view of head. Fig. 27. Spiracle. Fig. 28. Ventral view of mandible. Fig. 29. Inner view of mandible.



FIGURES 30-33. *Euparagia scutellaris* (prepupa). Fig. 30. Frontal view of head. Fig. 31. Spiracle. Fig. 32. Ventral view of mandible. Fig. 33. Inner view of mandible.

## APPENDIX

A generic list of the Masariidae according to Richards (1962); it includes some biological features of the family, (+ = yes; - = no; ? = not known)

	No. of species	Distribution	Nest location	Turrets	Cells in clusters	Progressive provisioning
Masariidae						
Euparagiinae						
<i>Euparagia</i>	7	Western North Amer.	in soil	+	-	-
Gayellinae						
<i>Gayella</i>	4	Chile, Argentina	exposed	-	+	-
<i>Paramasaris</i>	1	Central America	?	?	?	?
Masarinae						
Paragini						
<i>Paragia</i>	14	Australia	in soil	+	?	-
<i>Metaparagia</i>	2	Australia	?	?	?	?
<i>Rolandia</i>	1	Australia	?	?	?	?
<i>Riekia</i>	1	Australia	?	?	?	?
<i>Ceramiopsis</i>	1	South America	in soil	+	?	?
<i>Ceramius</i>						
(includes <i>Paraceramius</i> and <i>Ceramitoides</i> )	26	Africa, Eurasia	in soil	+	+	+
Masarini						
<i>Trimeria</i>	7	South America	?	?	?	?
<i>Microtrimeria</i>	1	South America	?	?	?	?
<i>Quartinia</i>	40	Africa	?	?	?	?
<i>Quartiniella</i>	5	Africa	?	?	?	?
<i>Quartinooides</i>	38	Africa	?	?	?	?
<i>Masaris</i>	2	Middle East	exposed	-	+	?
<i>Masarina</i>	3	Africa	?	?	?	?
<i>Jugurtia</i>	20	Africa	?	?	?	?
<i>Pseudomasaris</i>	15	No. Amer., Africa	exposed	-	+	-
<i>Celonites</i>	37	Africa, Middle East	exposed	-	+	-

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A REVIEW OF THE EXTINCT AVIAN GENUS, *MANCALLA*

BY HILDEGARDE HOWARD



LOS ANGELES COUNTY MUSEUM OF NATURAL HISTORY • EXPOSITION PARK  
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*Editor*

# A REVIEW OF THE EXTINCT AVIAN GENUS, *MANCALLA*

BY HILDEGARDE HOWARD<sup>1</sup>

**ABSTRACT:** With the large number of fossil bones of the flightless auk, *Mancalla* (Charadriiformes: Alcidae: Mancallinae) now at hand, it has been possible to study variability within the genus, verify the assignment of the Corona del Mar specimens to the genotype, *Mancalla californiensis*, and demonstrate statistically the presence of two species in the San Diego Formation. The name *Mancalla diegense* must now be applied to the larger (and less well represented) of the two San Diego species. The smaller, more abundant species is described here as *Mancalla milleri*.

New locality records for the genus are cited, extending its range to Crannell, Humboldt County, California, in the north, and to Cedros Island, Baja California, in the south.

## INTRODUCTION

Since the last major report on the genus *Mancalla* (Miller and Howard, 1949), much additional material has become available from the previously recorded localities within the city of San Diego, California and from the Corona del Mar site near the upper end of Newport Bay, Orange County, California. Where before there were but four bones from the latter locality, representing only carpometacarpus, tarsometatarsus (2) and vertebra, there are now fourteen, including another tarsometatarsus and three more carpometacarpi, and adding coracoid, two humeri (proximal and distal ends), ulna, radius and tibiotarsus. From the several San Diego sites, over 350 specimens are added, bringing the total now available close to 500, in contrast to 145 in 1949. This material is included in the collections of the Los Angeles County Museum of Natural History (LACM, approximately 400), University of California Museum of Paleontology (UCMP, 48), the Loye H. Miller collection of the University of California at Los Angeles (LHM, 50), and the San Diego State College (SDSC, 3).

Besides the material from these previously discussed sites, three new areas of occurrence of *Mancalla* have come to light. One is located in northern California, near the small town of Crannell (Humboldt County), another in southern California, in Laguna Hills (Orange County), and the third on Cedros Island, Baja California, Mexico. A perfect humerus at Humboldt State College (HSC) is the sole representative from the northern locality (HSC locality 197). Localities LACM 65120 and 65121 in the Laguna Hills area have yielded 26 bones, most of which are incomplete with contours obscured by mottled coloring and roughened surfaces. The 55 bones from Cedros Island were collected on an expedition from the University of California,

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Riverside (UCR), and were donated to the Los Angeles County Museum of Natural History (LACM localities 65144 to 65154 inclusive). Although many of the Cedros bones are incomplete, the contours are clear and preservation is good. In several instances skeletal elements of one individual were found together.

The increased representation of *Mancalla* has provided the opportunity of determining variability within the genus, and the associated skeletal material from Cedros Island has contributed to an understanding of skeletal proportions. The present Catalogue of Fossil Birds (Brodkorb, 1967) lists *Mancalla californiensis* from the type locality in Los Angeles and from the Corona del Mar site, and only *M. diegensis* from San Diego. Both Miller (1956) and Howard (1966), however, have indicated increasing confidence that the great size range in specimens from San Diego indicates that more than one species of *Mancalla* is represented there. The present study not only corroborates this belief, but clarifies the species assignments, resulting in the recognition and description of a new species from San Diego.

The Humboldt County humerus and the Laguna Hills bones resemble the San Diego specimens, but the Cedros Island material is distinct. The description of this species will be included in a report on the entire fossil avifauna from the Cedros Island localities.

#### ANALYSIS OF SPECIES

##### *Mancalla californiensis* Lucas

The type of *Mancalla californiensis* (a humerus lacking the distal end) is the only representative of the species recorded from the type locality—the Third Street tunnel excavation in Los Angeles (Lucas, 1901).

The later record of *M. californiensis* from Corona del Mar (Howard, 1949) was based on the large size of the carpometacarpus (no humerus being represented). At San Diego, the few fragments of large humeri among the much more abundant small specimens suggested *M. californiensis* (Miller, 1956), but these were too imperfect for anything except a size comparison.

Later excavations have brought to light a proximal end of a humerus from Corona del Mar and several well-preserved specimens of the element from San Diego that equal or closely approximate the type of *M. californiensis* in length and/or breadth of proximal end. It is, therefore, at last possible to make direct comparison with the type of *M. californiensis*—a good cast of which is at hand.

It was previously noted by Miller and Howard (1949) that the type humerus of *M. californiensis* differed from the then available San Diego humeri not only in its large size, but in the position of the muscle scar at the median border of the pneumatic fossa, and the character of the adjacent depression. The difference was described as follows (*op. cit.*: 209): "In the type of *Mancalla californiensis* the proximal tip of this scar is situated farther

within the fossa than in any of the San Diego specimens, and the depression is thus allowed to extend farther proximally as well, taking the form of a distinct groove with clear-cut, ridgelike edges running up alongside the median partition of the fossa." The specimen from Corona del Mar (LACM 2576) matches the type of *M. californiensis* precisely. It is further notable that in both the type and the Corona del Mar humeri these "ridgelike edges" remain separate for their full extent up into the pneumatic fossa, whereas in the San Diego specimens they converge proximally.

Other distinctions in the type humerus of *M. californiensis* and the large humeri from San Diego pertain to the greater curvature of the shaft in the former and the less prominent projection of the distal contour of the bicipital crest. The shaft character can be observed only in the type of *M. californiensis*, the Corona del Mar humerus is broken below the bicipital crest.

Distinction between the Corona del Mar and the San Diego material is evidenced also in the coracoid, ulna, radius, carpometacarpus, tibiotarsus and tarsometatarsus. Characteristics of these elements from Corona del Mar are now assumed to apply to the species *M. californiensis*. See Table I. With the exception of the carpometacarpi, all available specimens from Corona del Mar fall within the range in size of the San Diego bones in linear dimension. The carpometacarpi are longer and have a longer process of metacarpal 1.

Measurements of Corona del Mar specimens assigned to *Mancalla californiensis*: Humerus (LACM 2576) greatest breadth of proximal end 19.4 mm; (LACM 2577) breadth and depth of shaft above ectepicondylar process 4.7 x 10.2 mm. Coracoid (LACM 2581) height from below scapular facet to middle of head 18.8 mm; breadth across furcular facet 8.7 mm; breadth through triosseal canal, 5.9 mm; height of furcular facet at tip 5.1 mm. Ulna (incomplete, LACM 2580) depth of shaft 6.7 mm; depth of proximal end (estimated) 10.7 mm. Radius (LACM 2579) greatest length 29.7 mm; greatest depth of shaft 6.8 mm. Carpometacarpus (LACM 2578) greatest length 41.3 mm; height of process of metacarpal 1, 17.7 mm; greatest depth of proximal end through process of metacarpal 1, 11.0 mm; breadth of proximal trochlea 4.8 mm. Tibiotarsus (LACM 2424) estimated length 87.5 mm; breadth of proximal end 8.6 mm; least breadth of shaft 6.1 mm. Tarsometatarsus (LACM 2250) length from intercotylar tuberosity to external trochlea (middle trochlea broken) 39.3 mm; breadth of distal end 9.3 mm; breadth of proximal end 9.9 mm; breadth of shaft (middle) 4.8 mm.

#### *Mancalla diegensis* (Miller)

The large collection of *Mancalla* bones now available from San Diego exhibits a greater size range than was previously suggested by the material available in 1949. The humerus is the best represented element. Of over 130 humeri now at hand, 100 can be measured for proximal or distal breadth

TABLE I  
Comparison of *Mancalla californiensis* and *M. diegense*

Element	<i>M. californiensis</i>	<i>M. diegense</i>
HUMERUS	Muscle scar well within pneumatic fossa and ridgelike edges of depression parallel	Scar less extended within fossa and ridges converging.
	Curvature of shaft pronounced	Shaft straighter
	Contour of bicipital crest rounded distally	Crest prominently projected distally (angular)
CORACOID	Anterior border of triosseal canal slightly posterior to anterior border of shaft	Border of triosseal canal forming anterior border of the bone
	Upper surface of head broad; smoothly rounded	Upper surface of head narrow with central ridge
ULNA	Tip of furcular facet blunt; no upturned point	Tip of furcular facet with up-turned point
	Proximal profile from olecranon to cotylae broad and shallow; olecranon blunt	Profile depressed; olecranon more bulbous
	Palmar side of shaft above distal end flat, bordered by well-marked intermuscular lines	Palmar side of shaft rounded; slanting from internal to external side
RADIUS	External surface smooth; no depression below head	External surface rugose, with marked depression below head
	Groove on lateral edge extending nearly halfway up shaft	Groove extending less than $\frac{1}{3}$ length of bone
CARPOMETACARPUS	Length 41 mm; length process metacarpal 1, 16.6-17.7 mm	Maximum: length 37 mm; length process metacarpal 1, 15.4 mm
	Internal trochlear crest not clearly separated from M 3	Base of internal trochlear crest clearly separated from M 3
TIBIOTARSUS	Proximo-internal ligamental attachment short, broad, flat and partly on posterior surface of shaft	Attachment long, thin straight ridge on internal edge shaft
TARSOMETATARSUS	Center of shaft (anteriorly) level or convex; external border indistinctly raised	Marked groove extending proximally from distal foramen to external edge; external border raised for full shaft length

and 34 of these also provide a linear measurement. In length, the maximum bone is 151 per cent of the minimum, with a coefficient of variability (V) of 10.2 for the series. In a series of 300 humeri of the flightless auk, *Pinguinis impennis*, recorded by Lucas (1888:521), the maximum bone is only 114 per cent of the minimum in greatest length, and the series has a V of 3.0.

The distribution curve for length of the *Mancalla* humeri is roughly bimodal. The 26 specimens that fall below 66.6 mm form a normal curve with a mode of 63 mm and a mean of 62.7 mm. The remaining seven specimens are scattered from 71 to 85 mm with a mean of 76.5 mm. The 64 specimens in which proximal breadth can be measured provide a distinct bimodal curve where the smaller specimens range from 14.2 to 16.4 mm with a mean of 15.3 mm, and the larger bones range from 17.3 to 20.3 mm with a mean of 18.7 mm.

Bimodality of curve plus a large coefficient of variability is suggestive of heterogeneity of the sample according to Simpson, Roe and Lewontin (1960:102 and 205). They state further (*op. cit.*: 207) that unless changes due to growth are involved, a homogeneous sample for a linear dimension usually has a V of 3 to 7 in mammals, and is lower in birds. That the range in *Mancalla* cannot be attributed to age is evidenced by the state of ossification of the bones measured.

TABLE II  
Size Range and Variability in Length<sup>1</sup> of Limb Elements  
of *Mancalla* from San Diego

Element	Number of specimens	Length in mm			Ratio of maximum to minimum (in percent)	Coefficient of variability (V)
		max.	mean	min.		
Coracoid	21	54.0	43.5	39.0	138	11.1
Humerus	34	85.2	65.9	56.4	151	10.2
Ulna	23	32.1	26.3	23.6	135	7.8
Radius	9	31.8	27.1	24.2	131	11.5
Carpometacarpus	14	37.2	33.4	29.6	125	7.5
Femur	14	57.0	50.1	44.9	127	7.6
Tibiotarsus	15	98.7	82.8	72.0	137	11.2
Tarsometatarsus	9	43.6	36.6	31.1	140	11.4

<sup>1</sup>Lengths are measured as follows: coracoid from head (lateral to furcular facet) to sternal facet (lateral to internal distal angle); humerus, from head to internal condyle; ulna, from intercotylar ridge to internal condyle; carpometacarpus, from external crest of trochlea to distal end of metacarpal 2; tibiotarsus, from proximal articular surface to distal end; radius, femur and tarsometatarsus, greatest length.

These statistical criteria applied to the *Mancalla* humeri indicate heterogeneity of the San Diego sample, and comparison with the lesser range and small V of the *Pinguinis* humeri lends further support. As the large and small bones are intermingled throughout the deposits, it seems reasonable to assume that the distinction is specific rather than subspecific. Previously it was assumed that, if two species were represented, the larger one was *M. californiensis*. We have seen above (Table I), however, that none of the San Diego material can be assigned to *M. californiensis*.

The size range and coefficient of variability has been determined for all of the limb elements of the San Diego *Mancalla*. Each shows a wide range in measurement of length and a V greater than 7 (see Table II). For the type element of *M. diegensis*, the femur, exact measurement of greatest length can be made on 10 specimens and estimated on another four. Breadth of distal end can also be measured. Five bones have a length from 57.0 to 53.8 mm and a distal breadth from 11.1 to 9.7 mm. The other nine measure from 51.1 to 45.0 mm in length with a distal breadth from 9.3 to 8.4 mm. The type of *M. diegensis* (UCMP 33409) measures 56.3 mm in length and 11.0 mm in distal breadth—next to the maximum in both measurements and 25 per cent longer than the minimum specimen. From these figures it is concluded that the name *Mancalla diegensis* must now be applied to the large San Diego species rather than to the more abundant small form. The small form is, therefore, here described as new.

In some elements the point of linear separation between the large and small species is not clearly demarcated. To determine the placement of "borderline" specimens, measurements of breadth and qualitative characters were taken into account (see Tables III and IV). Comparisons with the partial skeletons from Cedros Island were also helpful, as this island species was apparently near in size to *M. diegensis*.

In the San Diego collection, approximately 50 complete limb elements and an equal number of incomplete specimens are now identified as *M. diegensis*. Among these, the following were illustrated by Miller and Howard (1949): scapula LACM 2176 and 2049 (Pl. 4, Figs. 5 and 7); coracoid LACM 2087 and 2067 (Pl. 3, Figs. 2 and 3); humerus LHM 2270 and 2220 (Pl. 3, Figs. 6 and 14); ulna LACM 2064 (Pl. 3, Fig. 7); carpometacarpus LACM 2068 (Pl. 4, Fig. 16); femur LHM 2220 (Pl. 4, Fig. 2); tibiotarsus LACM 2125 and LHM 2270 (Pl. 4, Figs. 9 and 11), and LACM 2177 (Pl. 5, Fig. 1); tarsometatarsus LACM 2178 and 2177 (Pl. 5, Figs. 4 and 5). One sternal fragment (LACM 2333) and one cranium with associated rostrum (LACM 2633) are outstandingly large and are tentatively assigned to *M. diegensis*.

The humerus from Humboldt County conforms in all respects with humeri of *M. diegensis* and is so assigned. Measurements of this bone are as follows: length 81.3 mm, breadth of proximal end 19.5 mm. Preservation of the Laguna Hills specimens is poor, but all are clearly distinct from *M. californiensis*. With the exception of two small ulnae, all appear to resemble *M. diegensis* and are tentatively so assigned.

*Mancalla milleri*, new species

*Holotype*: Complete left femur, LACM 2185, collected by Clifford Kennell, Dec. 26, 1947. Illustrated in Miller and Howard, 1949, Plate 5, Fig. 3, as "*Mancalla diegense*."

*Locality*: LACM locality 1070, east side of Curlew Street, across from end of Ostego Drive, San Diego, California.

*Paratype*: Complete left humerus, LACM 2813, collected July, 1962 from type locality.

*Formation and Age*: San Diego Formation, Middle (?) Pliocene.

*Referred Material*: In addition to the type and paratype, 87 limb elements on which a measurement of length can be made are referred to

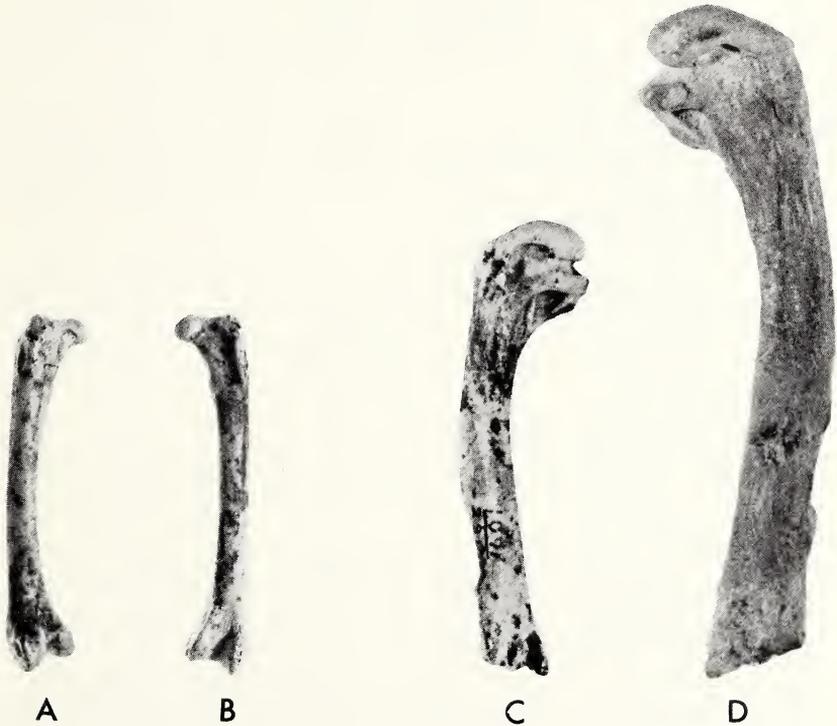


FIGURE 1. A.-C. *Mancalla milleri*, new species: A. Type femur (LACM 2185) posterior view; B. type femur anterior view; C. paratype humerus (LACM 2813) anconal view. D. *Mancalla diegense* Miller, maximum available humerus (LACM 2670) for comparison with *M. milleri*. Natural size. Los Angeles County Museum of Natural History Photos.

*M. milleri*, as follows: 12 coracoids, 25 humeri, 16 ulnae, 6 radii, 7 carpo-metacarpi, 8 femora, 8 tibiotarsi and 5 tarsometatarsi. There are also 13 scapulae and at least five incomplete sterna, two pelves, a cranium, and numerous incomplete limb bones whose size indicates assignment to *M. milleri*. The following elements illustrated by Miller and Howard (1949) as "*Mancalla diegensis*" are now assigned to *Mancalla milleri*: scapulae LACM

TABLE III  
Estimated Size Range (in millimeters) of Specimens of  
*Mancalla diegensis* and *M. milleri*

Element	<i>M. diegensis</i>			<i>M. milleri</i>		
	Max.	Mean	Min.	Max.	Mean	Min.
Scapula						
Breadth articular end	14.4	13.5	12.5	11.8	10.9	10.3
Coracoid						
Length	54.0	49.1	47.5	43.5	40.0	38.5
Breadth below furcular facet	6.3	5.8	5.4	5.1	4.9	4.0
Humerus						
Length	85.2	76.5	71.0	66.6	62.7	56.4
Breadth proximal end	20.3	18.7	17.3	16.4	15.3	14.2
Ulna						
Length	32.1	29.4	28.0	27.0	25.3	23.6
Breadth proximal cotylae	6.6	6.4	5.9	5.7	5.2	4.5
Radius						
Length	31.8	30.9	29.6	26.9	25.1	24.2
Greatest depth shaft	6.4	6.35	6.3	5.6	4.9	4.6
Carpometacarpus						
Length	37.2	35.6	35.0	33.2	31.6	29.6
Depth proximal end through metacarpal I	11.0	10.3	9.7	9.5	9.1	8.8
Femur						
Length	57.0	55.2	53.8	51.1	47.9	45.0
Breadth distal end	11.0	10.2	9.7	9.3	9.0	8.4
Tibiotarsus						
Length	98.5	90.2	81.0	77.5	74.9	72.0
Breadth distal end	10.7	9.0	8.2	7.9	7.2	6.5
Tarsometatarsus						
Length	43.6	39.9	38.0	36.0	34.0	31.1
Breadth proximal end	10.7	9.6	8.7	8.4	8.0	7.2

2070 and LHM 2270 (Pl. 4, Figs. 4 and 6); coracoid LHM 2270 (Pl. 3, Fig. 1); humeri LHM 2218 (Pl. 1, Fig. 1), LHM 2269, LACM 2066, 2096, and LHM 2281 (Pl. 2, Figs. 1, 2, 3 and 4); ulnae LACM 2069 (Pl. 1, Fig. 1), LACM 2082 (Pl. 1, Fig. 2 and Pl. 3, Fig. 8), LACM 2079 and 2101 (Pl. 3, Figs. 9 and 10), and LACM 2179 (Pl. 5, Fig. 2); radius LHM 2270 (Pl. 1, Figs. 1 and 6, and Pl. 4, Fig. 3); carpometacarpi LHM 2068 (Pl. 1, Figs. 1 and 3, and Pl. 4, Fig. 15), and LHM 2281 (Pl. 4, Fig. 17); femur LACM 2097 (Pl. 4, Fig. 1); tibiotarsi LACM 2083, 2100 LHM 2270, LACM 2108 and 2134 (Pl. 4, Figs. 8, 10, 12, 13 and 14); sterna LHM 2220 and LACM 2063 (Pl. 2, Figs. 6 and 7) and LACM 2180 (Pl. 6, Fig. 1); pelvis LHM 2281 (Pl. 2, Fig. 5) and LACM 2182 (Pl. 6, Fig. 2).

TABLE IV  
Qualitative Characters  
Distinguishing *Mancalla diegensis* and *M. milleri*

<i>Mancalla diegensis</i>	<i>Mancalla milleri</i>
<i>Coracoid:</i> anterior edge of furcular facet projected anteriorly; tip raised slightly and gradually.	<i>Coracoid:</i> anterior edge of furcular facet nearly on line with anterior contour of triosseal canal; tip up-swept anteriorly, with abruptly raised high, pointed tip.
<i>Humerus:</i> distal contour of bicipital crest (viewed anconally) almost a right angle, with prominent ligamental attachment at base of bicipital crest.	<i>Humerus:</i> distal contour of bicipital crest less angular, and ligamental attachment less projected.
<i>Ulna:</i> olecranon blunt, and straight with respect to shaft contour (in lateral view); very faint depression internal to olecranon.	<i>Ulna:</i> olecranon as in <i>M. diegensis</i> but internal depression deeper.
<i>Femur:</i> obturator ridge relatively short, with generally rounded contour; very slight depression internal to ridge.	<i>Femur:</i> obturator ridge relatively long, with angular contour sharply defined by deep depression along internal edge of ridge.
<i>Tibiotarsus:</i> posterior contour of proximal articular surface with deep notch separating the external and internal portions of surface.	<i>Tibiotarsus:</i> slight indentation between external and internal portions of proximal articular surface, but no deep separation.
<i>Tarsometatarsus:</i> Viewed anteriorly, proximal end flared; external border of shaft sharper than internal; shaft moderately depressed.	<i>Tarsometatarsus:</i> Bone columnar in appearance; both borders of shaft (anteriorly) sharply defined; shaft well depressed anteriorly.

*Diagnosis:* Type femur 16 per cent shorter than type of *M. diegensis*; deep excavation on internal side of obturator ridge. Mean of nine femora 13 per cent shorter than mean of five femora of *M. diegensis*. Paratype humerus 25 per cent shorter than type of *M. californiensis* (using dimension of length from proximal end to distal tip of deltoid crest to accommodate to incomplete specimen of *M. californiensis*); mean of 25 humeri 18 per cent shorter in over all length than mean of 7 humeri of *M. diegensis*.

*Description:* The smallest known species of *Mancalla*; averaging 12 to 19 per cent smaller than *M. diegensis* in comparable elements (see Table III). Poor preservation of the San Diego material, and considerable variability make qualitative distinctions from *M. diegensis* difficult to observe. Those which appear to be constant are shown in Table IV.

Of ten specimens of tibiotarsi in which the supratendinal bridge is fully ossified and intact, seven are clearly assignable to *M. milleri*. This fact indicates that the small size of the tibiotarsi cannot be attributed to immaturity.

Measurements of type and paratype: Femur LACM 2185, greatest length 47.3 mm; depth through trochanter and obturator ridge 6.3 mm; breadth of distal end 8.2 mm; least breadth of shaft 4.0 mm. Humerus LACM 2813, length to internal condyle 58.1 mm; breadth of proximal end 14.8 mm; breadth of distal end 5.2 mm; length from head to distal tip of deltoid crest 38.7 mm.

See Table III for size range of all specimens assigned to *M. milleri*.

#### A MOUNTED SKELETON OF MANCALLA

A composite mount of *Mancalla* is displayed at the Los Angeles County Museum of Natural History (see Howard, 1953). At the time of selection of material for the mount, in 1953, there were 224 bones of *Mancalla* in the museum collection, representing at least fragmentary specimens of the main elements. Vertebrae, ribs and phalanges, however, were incompletely represented, and these elements were supplied from a modern skeleton of *Uria aalge californica*.

For the skull and pelvis the choice was limited to one good specimen each (LACM 2205 and 2182 respectively). The two available sterna appeared to correlate in size with the pelvis, and the better specimen was chosen (LACM 2063). The choice of coracoids (LACM 2243 and 2208) was based on the proper fit of the sternal facet into the coracoidal sulci of the sternum. Two scapulae (unnumbered) appeared suitable for articulation with the coracoids, and two humeri (LACM 2442 and 2303), in turn, seemed to conform reasonably well to the glenoid area formed by the coracoid and scapula.

In accordance with the size now established for these elements of the two San Diego species, the humeri and scapulae are found to be of average size for *M. milleri*; the right coracoid is slightly above average, the other slightly below; the single radius (LACM 2335) available at the time proves to be slightly above average for *M. milleri*; the ulnae (LACM 2543 and

2544) and carpometacarpi (LACM 2213 and an unnumbered specimen) fall within the size range for *M. diegensis*. Femora were scarce, but one complete (LACM 2097) and one proximal end (unnumbered) seemed appropriate for the size of the acetabulae of the pelvis. The complete left femur proves to be considerably above the average for *M. milleri*, but still within its size range. The right tibiotarsus and tarsometatarsus (LACM 2177) that were found together in the matrix (see Miller and Howard, 1949: 226) were chosen for the other two elements of the leg. Both specimens are near the borderline between *M. diegensis* and *M. milleri* in length but are now considered to be of minimum size for *M. diegensis*. Also the contours of the tarsometatarsus and the stocky proportions of the tibiotarsus are characteristic of *M. diegensis*. The character of the proximal articular surface of the tibiotarsus described in Table IV cannot be ascertained now that the bone is in the mount. However, the illustration of the specimen (Miller and Howard, 1949: Pl. 5, Fig. 1b) suggests the separation of the two surfaces as in *M. diegensis*.

In the light of our present knowledge of *Mancalla*, the mount which we hoped would represent an average-sized specimen of the dominant San Diego species, is above the average of *M. milleri* in many of its elements and disproportionately large in the terminal segments of the wing and leg. If our judgment is correct concerning the size break between *M. diegensis* and *M. milleri*, the skull, limb girdles, sternum, humeri, radius and femora represent *M. milleri*. But the ulna, carpometacarpus, tibiotarsus and tarsometatarsus represent *M. diegensis*. Herein lies an excellent example of the pitfalls of building a composite mount!

#### SUMMARY AND CONCLUSIONS

With three times more specimens at hand, than were available to Miller and Howard (1949) at the time of their comprehensive report on *Mancalla*, the present study has contributed considerably to an understanding of the taxonomy and distribution of the genus.

1. The geographic distribution of the genus is enlarged from southern California to a wide extent along the west coast of North America from Humboldt County, California in the north to Cedros Island, Baja California, Mexico in the south.

2. Identification of *Mancalla californiensis* from the Corona del Mar locality, formerly based only on size, is confirmed by the discovery of a humerus at the latter locality comparable to the type specimen from Los Angeles.

3. The greatly enlarged collection of *Mancalla* bones from the San Diego sites exhibits so great a range in size that the presence of two species, as previously postulated, can be statistically demonstrated.

4. The larger of the two San Diego species conforms with *Mancalla californiensis* in size, but differs qualitatively. The type femur of *M. diegensis*

is found to be one of the largest of the femora in the collection, and the large San Diego species, therefore, takes the name of *M. diegense*.

5. The smaller, more abundant species from San Diego is described in honor of the late Professor Loye Miller, whose contributions have formed the basis for the growth of paleornithology on the west coast.

#### ACKNOWLEDGMENTS

I wish to express my appreciation to the University of California Museum of Paleontology in Berkeley, the University of California at Los Angeles and the San Diego State College for the loan of fossils, and for their indulgence in permitting the extensions of these loans for the long period of time necessary to study this complicated problem. Personal thanks are extended to Mr. Roy Kohl for sending the Humboldt County specimen, to Mrs. Jean Cohn for assistance and information regarding the San Diego State College material, and to Dr. Richard Tedford and Dr. Frank Kilmer for geological information concerning the fossil deposits in which *Mancalla* occurs. Dr. Tedford is also responsible for the gift of the Cedros Island material to the Los Angeles County Museum of Natural History. To the Los Angeles County Museum of Natural History I am continually grateful for the opportunity to use the collections, and to the museum staff for their many kindnesses.

It has been a privilege to have had numerous conferences with the late Professor Loye Miller during the period of this study, and to have had his blessing on the conclusions reached.

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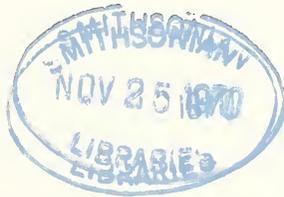
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A NEW MOTH FLY OF THE GENUS *PSYCHODA*  
FROM CRABHOLES ON THE KENYA COAST  
(Diptera: Psychodidae)

By CHARLES L. HOGUE



LOS ANGELES COUNTY MUSEUM OF NATURAL HISTORY • EXPOSITION PARK  
LOS ANGELES, CALIFORNIA 90007

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A NEW MOTH FLY OF THE GENUS *PSYCHODA*  
FROM CRABHOLES ON THE KENYA COAST  
(Diptera: Psychodidae)

By CHARLES L. HOGUE<sup>1</sup>

ABSTRACT: A new species of Psychodidae, *Psychoda martini*, is described and figured. Material consists only of adult males and females collected on the Kenya Coast from land crab burrows of two species, *Cardisoma carnifex* and *Sesarma meinerti*.

The number of *Psychoda* species known from the vast Ethiopian Region is estimated to be 40, including available undescribed species (Satchell, 1955, Tonnoir, 1939). This appears to be far less than what the actual fauna must be judging from the size of the genus in other much smaller and ecologically less diverse areas, viz: Papuan Region, 80; Philippines, 51; Borneo, 38; Micronesia, 23 (Quate, 1967: 211). It is, therefore, not surprising that another new species was recognized, especially since it comes from a coastal locality in contrast to the inland and mountain origins of its African congeners.

*Psychoda martini* Hogue, new species  
Figures 1-7

DESCRIPTIONS (terminology mainly after Quate, 1955: 108-114).

**Adult female:**

*General.*—Typical, unicolored *Psychoda*.

*Size.*—Average for *Psychoda*; measurements in mm as follows (= means lengths; ranges in parentheses; N = 10 = random sample from type series).

Wing length	1.55 (1.53-1.60)	width	.64 (.55-.68)
Legs	fore	mid	hind
femur	.33 (.29-.37)	.39 (.31-.435)	.39 (.36-.415)
tibia	.29 (.22-.34)	.51 (.46-.54)	.57 (.475-.635)
tarsus 1	.25 (.21-.27)	.27 (.24-.30)	.24 (.215-.27)
2	.08 (.07-.09)	.08 (.065-.09)	.08 (.065-.085)
3	.06 (.05-.065)	.06 (.05-.06)	.06 (.05-.065)
4	.05 (.045-.06)	.05 (.04-.05)	.05 (.045-.05)
5	.06 (.05-.07)	.06 (.05-.065)	.06 (.055-.06)
Palpus	1 .06 (.05-.075)		
	2 .13 (.10-.15)		
	3 .16 (.13-.17)		
	4 .19 (.165-.21)		

<sup>1</sup>Senior Curator of Entomology, Los Angeles County Museum of Natural History.

*Coloration*.—Uniformly grayish brown without markings or pattern of any kind.

*Head* (Figs. 3, 6).—Eye bridges four facets wide, separated by a width of four facets. Antenna (Fig. 3) 16 segmented, per cent proportions 100: 67: 177: 140: 133: 133: 130: 127: 123: 117: 117: 117: 110: 73: 3: 3: 3. Scape 1.5 times as long as broad, pedicel spherical, flagellar segments with necks approximately 1.5 times longer than bulbs, except 13 in which neck is slightly shorter than bulb; 14-16 clearly separated; a single small sensory cone on 13; a pair of Y-shaped sensory filaments on each of segments 3-13. Palpal segment per cent proportions 100: 218: 266: 316.

*Wing*.—2.42 times as long as wide. Both wing forks complete, ratio of  $R_{2+3}:R_3 = .75$ ,  $M_{1+2}:M_2 = .38$ .

*Genitalia*.—As figured (Fig. 2); subgenital plate shallowly U-shaped, basal part broad.

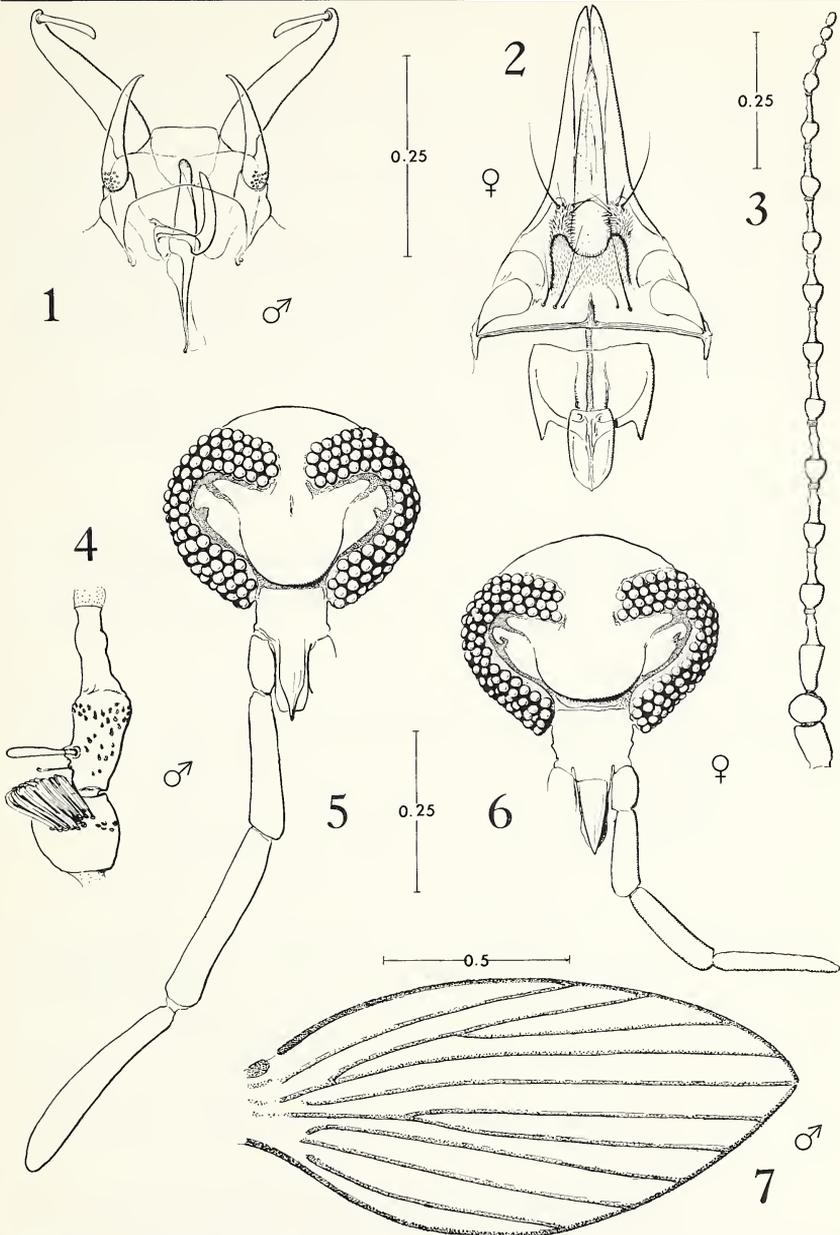
#### Adult male:

*General*.—Similar to female in coloration and basic structure.

*Size*.—Slightly smaller than female; measurements in mm as follows (= means lengths; ranges in parentheses; N = 10 = random sample from type series):

Wing length	1.44 (1.34-1.58)	width	.70 (.64-.75)
Legs	fore	mid	hind
femur	.34 (.315-.365)	.39 (.355-.40)	.40 (.365-.43)
tibia	.25 (.235-.38)	.49 (.455-.515)	.56 (.50-.60)
tarsus 1	.29 (.265-.30)	.29 (.270-.295)	.26 (.245-.270)
2	.09 (.08-.09)	.09 (.075-.095)	.08 (.07-.09)
3	.06 (.055-.065)	.06 (.055-.065)	.06 (.055-.065)
4	.05 (.045-.055)	.05 (.04-.05)	.05 (.045-.05)
5	.06 (.055-.065)	.06 (.055-.06)	.06 (.055-.065)
Palpus	1 .08 (.075-.09)		
	2 .21 (.175-.23)		
	3 .28 (.25-.29)		
	4 .33 (.275-.365)		

*Head* (Figs. 4, 5).—Eye bridges separated by a width of two facets. Pedicel of antenna provided with an isolated, drosomesal dense patch of 25 to 30 slender scales with sharply recurved tips (Fig. 4); basal flagellar segment with a conspicuous dorsal, round-tipped seta projecting perpendicularly from its base at about the proximal third of the bulb, and a second smaller (one-



FIGURES 1-7. *Psychoda martini*, new species. Fig. 1. genitalia of male; Fig. 2. genitalia of female; Fig. 3. antenna of female (sensory filaments not shown); Fig. 4. pedicel and basal flagellar segment of antenna of male, mesal view; Fig. 5. head of male; Fig. 6. head of female; Fig. 7. wing of male.

half length of preceding) club-tipped seta alongside and proximal to the larger (Fig. 4). Inconspicuous sensory cones usually on segments 13 and 15. Palps longer than in female, segments increasingly longer than in female distad, segment per cent proportions 100: 261: 350: 412.

*Wing* (Fig. 7).—Noticeably broader than in female, 2.1 times as long as wide.  $R_{2+3}:R_3 = .58$ ,  $M_{1+2}:M_2 = .39$ .

*Genitalia*.—As figured (Fig. 1). Surstyle slightly less than twice as long as 9th tergite, with single tenaculum. Lateral shaft of aedeagus slightly shorter than main shaft, tip subulate, base expanded and extended across the main shaft to form an oval, collarlike flange; main shaft heavier than lateral, with a rounded tip.

#### DISTRIBUTION

Known only from the type locality on the Kenya Coast, East Africa.

#### MATERIAL

**Holotype** ♂: Kilifi Creek, Kenya, East Africa; 23 January 1968; collected by C. L. Hogue (CLH 210); deposited in Los Angeles County Museum of Natural History (LACM); slide mount, in euparal.

**Allotype** ♀: Same data as holotype, except 3 February 1968; (CLH 211); deposited at LACM.

**Paratypes**: 15 ♂♂, 41 ♀♀; same locality as holotype, 23 January (CLH 210), 3 February (CLH 211), 4 February (CLH 214B), 1968; deposited at LACM, British Museum of Natural History, and National Museum of Natural History, Washington.

All specimens were collected from burrows of the tropical land crabs, *Cardisoma carnifex* (Herbst) and *Sesarma meinerti* de Man.

#### BIOLOGICAL NOTES

*Psychoda martini* was discovered and collected during the course of excavating and studying the burrows of land crabs on the north and south shores of the large bay (Kilifi Creek) west of the town of Kilifi. The results of these investigations are reported by Hogue and Bright (in press).

The flies were found to be fairly abundant resting on the walls within the burrows of both species of crabs at the site. When disturbed by jets of air from an aspirator, they readily crawled and flew from the burrows in company with abundant individuals of the mosquito *Aedes (Skusea) pembaensis* Theobald.

Although water samples from all the excavated burrows and other sources in the vicinity were examined carefully, no immature *P. martini* were discovered.

All collections were made during midday and afternoon hours of warm humid days. Seasonally, the time was in the mid-dry period of the year.

## DIAGNOSIS

With the following combination of characters, *Psychoda martini* segregates with *filipenis* Satchell 1955, *scuticopenis* Satchell 1955, *angustisternata* Satchell 1955, *maxima* Tonnoir 1939, *reducta* Tonnoir 1939 and *modesta* Tonnoir 1935 in Satchell's key (1955: 345) to the tropical African species: sensory filaments ("ascoids") Y-shaped, both wing forks complete, antenna 16-segmented in which the three diminutive terminal segments are clearly separated from each other and with sensory cones on at least one of segments 13, 14 and 15. It disagrees with all these in the shape of the various elements of the male and female genitalia, being most like *filipenis* in the character of the male aedeagus, that is with the lateral shaft expanded and extended basally across the main shaft to form an oval flange. However, *martini* lacks the distal filiform extension of the lateral shaft.

## ACKNOWLEDGMENTS

I would like to thank Dr. Purvis L. Martin of San Diego, California, for making possible the discovery of this new species by sponsoring a general zoological expedition to Kenya, in January-February of 1967 of which I was a member. In recognition of his help it is estimably named for him.

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FURTHER INFORMATION ON THE BREEDING BIOLOGY  
OF THE HONEY GUIDES

By HERBERT FRIEDMANN



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VIRGINIA D. MILLER  
*Editor*

# FURTHER INFORMATION ON THE BREEDING BIOLOGY OF THE HONEY GUIDES

By HERBERT FRIEDMANN<sup>1</sup>

ABSTRACT: In this paper recent additions to our knowledge of the reproductive biology of four of the African species of honey guides of the genus *Indicator* are presented with comments for their proper evaluation and correlation with earlier information. The egg of *Indicator maculatus maculatus* is described for the first time; five new host species are given for *I. indicator* (*Merops superciliosus chrysocercus*, *M. orientalis viridissimus*, *M. nubicus*, *M. pusillus pusillus*, and *M. bulocki bulocki*), and one each for *I. minor* (*Lybius leucocephalus senex*) and *I. conirostris* (*Gymnobucco bonapartei cinereiceps*).

Our knowledge of the breeding biology of the honey guides is still far from complete, but the various bits of new information recently made available help to fill some of the existing gaps. These are given below for each of the four African species of *Indicator* to which they apply. I hope that competent observers and students of birds in various parts of Africa may use their opportunities to further our knowledge of these difficult but fascinating birds.

## 1. Spotted Honey guide. *Indicator maculatus* G. R. Gray

The egg of the nominate race of the spotted honey guide has remained undescribed. The first known example, now in the collection of the Los Angeles County Museum of Natural History, was collected at Boron, in the Ivory Coast, toward the end of June, 1968, by Daniel Parelius, who sent it to me. The egg is pure white with slight gloss, like those of all species of *Indicator* whose egg shells are known, and measures 23.4 x 18 mm. It is very similar to, but slightly larger than, the single recorded egg of the central African race of this species, *I. maculatus stictithorax*, which measures 21.6 x 17.7 mm.

These two eggs, one of each of the two subspecies of this honey guide, were collected under precisely similar conditions. Parelius had set a trap of fine net very close to the ground, and he caught in it a female spotted honey guide, which, on dissection, proved to be in active breeding condition. The *maculatus* egg was on the ground immediately beneath the net and must have been laid by the captured bird, although it was not noticed until the next morning when another female spotted honey guide was taken in the trap. The second bird could not have been responsible for the egg as it was in non-breeding condition.

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In like manner, the egg of *I. maculatus stictithorax*, taken in Rio Muni (now Spanish Continental Guinea) in January, 1952, by Jorge Sabater, was also found on the bare earth just beneath a net trap close to the ground, in which a female spotted honey guide was taken at the time.

Lest it be thought that the typical race of this species is new to the Ivory Coast, it may be recalled that Bigot and Roux (1966: 148) reported three examples from there in 1962. These were the first actual specimen records from that country, and were followed by those obtained by Parelius six years later. Bigot and Roux noted that the stomach contents of their specimens contained remains of chiton from beetles and spiders. This caused them to comment that the spotted honey guide was far from being exclusively a wax eater, but fed equally on small terrestrial arthropods.

I emphasize once more that beeswax is not the whole, or, so far as we know, even the most important element of, food of this or of any of the species of *Indicator*, but is something added to the regular insectivorous diet of these birds, although with apparent desire on their part. In the honey guides of the genera *Melignomon* and *Prodotiscus* the wax found in their stomachs is not wax from becomb, but is from scale insects, Coccidae.

## 2. Greater Honey guide. *Indicator indicator* (Sparman)

Five additional hosts for the greater honey guide have recently been reported in Nigeria, all of them species of bee eaters. It was known previously that members of this family are highly favored as hosts by the greater honey guide, so it is not surprising to find that additional species of the group are similarly parasitized. Four of the five are species new to the host list; the other one is a sub-species previously unrecorded in this capacity, but conspecific with another race already known to be victimized in other parts of Africa by the same species of honey guide. The new data, given below, together with the information previously assembled by me (Friedmann, 1955, 1958, 1968), show that nearly 30 per cent of all recorded instances of parasitism by the greater honey guide, actually 47 out of 161 cases, have involved bee eaters as the hosts.

The additions are as follows:

Blue-cheeked bee eater. *Merops superciliosus chrysocercus* Cabanis and Heine.

Walsh (1966: 74) first recorded this bee eater breeding in a sand bank on the Niger River about 20 kilometers south of Kainji Dam, Kontagora Division, Nigeria. This constituted a considerable southern extension of its known breeding range, as until then the bird was not known to nest south of 15° 8' N, approximately 60 kilometers south of Ansongo, on the Niger River, in the French Sudan. From June 29, 1966, Walsh studied the Kainji Dam colony of some 14 nest holes to which the birds were seen carrying food, either to incubating mates, or, more probably, to young in the recesses of the tunnel nests. On July 16, Walsh dug out one of these nests and found it to contain as its sole inmate a young greater honey guide nearly ready to leave the nest. From data on other nestlings of this honey guide it is known

that the period from hatching to fledging is approximately a month. This would place the date of egg laying around the beginning of June.

This is the first record for the blue-cheeked bee eater as a host of the greater honey guide. It is apparently the same instance that was listed later by Wells and Walsh (1969: 14). Additional reports may be anticipated as the blue-cheeked bee eater seems to be spreading southward in Nigeria. Walsh (in litt., September, 1969) informed me that the 1966 colony of 14 nest holes had increased to 90 nest holes in 1967, and in 1968 he discovered another colony of about 150 nest holes about eight kilometers farther south on the Niger River.

Little green bee eater. *Merops orientalis viridissimus* Swainson

Fry (1967: 12) added the little green bee eater to the list of victims of the greater honey guide in Nigeria. No details were given, and it is not possible to say whether but a single such instance or more than one came to his notice.

Nubian carmine bee eater. *Merops nubicus* Gmelin

Wells and Walsh (1969: 14) reported this bee eater to be parasitized by the greater honey guide near the Kainji Dam, Nigeria. In reply to my inquiry Walsh (in litt., September, 1969) informed me that the report was based on seeing recently fledged young of *Indicator indicator* at the colony of carmine bee eaters, but as the observations were made by Wells he could not elaborate on them, and Wells had departed for Malaya and could not be reached readily. It is unfortunate that the observations as recorded did not specifically mention feeding of the young parasites by the adults of the host species, but the fact that there were more than one of the young honey guides in immediate proximity to the nesting colony adds substance to the record, the exact wording of which is as follows ". . . At the Shugunu *nubicus* colony in 1966 young honey guides were on the wing in V (May), before the majority of young bee eaters had left the next (nest) . . ."

Least bee eater. *Merops pusillus pusillus* Müller

In eastern and southern Africa the race *M. p. meridionalis* has long been known to be one of the most frequent, if not the very most frequent, of the victims of the greater honey guide. It is therefore not surprising to find that in Nigeria the nominate race of this bee eater is also similarly imposed upon by the parasite. The first such instance was reported by Dodds (1959: 118) in a paper overlooked by me until recently, and then additional and wholly independent observations were published by Fry (1967: 12).

White-fronted bee eater. *Merops bulocki bulocki* Vieillot

The nominate race of this bee eater has been found to be a frequent victim of the greater honey guide in Nigeria by Fry (1965: 78, and 1967: 12). If we were to follow White (1965: 234) in considering *bullockoides* conspecific with *bulocki* it would be pertinent to state that the former taxon is known

to be parasitized in Kenya and Rhodesia, where, indeed, it seems to be a regularly selected host, for which at least six records have been reported (Friedmann, 1968: 3). However, Fry (1969: 574) after extensive field as well as museum studies, considers *bullockoides* and *bullocki* to be valid taxa, although closely related species, and I concur.

Boehm's bee eater. *Merops boehmi* Reichenow

In my 1968 paper (Friedmann, 1968: 3) I cited Benson, Brooke, and Vernon (1964: 67) as reporting a Zambian instance of this bee eater serving as a honey guide host. In this capacity it was known earlier only from a single case found in Malawi. Since then Benson has informed me that there was no Zambian record and that he and his co-authors had combined Malawi and Zambia data in their paper.

While additional instances of parasitism by the greater honey guide have come to my notice since my 1968 paper, they have contributed no new information, but merely added to earlier, similar occurrences. In two other species of *Indicator* there are, however, one new host record for each.

3. Lesser Honey guide. *Indicator minor* Stephens

An additional host for the lesser honey guide (n nominate sub-species) may be reported solely on a set of eggs of the white-headed barbet, *Lybius leucocephalus senex* (Reichenow), with one of the lesser honey guide. These are currently on display in the exhibition galleries of the National Museum in Nairobi. The set apparently was acquired by the Museum from Sir Charles F. Belcher, but I was unable to learn the locality or date of collection when visiting the Museum in October, 1969.

4. Thick-billed honey guide. *Indicator conirostris* (Cassin)

Mr. Gorman M. Bond informed me that in the second week of June, 1965, A. Forbes Watson collected a nestling female of this honey guide from a nest of a grey-throated barbet, *Gymnobucco bonapartei cinereiceps* Sharpe, in the Kakamega Forest, western Kenya. This is the first record for the subspecies *cinereiceps* as a victim of the thick-billed honey guide, although the nominate race of the barbet had been known earlier to be parasitized in Cameroon. The Kakamega bird is now in the National Museum of Natural History, Washington.

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