BREVIORA

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CAMBRIDGE, MASS. 11 OCTOBER, 1968 NUMBER 296

THE GENUS *DYSDERINA* (ARANEAE, OONOPIDAE) IN CENTRAL AMERICA AND THE WEST INDIES

Arthur M. Chickering

ABSTRACT. A total of twenty-four species of the genus *Dysderina* are recognized in this paper. Seventeen species are described as new. Nine of these are from Panama, two are from Costa Rica, two are from Trinidad, W. I., one is from Jamaica, W. I., two are from St. Vincent, B. W. I., and the remaining one is from Dominica, B. W. I. *Dysderina principalis* Simon from St. Vincent, B. W. I. is not *D. principalis* (Keyserling) from Colombia and, therefore, is described as a new species, *D. soltina* sp. nov. *Dysderina antillana* Bryant, described from St. Croix, U. S. Virgin Islands in 1942 and reported from Hispaniola in 1948, has been shown to be *Ischnothyreus peltifer* (Simon) and is treated in another publication.

The Oonopidae include a group of very small spiders usually occupying concealed habitats such as leaf litter, debris, especially grass and weed debris, and other similar habitats. They are particularly numerous in tropical and subtropical regions but are now known from many other parts of the world. The distinctive features of the family are treated in such publications as the following: Simon, 1892-1895; Petrunkevitch, 1939; Comstock, 1940; Kaston, 1948, and others, and will not be treated in this paper. Since early in my work of collecting and studying spiders in Panama, I have continued to be interested in these minute members of the order Araneae. For the past several years I have made a special effort to collect members of the family Oonopidae in Central America and the West Indies. As a result of this effort I have accumulated a rather large number of species of several genera belonging to this family, and the time has arrived for me to put the results of these years of study and collecting into a permanent record. It had been my intention to publish the results of these studies in a single monograph. Recently, however, the decision was made to publish a series of shorter papers each dealing with a single genus or a group of genera as conditions seem to warrant. The genus *Dysderina* is one of a group of genera to be treated early in the series.

My appreciation and gratitude are again expressed for the continued aid and encouragement in the pursuit of my studies extended by the staff of the Museum of Comparative Zoology. My thanks are also extended to Dr. W. J. Gertsch, American Museum of Natural History, Dr. G. Owen Evans and Mr. D. J. Clark, Department of Zoology, British Museum (Natural History) for the loan of important species of the genus *Dysderina*. Grants GB-1801 and GB-5013 from the National Science Foundation have made it possible for me to continue my work in the Museum of Comparative Zoology and to spend a total of nearly twelve months during the last four years collecting in Panama, Costa Rica, and the West Indies.

Except as otherwise stated in later parts of this paper, all types together with my entire collection of the genus *Dysderina* will be deposited in the Museum of Comparative Zoology.

Genus DYSDERINA Simon, 1891

The type species is *Dysderina principalis* (Keyserling) by monotypy. The genus was established on the basis of a male from Colombia identified by Keyserling as *Oonops principalis*. Simon (1891) correctly recognized that this species could not be regarded as belonging to the genus *Oonops* and, therefore, placed it in a new genus *Dysderina*. Simon also described two additional species from St. Vincent Island, B. W. I. *Dysderina plena* O. P.-Cambridge was described from Mexico in 1894. *Dysderina antillana* Bryant was described from St. Croix, U. S. Virgin Islands in 1942, and also reported from Hispaniola in 1948, but is now known to be *Ischnothyreus peltifer* (Simon) as will be shown in another paper. In 1951 I reported four species of *Dysderina* from Panama. Since that time I have collected these small spiders at every opportunity and as a result I now have a rather large collection consisting of numerous species from parts of Central America and the West Indies but none has appeared east of Dominica, W. I. The most important features of this genus observed during my study of the group may be stated as follows: Total length varies from about 1.6 mm to 2.75 mm, with females usually somewhat larger than males. There is a remarkable similarity of general appearance among the species recognized in this paper. Males can be readily separated into species on the basis of the distinctive features of the palpal tarsi. Females, on the other hand, are very difficult to separate into species with any degree of certainty. In my treatment of this sex I have placed great emphasis on the epigynal areas which occasionally are quite distinctive but more frequently are at best only obscurely so. Nearly all outer parts are strongly chitinized. The carapace is moderately high; regularly arched from posterior eyes to beginning of posterior declivity; about three-fourths as wide as long nearly opposite second coxae; surface irregularly granulate; usually with no indication of a median groove or pit. Eyes: six in two rows; AME lacking; posterior row gently recurved as viewed from above; quite compactly arranged; little difference in size of eyes but shape often varies (long diameter always used for measurements); clypeus typically heavily bordered. Chelicerae moderately developed; usually vertical, parallel; with fang typically slender and evenly curved; fang groove with a single tooth, at least in certain species. Maxillae with a peculiar terminal notch seen only in males and thus far only in a few species (Fig. 2). Lip: strongly chitinized; considerably wider than long; transversely concave in middle. Sternum: strongly chitinized; usually deeply grooved with conspicuous lobules opposite the coxae; continued laterally between coxae and united with a sclerite surrounding the cephalothorax to make a strong enclosure; sternal suture strongly procurved; fourth coxae usually widely separated. Legs: usually 4123 in order of length but with minor variations occasionally; first and second legs with conspicuous ventral spines which vary somewhat among different species; third and fourth legs without true spines. Male palp: all segments except tarsus simple and unmodified; apparently without true spines; tarsus somewhat inflated and with more or less distinctive terminal structures. Abdomen: ovoid; with pedicel strongly chitinized and deeply corrugated; dorsal scutum varies somewhat in size but typically covers most of dorsum; epigastric scutum continued around pedicel and far dorsally (Fig. 8); ventral scutum covers much of remainder of venter but varies in extent; a sclerite typically partially surrounds the spinnerets on ventral side; black bristles may mark the position of the reduced colulus; openings of book-lungs, tracheal spiracles, and genital organs more or less distinct. Genital area somewhat distinctive but usually obscure. Where the species under consideration agrees fully with the stated features of the genus no mention will usually be made of the specific characteristics in the description of the species.

As a result of my study of the genus *Dysderina* presented in this paper I am obliged to recognize a total of twenty-four species from the region under study (exclusive of *D. principalis* (Keyserling) from Colombia). The number is undoubtedly inflated because of the great difficulty in accurately matching up males and females.

Thirteen of these species are from Panama; two are from Costa Rica; one is from Mexico; two are from Trinidad, W. I.; one is from Jamaica, W. I.; four are from St. Vincent, B. W. I.; and one is from Dominica, B. W. I. Fifteen of these species, ten of which are regarded as new, are represented by males; nine are represented only by females of which seven are regarded as new; six of the different kinds of males are accompanied by what are believed to be properly assigned females. It should be remembered, however, that matching females with the proper males is a very uncertain task.

Key to the males of DYSDERINA *from Central America and the West Indies*

1a. Species in which the palpal tarsus terminates in a pair of slender distal apophyses, one sickle-shaped and one somewhat feather-shaped (Fig. 43) .... *D. obtina*, p. 21
1b. Species without such palpal, tarsal, distal structures as given above 2
2a. Species with a group of four or five distal, terminal apophyses on the palpal tarsus (Fig. 30) .... *D. globina*, p. 14
2b. Species without such palpal, tarsal, distal structures as given above .. 3
3a. Species with three definite, distal, palpal, tarsal apophyses (Figs. 41, 77) (*meridina, spinigera*) 4
3b. Species without such distal, palpal, tarsal structures as given above .. 5
4a. Species with distal, palpal, tarsal apophyses as in Figure 41 .... *D. meridina*, p. 20
4b. Species with distal, palpal, tarsal apophyses as in Figure 77 .... *D. spinigera*, p. 31
5a. Species with a single, short, broad, distal, palpal, tarsal apophysis divided into an opaque half and a transparent half (Fig. 4) .... *D. abdita*, p. 5
5b. Species without such a single distal apophysis as given above 6
6a. Species with a long, slender, distal, palpal, tarsal spine and a relatively massive, somewhat twisted, closely associated apophysis (Figs. 20-22) .... *D. craneae*, p. 10
6b. Species without such a pair of distal, palpal, tarsal structures as given above 7
7a. Species in which the distal, palpal, tarsal apophysis turns at a right angle near its base and then divides into a pair of flattened structures (Figs. 37-38) .... *D. intempina*, p. 19
7b. Species without such a distal, palpal, tarsal apophysis as given above 8
8a. Species with a single, distal, palpal, tarsal extension divided into a pair of relatively short, incurved apophyses (Figs. 46-47) .. *D. plena*, p. 23
8b. Species without such a pair of apophyses as given above 9

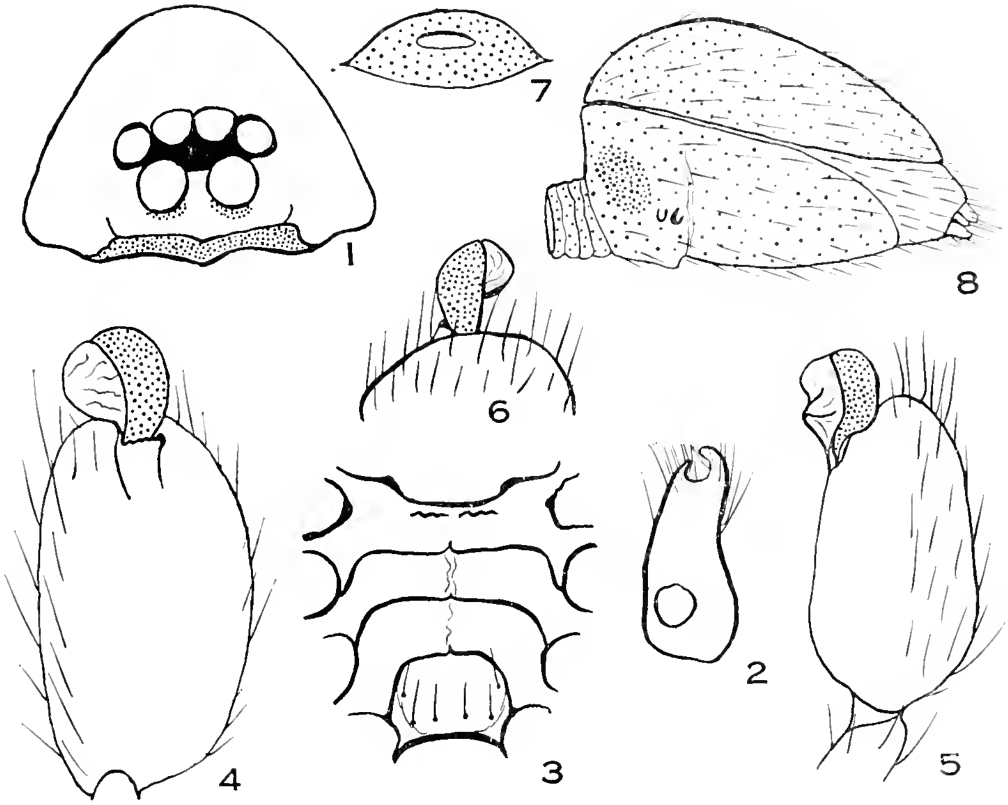
9a. Species with two distal, palpal, tarsal structures, a slender curved spine and a relatively large, broad, compound apophysis (Fig. 63) .... *D. seclusa,* p. 27
9b. Species without such a pair of distal, palpal, tarsal structures as given above 10
10a. Species with palpal, tarsal, distal apophysis terminating in a broad, angular, somewhat concave structure (Fig. 16) .... *D. concinna,* p. 9
10b. Species without such a distal, palpal, tarsal structure as given above 11
11a. Species with palpal, tarsal, distal apophysis a single robust structure divided distally into a short, slender spine and a sharply pointed robust spine (Fig. 65) .... *D. simla,* p. 29
11b. Species without such a palpal, tarsal, distal apophysis as given above 12
12a. Species with a main palpal, tarsal, distal apophysis sharply bent midway, enlarged and flattened distally and with a minute spine (Figs. 58-59) .... *D. recondita,* p. 25
12b. Species without such palpal, tarsal, distal structures as given above 13
13a. Species with a robust palpal, tarsal, distal apophysis terminating in a series of short, pointed structures obscured by a cluster of hairs (Figs. 69-70) .... *D. soltina,* p. 30
13b. Species without such a palpal, tarsal, distal apophysis as given above 14
14a. Species with a pair of palpal, tarsal, distal apophyses curved toward one another; clypeus about three-fourths as high as diameter of ALE (Chickering, 1951, figs. 2, 3; and Fig. 24 this paper) ..*D. dura,* p. 12
14b. Species with a long, curved, palpal, tarsal, distal apophysis together with a slender spine and a short, blunt process between the two; clypeus about as high as diameter of ALE (Fig. 81) ..*D. watina,* p. 33

DYSDERINA ABDITA sp. nov.

Figures 1-8

Holotype. The male is from El Volcan, Republic of Panama, August, 1950. The name of the species is a Latin adjective referring to its concealed habitat.

Description. Total length 2.28 mm. Carapace 1.04 mm long; 0.85 mm wide opposite second coxae where it is widest; well rounded along ventral border from opposite base of palp to posterior margin; 0.52 mm tall; quite evenly arched from PME to beginning of posterior declivity which begins opposite interval between second and third coxae; with surface unevenly granulate with median arched area nearly devoid of granulations; without a median, longitudinal thoracic groove or pit; with sparsely situated short recurved hairs or fine bristles. Eyes: six in two rows as usual; posterior row occupies about five-sixths of width of carapace at that level; viewed from above, posterior row gently recurved; viewed from in front, posterior row gently procurved (Fig. 1). Ratio of eyes ALE : PME : PLE = 10 : 9 : 9; boundaries of ALE somewhat irregular but nearly circular, others somewhat oval. ALE separated from one another by nearly their radius, from PLE by one-sixth of their diameter, from PME by a little less than one-third of their diameter. PME contiguous only for a short distance and separated from PLE by about one-ninth of their diameter. Height of clypeus (Fig. 1) slightly less than the diameter of ALE. Chelicerae: vertical; essentially parallel; basal segment 0.29 mm long; apparently without a basal boss; fang slender and evenly curved; fang groove apparently with a very small tooth, probably promarginal. Maxillae: moderately long; slender; distinctly convergent and almost meeting anterior to lip; palp inserted into basal third; with a well developed distal scopula; distal end divided (Fig. 2). Lip: strongly chitinized; extended posteriorly into sternal area and with an obscure groove separating the horizontal part from the more vertical portion; wider at base than long in ratio of about 9 : 7; anterior border with a row of stiff bristles. Sternum: scutiform in general; as wide as long; widest between second coxae; strongly chitinized and distinctly but less intricately grooved than in several other species (Fig. 3); posterior border recurved and not continued between fourth coxae which are separated by about 1.5 times their width; coxae three and four short and stout; coxae one and two somewhat more elongated; sternal suture procurved. Legs: 4213 in order of length; tibial index of first leg 10, of fourth leg 9; trichobothria present but exact number and placement undetermined. Tarsal claws apparently as recorded for *D. seclusa* (Chickering, 1951). First femur with two pairs of ventral spines in distal half; first tibia with five pairs of ventral spines, first very long but diminishing distally so that last pair is hardly more than a pair of bristles; first metatarsus with three pairs of ventral spines, irregularly spaced. Second femur apparently with only one conspicuous spine on prolateral surface at beginning of distal third; second tibia with four pairs of ventral spines; second metatarsus apparently with only two pairs of ventral spines, irregularly spaced. Third and fourth legs lacking true spines. Palp: only tarsus inflated; important features, more or less distinctive, shown in Figures 4-6. Abdomen: with a well developed and strongly corrugated pedicel; 1.24 mm long exclusive of pedicel; 0.9 mm wide near middle; spinnerets as usual in the genus; genital aperture as in Figure 7; dorsal scutum covers nearly the entire dorsum; epigastric scutum continued around anterior end of abdomen; boundaries between epigastric and ventral scuta not clear; ventral scutum covers



Figs. 1-8. *Dysderina abdita* sp. nov. Fig. 1. Eyes and clypeus; from in front. Fig. 2. Right maxilla; nearly lateral view (from dissected paratype). Fig. 3. Sternum; from below. Figs. 4-5. Left palpal tarsus; nearly ventral and retrolateral views, respectively. Fig. 6. Tip of left palpal tarsus; nearly dorsal view. Fig. 7. Genital aperture. Fig. 8. Abdomen; left side (from paratype.)

nearly the entire venter except for a small area at posterior end and laterally where the two scuta nearly meet (Fig. 8). Color in alcohol: in general, a rich reddish brown, essentially as described for *D. dura* and others (Chickering, 1951).

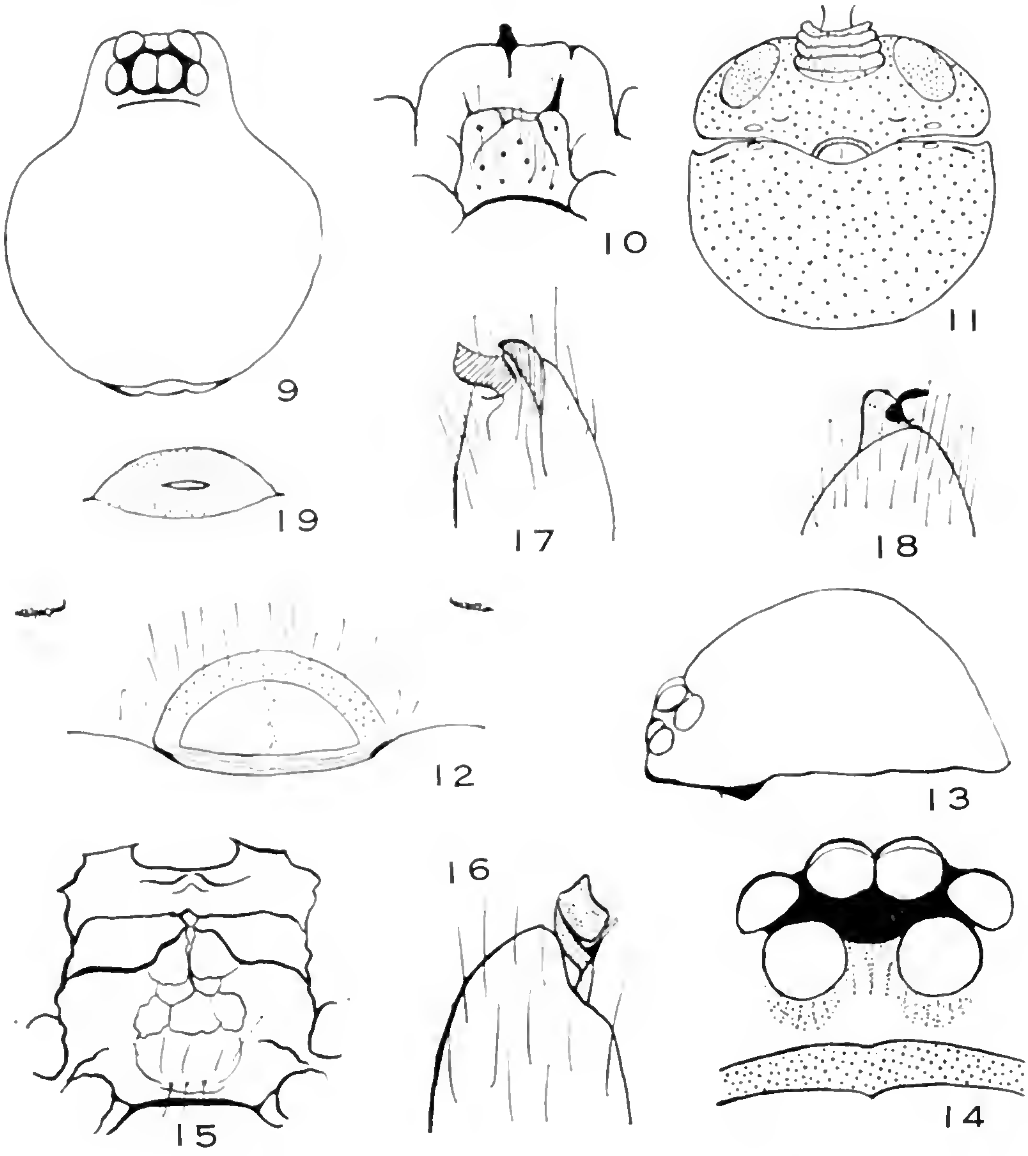
Records. Seven paratype males from El Volcan, Panama, August, 1950. It seems probable that one of the two kinds of females described from the same locality and collected during the same period should be matched with these males but this is not at present possible to do with any certainty.

DYSDERINA BELINDA sp. nov.

Figures 9-12

Holotype. The female is from Boquete, Panama, August, 1950. The name of the species is an arbitrary combination of letters.

Description. Total length 2.5 mm. Carapace: 1.08 mm long; 0.9 mm wide opposite posterior border of second coxae where it is widest (Fig. 9); 0.49 mm tall opposite interval between second and third coxae where it is tallest; distinctly arched from PME to beginning of steep posterior declivity; surface distinctly granulate and with granulations often in rows; with a recurved groove just



Figs. 9-12. *Dysderina belinda* sp. nov. Fig. 9. Carapace; dorsal view. Fig. 10. Posterior end of sternum; from below. Fig. 11. Venter, from below. Fig. 12. Epigynal area; from below. Figs. 13-19. *Dysderina concinna* sp. nov. Fig. 13. Carapace; left side. Fig. 14. Eyes and clypeus; from in front. Fig. 15. Sternum; from below. Figs. 16-18. Distal end of left palpal tarsus; nearly prolateral, nearly ventral and nearly dorsal, respectively. Fig. 19. Genital aperture.

behind posterior eyes; thoracic part regularly rounded along ventral margin and sharply narrowed shortly behind eyes. Eyes: six as usual in a fairly compact group; posterior row occupies about two-thirds of width of carapace at that level; viewed from above, posterior row slightly recurved, measured by posterior borders. Ratio of eyes ALE : PME : PLE = 9.5 : 9 : 8.5. ALE separated from one another by about one-half their long axis; separated from PME by about one-fourth of their long axis and from PLE by a line at one point. PME contiguous for nearly one-fourth of their circumference; separated from PLE by a line at one point. Posterior row only slightly wider than anterior row. Height of clypeus equal to fully three-fourths of the long axis of ALE. Chelicerae, maxillae and lip typical of females of the genus as far as observed. Sternum: rather strongly convex; with the usual intricate grooves and lobes typical of the genus; posterior end very bluntly terminated and only extended between bases of fourth coxae which are separated by nearly 1.5 times their width (Fig. 10). Legs: tibial index of first and fourth legs 9; spines essentially as described for *D. silvatica* Chickering (1951) with no very important differences. Abdomen: essentially as described for *D. silvatica* Chickering (1951); scuta and sclerite partly surrounding spinnerets quite typical of the genus (Fig. 11). Epigynal area: very simple as usual (Fig. 12). Color in alcohol: essentially as described for other species; with no important differences.

This species appears to be closely related to *D. silvatica* Chickering, 1951 (Fig. 6) but differs from that species definitely with respect to the features of the epigynal area. In the former species the epigynal area is a nearly semicircular area with a minute dot near the posterior border. In *D. belinda* sp. nov. the epigynal area (Fig. 12) appears as a nearly semicircular area with a complete, conspicuous border and a faint central, longitudinal stripe.

Records. Three females taken in the same locality with the holotype and during the same short period of nine days in Boquete, Panama, August, 1950, appear to belong here as paratypes.

DYSDERINA CONCINNA sp. nov.

Figures 13-19

Holotype. The male holotype is from El Volcan, Panama, August, 1950. The name of the species is a Latin adjective referring to its neat, pleasing appearance.

Description. Total length 2.27 mm. Carapace 1.01 mm long; 0.86 mm wide opposite interval between first and second coxae where it is widest; 0.44 mm tall, and therefore, about half as tall as wide (Fig. 13); otherwise essentially as described for *D. abdita* sp. nov. Eyes: posterior row occupies about seven-ninths of width of carapace at that level; gently recurved as seen from above. ALE separated from one another by about five-eighths of their diameter; separated from PLE by one-eighth of their diameter and from PME by about three-eighths of their diameter. PME contiguous for about one-fifth of their circumference; only slightly separated from PLE. Posterior row wider than anterior row in ratio of 9 : 7. Height of clypeus equal to about nine-eighths of the diameter of ALE. Viewed from in front, posterior row gently procurved (Fig. 14). Chelicerae: basal segment 0.33 mm long; fang slender and evenly curved; otherwise essentially as recorded for *D. abdita* sp. nov. No teeth observed along fang groove. Maxillae and lip: apparently as described for *D. abdita* sp. nov. but no distal notch observed on maxillae (scarcity of paratypes prevents dissection for closer examination). Sternum: scutiform in general; slightly longer than wide; intricately and obscurely grooved (Fig. 15); not continued between fourth coxae which are separated by twice their greatest width; right first coxa abnormally small. Legs: tibial index of first leg 9, of fourth leg 10; several trichobothria observed but exact number and placement not determined; two tarsal claws. Spines: first leg with femoral ventral spines 0-1r-1r-2-2, with last two on retromargin reduced to little more than bristles; tibia with ventral spines 2-2-2-2-2-0; metatarsus with five ventral spines, three along promargin and two along retromargin, all irregularly placed. Second tibia with five ventral spines along promargin and four along retromargin; second metatarsus with two pairs of ventral spines; no true spines observed on legs three and four or on palp. Palp: essential features shown in Figures 16-18. Abdomen: 1.17 mm long; 1.04 mm wide near middle; pedicel, scuta, tracheal spiracles, openings to book lungs and spinnerets all essentially as described for *D. abdita* sp. nov.; genital aperture as indicated in Figure 19. Color in alcohol: essentially as described for other species in this paper with slight variations.

Records. Two male paratypes were taken at El Volcan, Panama, August, 1950.

DYSDERINA CRANEAE sp. nov.

Figures 20-23

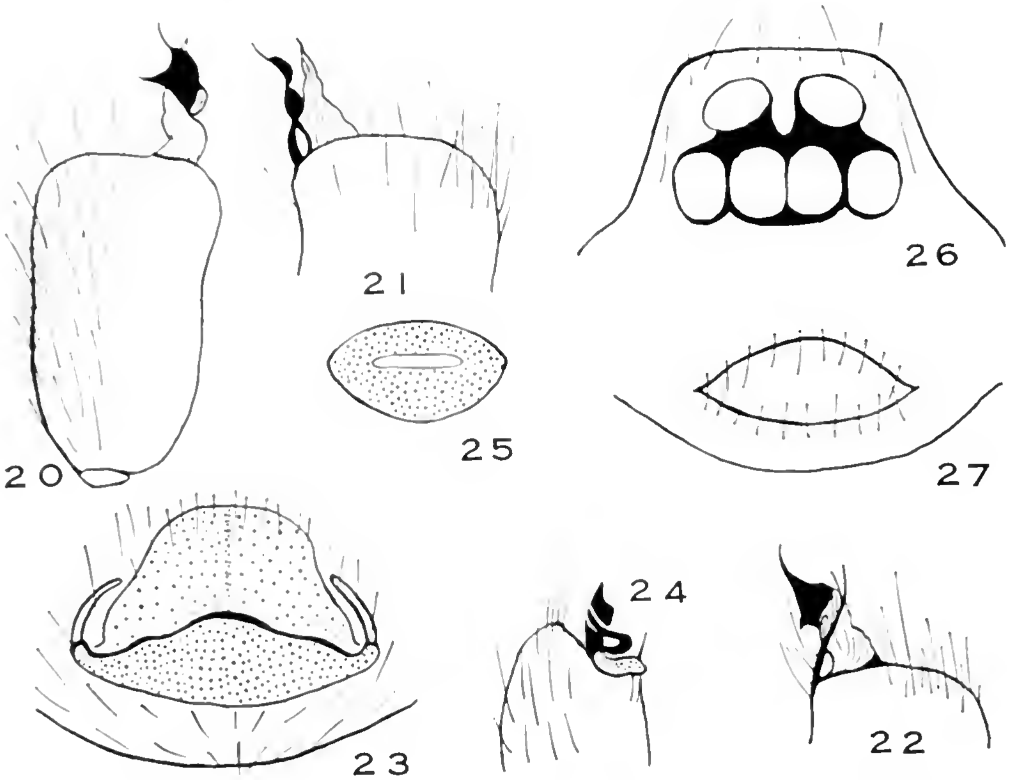
Holotype. The male is from Simla, Arima Valley, Trinidad, W. I. in the close vicinity of the William Beebe Tropical Research

Station, April 25, 1964. The species is named after Miss Jocelyn Crane, Director of the Station.

Description. Total length 2.2 mm. Carapace 1.05 mm long; 0.79 mm wide opposite second coxae where it is widest; 0.42 mm tall; surface conspicuously but very irregularly granulate. Eyes: eye group occupies fully four-fifths of width of carapace at level of PE; viewed from above, posterior row gently recurved; ratio of eyes ALE : PME : PLE = 10 : 9 : 9; positions and relationships essentially as stated for *D. globina* sp. nov. Chelicerae, maxillae and lip: all essentially typical of the genus as observed in this study. Sternum: deeply grooved in general pattern usually found in this genus; anterior third with a conspicuous transverse groove but otherwise nearly smooth; posterior two-thirds intricately grooved with primary and secondary grooves; fourth coxae separated by about six-fifths of their width. Legs: tibial index of first and fourth legs 9; spines almost identical with those recorded for *D. globina* sp. nov. Palp: all segments typical of males of the genus except the enlarged tarsus with its embolus and associated structures (Figs. 20-22); the degree of twisting of these structures seems to vary somewhat among the observed male paratypes. Abdomen: typical of males of the genus with respect to scuta, indistinctive genital region, spinnerets, book lungs, tracheal openings, etc.; spinnerets partly surrounded by a ventral semicircular sclerite. Color in alcohol: carapace brown with heavily granulate areas darker than middorsal and nongranulate areas; dorsal abdominal scutum lighter brown; other parts as usual with variations yellowish and light brown.

Female paratype. Total length 2.45 mm. Carapace 1.12 mm long; 0.88 mm wide; 0.45 mm tall; granulate essentially as in male. Eyes: eye group occupies about three-fourths of width of carapace at level of PE; seen from above, posterior row gently recurved; ratio of eyes ALE : PME : PLE = 10.5 : 10 : 9; ALE separated from one another by slightly less than their radius; other relationships typical of females of the genus as seen in this study; clypeus heavily bordered; height equal to about seven-tenths of the diameter of ALE. Mouth parts essentially typical of females of the genus. Sternum: essentially as in male except that anterior region is more irregular because of secondary grooves. Legs: 41=23 in order of length; tibial index of first and fourth legs 10; first leg with femoral ventral spines 0-0-1r-2-2-0, tibial ventral spines 2-2-2-2-2-0, metatarsal ventral spines 2-2-2-0; second leg essentially as in first; third and fourth legs devoid of true spines. Abdomen: dorsal and ventral scuta nearly cover this part of body; chitinous sclerite completely surrounds spinnerets and anal tubercle but is very narrow dorsally. Epigynal area quite distinctive (Fig. 23).

Records. Described female paratype taken with holotype from hay and weed debris by sifting, Simla, Arima Valley, Trinidad, W. I., April 25, 1964. Five male and seven female paratypes taken in vicinity of Simla, Arima Valley, or along roadside to Blanchesseuse, Trinidad, W. I., April, 1964.



Figs. 20-23. *Dysderina craneae* sp. nov. Fig. 20. Left male palpal tarsus; nearly prolateral view. Figs. 21-22. Tip of left male palpal tarsus; dorso-retrolateral view and nearly retrolateral view, respectively. Fig. 23. Epigynal area; from below. Figs. 24-25. *Dysderina dura* Chickering. Fig. 24. Tip of left palpal tarsus; nearly prolateral view. Fig. 25. Genital aperture of male. Figs. 26-27. *Dysderina furtiva* sp. nov. Fig. 26. Eyes from above. Fig. 27. Epigynal area; from below.

DYSDERINA DURA Chickering

Figures 24-25

Dysderina dura Chickering, 1951: 208. The male holotype is in the Museum of Comparative Zoology; collected on Barro Colorado Id., Panama Canal Zone, July, 1936.

A detailed description of this species was published in 1951 together with two figures illustrating certain features of the palp. Two more figures are added here to still further clarify the description. About three dozen specimens have been added to the collection since the recognition of the holotype. All of these have come from the vicinity of the Panama Canal Zone. The species is by far the most numerous in the collection from Panama. The female is still not certainly known but is suspected of being *D. silvatica* Chickering.

DYSDERINA FURTIVA sp. nov.

Figures 26-27

Holotype. The female holotype is from Jamaica, W. I., St. Catherine Parish, 3 mi. north of Spanishtown, Oct. 16, 1957. The name of the species is a Latin adjective referring to its concealed habitat.

Description. Total length 1.98 mm. Carapace 0.84 mm long; 0.69 mm wide opposite second coxae where it is widest; well rounded from just behind PE to posterior border which is only slightly notched; gently rising along median region from PME to beginning of steep posterior declivity; 0.25 mm tall; with no thoracic groove; with a sparse covering of black hairs most conspicuous at beginning of posterior declivity. Eyes: posterior row occupies about eleven-fifteenths of width of carapace at that level; seen from above, posterior row very gently recurved measured by posterior borders but nearly straight (Fig. 26); ratio of eyes ALE : PME : PLE = 7.5 : 7 : 6.5; ALE separated from one another by a little less than one-third of their diameter, from PLE by about one-fifth of their diameter and from PME by about one-third of their diameter; PME contiguous for a short distance, barely separated from PLE; posterior row wider than anterior row in ratio of about 22 : 17; viewed from in front, posterior row definitely procurved; height of clypeus equal to about four-fifths of the diameter of ALE. Chelicerae: basal segment 0.25 mm long; fang groove with a minute tooth on each margin near tip of the slender fang; otherwise essentially typical of females of the genus. Maxillae: somewhat more robust than described for *D. silvatica* Chickering (1951) but essentially as in that species. Lip: wider at base than long in ratio of about 13 : 10; slightly concave along distal border; sternal suture gently procurved. Sternum: scutiform in general; as wide as long; strongly convex; only faintly lobulated opposite coxae; grooves and ridges lacking; this last feature very unusual in the genus; posterior end not extended between fourth coxae which are separated by four-thirds of their width. Legs: 4123 in order of length; tibial index of first leg 8, of fourth leg 7; first leg with only one spine on prolateral side about two-thirds from base of femur; first tibia with ventral spines 2-2-2-2-1p; first metatarsus with ventral spines 2-2-1p; second leg with no femoral spines; second tibia with ventral spines 2-2-2-2-0; second metatarsus with three spines along promargin and two along retromargin with irregularity in placement; legs three and four probably to be considered lacking spines but some of the numerous bristles might be considered weak spines especially on fourth tibia; palp without terminal claw but with many stiff bristles resembling weak spines. Abdomen: pedicel shorter and less corrugated than in typical species; dorsal scutum covers about nine-tenths of dorsum; ventral scuta extend about seven-ninths of distance from pedicel to spinnerets; without a chitinous band guarding the spinnerets as in typical species; position of colulus barely indicated. Epigynal area: very simple as usual in the genus but its form (Fig. 27) seems to be more or less distinctive. Color in alcohol: essentially typical of the genus except that the highly chitinized cephalothorax and scuta are somewhat lighter in color.

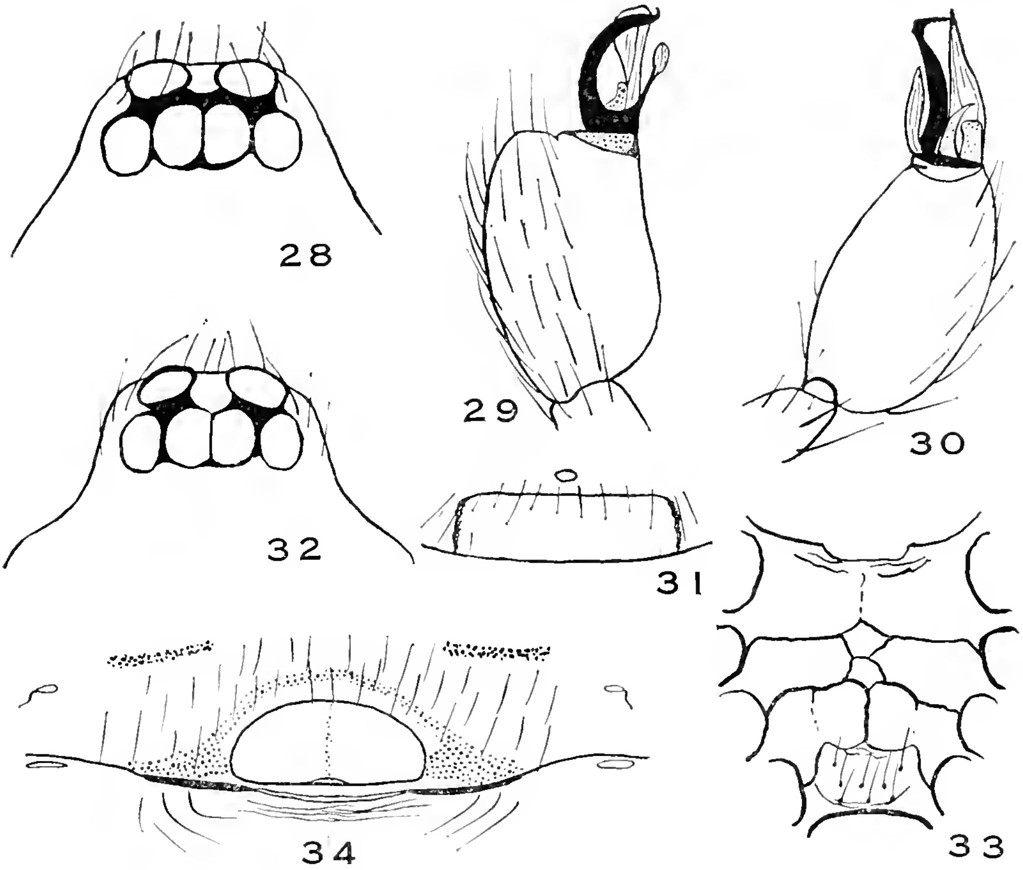
This species also appears to be closely related to *D. silvatica* Chickering, 1951, but the epigynal area is unlike that seen in any other species. In *D. furtiva* sp. nov. this region is a simple, broad, slit-like aperture with a narrow border surrounding a plain white area.

Records. Paratype females were taken with the holotype and numerous specimens are in the collection from the following localities: St. Andrew Parish, Stony Hill, May 26, 1956 (C. C. Hoff); Coopers Hill, Feb. 10, 1955 (P. F. Bellinger); Jack's Hill Road, Dec. 6, 1957; St. Ann Parish, vicinity of Moneague, Nov. 7, 1957; St. Catherine Parish, Evarton, Nov. 29, 1957. Numerous females from Trinidad, W. I., for some time regarded as representing a new species are now referred to this species. No males have yet been associated with these numerous females.

DYSDERINA GLOBINA sp. nov.

Figures 28-31

Holotype. The male holotype is from Dominica, B. W. I., Windward Islands, June 12, 1911. It will be deposited in the American Museum of Natural History, New York, N. Y. The name of the species is an arbitrary combination of letters.



Figs. 28-31. *Dysderina globina* sp. nov. Fig. 28. Eyes from above. Figs. 29-30. Male palpal tarsus; nearly prolateral and retrolateral views, respectively. Fig. 31. Genital region from below. Figs. 32-34. *Dysderina humphreyi* sp. nov. Fig. 32. Eyes from above. Fig. 33. Sternum from below. Fig. 34. Epigynal area from below.

Description. Total length 1.83 mm. Carapace 0.91 mm long; 0.73 mm wide opposite interval between first and second coxae where it is widest; 0.4 mm tall; other features essentially typical of males in the region under study. Eyes: eye group (Fig. 28) occupies about three-fourths of width of carapace at level of PE; seen from above, posterior row moderately recurved; ratio of eyes ALE : PME : PLE = 9 : 9 : 10 (some irregularities in outline noted); ALE separated from one another by three-tenths of their diameter and barely separated from PLE and PME; PME contiguous for more than one-fourth of their circumference and barely separated from PLE; height of clypeus equal to about three-fifths of the diameter of ALE. Chelicerae typical of males in the region under study; maxillae appear to be grooved and possibly divided distally. Lip wide at base and much narrowed distally. Sternum:

granulate; with a deep transverse groove shortly behind procurved sternal suture; with grooves, intricately developed in many species, here very much reduced and simplified; fourth coxae separated by nine-sevenths of their width. Legs: tibial index of first and fourth legs 9; 4123 in order of length; first femur with ventral spines 0-0-1r-1p-1p; first tibia with ventral spines 2-2-2-2-2 (last two little more than stiff bristles); first metatarsus with ventral spines 2-2-1p-0; second femur apparently only with ventral spines 0-0-1p-0; second tibia and second metatarsus essentially as in first with respect to ventral spines; third and fourth legs lacking true spines. Palp: all segments as usual in the genus except tarsus with its complicated embolus and associated apophyses (Figs. 29-30). Abdomen: essentially as described for *D. meridina* sp. nov.; genital region obscure but apparently distinctive (Fig. 31).

Records. One male paratype, somewhat damaged, accompanies the holotype. A female, recently moulted, is also with the holotype but is not in good condition for description.

DYSDERINA HUMPHREYI sp. nov.

Figures 32-34

Holotype. The female holotype is from Boquete, Panama, August, 1954. The species is named after Richard L. Humphrey, M.D., who, as an undergraduate student, was my assistant during a period of field work in Panama in the summer of 1954.

Description. Total length 2.24 mm. Carapace 0.97 mm long; 0.75 mm wide opposite second coxae where it is widest; 0.41 mm tall; somewhat less regularly arched along median dorsal region than usual in females of the genus; otherwise essentially typical of the genus. Eyes: posterior row occupies about three-fourths of width of carapace at that level; almost straight but very slightly recurved as viewed from above (Fig. 32); ratio of eyes ALE : PME : PLE = 8.5 : 8.5 : 7.5 (boundaries of eyes, especially of ALE, are quite irregular); ALE separated from one another by about their radius; ALE barely separated from PLE and from PME by about one-fourth of their diameter. Posterior row of eyes very closely crowded together; PME contiguous for one-fourth of their circumference; barely separated from PLE. Posterior row of eyes wider than anterior row in ratio of about 6 : 5; viewed from in front, posterior row of eyes definitely procurved; height of clypeus equal to about five-eighths of the diameter of ALE. Chelicerae, maxillae, and lip essentially as described for *D. silvatica* Chickering (1951) as far as observed. Sternum: general features as usual in the genus; fourth coxae separated from one another by a little less than 1.5 times their width; pattern of grooves essentially as represented in Figure 33. Legs: 4123 in order of length; tibial index of first leg 10, of fourth leg 9. Leg spines: first femur with five ventral spines, two on promargin and three on retromargin, not regularly paired; first tibia with five pairs of ventral spines; first metatarsus with five ventral spines irregularly placed; second femur with four ventral spines, one on promargin and three on retromargin; second tibia with four pairs of ventral spines; second metatarsus with five ventral spines, three on promargin and two on retromargin; legs three and four apparently without true spines. Abdomen: scuta, pedicel, tracheal spiracles, etc., all essentially typical of females of the genus. Epigynal area: very simple as usual; essentially as represented in Figure 34. Color in alcohol: essentially typical of the genus with no unusual features.

This species appears to be closely related to both *D. plena* O. P.-Cambridge and *D. silvatica* Chickering but the shape of the epigynal area is somewhat different than in the two previously known species and the dots along the posterior border are completely lacking.

Records. Eight paratype females collected August 4-11, 1954, in the close vicinity of Boquete, Panama.

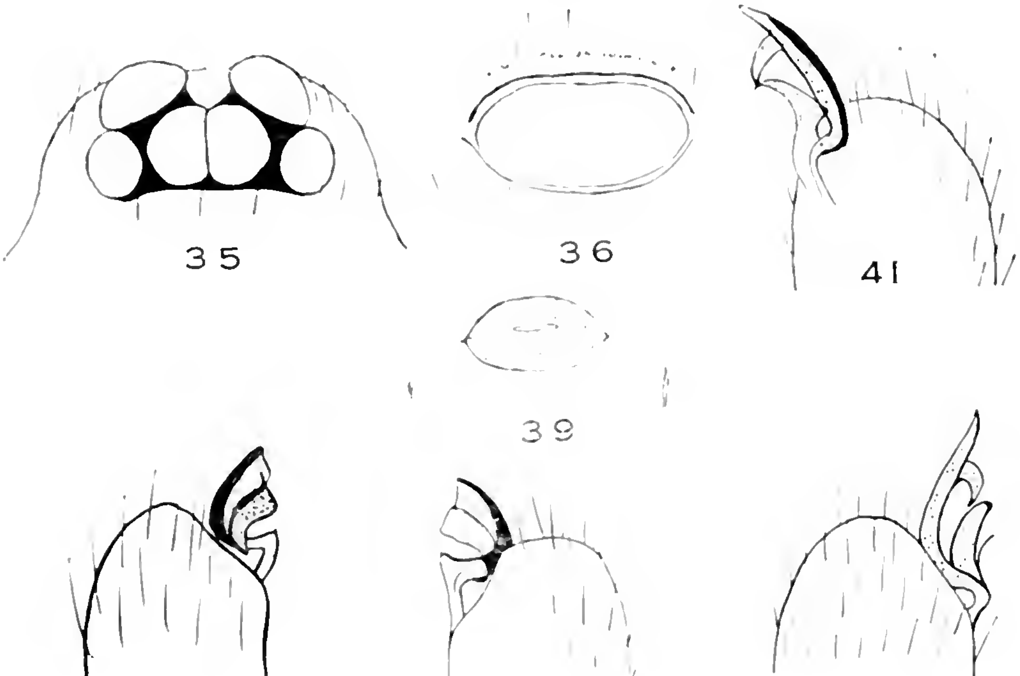
DYSDERINA IMPROVISA sp. nov.

Figures 35-36

Holotype. The female holotype is from Barro Colorado Island, Panama Canal Zone; collected in a Berlese funnel by Dr. James Zetek, May-October, 1946. The name of the species is a Latin adjective meaning unexpected.

Description. Total length 2.26 mm, exclusive of the slightly extended spinnerets. Carapace 0.95 mm long; 0.77 mm wide opposite second coxae where it is widest; 0.4 mm tall; otherwise essentially as in *D. silvatica* Chickering (1951). Eyes: posterior row occupies about three-fourths of width of carapace at that level (Fig. 35); viewed from above, gently recurved. Ratio of eyes ALE : PME : PLE = 8.5 : 7.5 : 7. ALE separated from one another by a little more than their radius; contiguous to PLE; separated from PME by nearly one-fourth of their diameter; PME contiguous for about one-fourth of their circumference; barely separated from PLE; posterior row wider than anterior row in ratio of 6 : 5; viewed from in front, posterior row definitely procurved. Height of clypeus equal to about three-fourths of the diameter of

ALE. Chelicerae, maxillae and lip essentially as described for *D. silvatica* Chickering (1951). Sternum: general features as usual in the genus; pattern of grooves rather complicated; fourth coxae separated from one another by about seven-fourths of their width. Legs: 4123 in order of length; tibial index of first leg 9, of fourth leg 10. Leg spines: first femur with irregularities of ventral spines on right and left; first tibia with five pairs of ventral spines; first metatarsus with three pairs of ventral spines; second femur with ventral spines 1r-1r-2-1p; second tibia with ventral spines 2-2-2-2-1p; second metatarsus with two pairs of ventral spines; third and fourth legs with few weak spines. Abdomen: essentially typical of females of the genus. Epigynal area: very simple as usual; essentially as shown in Figure 36. Color in alcohol: also essentially typical of the genus with minor variations.



Figs. 35-36. *Dysderina improvisa* sp. nov. Fig. 35. Eyes from above. Fig. 36. Epigynal area from below. Figs. 37-39. *Dysderina intempina* sp. nov. Figs. 37-38. Distal end of left male palpal tarsus; prolateral and retrolateral views, respectively. Fig. 39. Genital area from below. Figs. 40-41. *Dysderina meridina* sp. nov.; distal end of left male palpal tarsus; prolateral and retrolateral views, respectively.

D. improvisa sp. nov. is also regarded as closely related to *D. silvatica* Chickering but its epigynal area is distinctly oval in shape, as compared to the semicircular shape of this region in the previously known species. The pattern of grooves on the sternum appears to be somewhat distinctive also.

Records. Seven female paratypes from Barro Colorado Id., Panama Canal Zone, were collected in a Berlese funnel by Dr. James Zetek, May-Oct., 1946. Six females were taken in the same locality as follows: June-Aug., 1936; April-May, 1942 (Zetek); June-Oct., 1946 (Zetek); Aug., 1954; January, 1958. One female was taken in the Canal Zone Forest Preserve, February, 1958.

DYSDERINA INTEMPINA sp. nov.

Figures 37-39

Holotype. The male holotype is from Boquete, Republic of Panama, August, 1950. The name of the species is an arbitrary combination of letters.

Description. Total length 2.15 mm. Carapace 0.99 mm long; 0.79 mm wide opposite second coxae where it is widest; 0.53 mm tall; otherwise essentially typical of males of the genus. Eyes: posterior row occupies about five-sevenths of width of carapace at that level; slightly recurved as seen from above. Ratio of eyes ALE : PME : PLE = 8.5 : 8.5 : 9. ALE separated from one another by their radius; almost in contact with PLE; separated from PME by their radius. PME contiguous only for a short distance; only separated from PLE by a narrow line. Posterior row of eyes wider than anterior row in ratio of about 5 : 4. Height of clypeus equal to slightly less than the diameter of ALE. Viewed from in front, posterior row of eyes moderately procurved. Chelicerae: basal segment 0.31 mm long; essentially typical of males of the genus; no dissection conducted because of scarcity of paratypes. Maxillae and lip: apparently typical of males of the genus. Sternum: grooves quite clearly delineated; very similar to those in *D. obtina* sp. nov.; fourth coxae separated by slightly more than their width. Legs: 4123 in order of length; tibial index of first leg 11, of fourth leg 9; trichobothria observed but exact number and placement not determined. Leg spines: first femur with ventral spines 0-1r-1r-2-1p-0; first tibia with five pairs of long slender spines; first metatarsus with three pairs of ventral spines; second femur apparently with one weak ventral and two weak prolateral spines; second tibia with four pairs of ventral spines; second metatarsus probably with two pairs of ventral spines; these spines tend to be offset prolaterally or retrolaterally. Palp: apparently typical of males of the genus except for the tarsus whose distinctive features are shown in Figures 37-38. Abdomen: pedicel, scuta, etc., apparently typical of males of the genus; genital region as shown in Figure 39. Color in alcohol: essentially typical of the genus with minor variations.

Records. One paratype male was taken during the same period as the holotype and in the same locality. Females taken at the same time and in the same locality may also belong here but there can be no certainty at this time.

DYSDERINA MERIDINA sp. nov.

Figures 40-41

Holotype. The male holotype is from San José, Costa Rica (Enrique Schmidt). No date of collection is given but, presumably, the specimen was taken fairly recently. The name of the species is an arbitrary combination of letters. The holotype will be deposited in the American Museum of Natural History, New York, N. Y. The abdomen of the holotype is detached from the cephalothorax but otherwise is in a good state of preservation.

Description. Total length 2 mm. Carapace 0.94 mm long; 0.75 mm wide opposite second coxae where it is widest; about 0.4 mm tall; rises gradually from PME to opposite posterior border of second coxae and then descends steeply to posterior border where there is a narrow upturned shelf; surface finely granulate; median thoracic groove lacking. Eyes: six as usual; seen from above, posterior row gently recurved. Ratio of eyes ALE : PME : PLE = 8.5 : 8 : 7.5. ALE separated from one another by slightly more than their radius; barely separated from PLE; separated from PME by a little more than one-half their radius. PME contiguous for about one-fourth of their circumference; separated from PLE by a line. Height of clypeus equal to slightly less than the diameter of ALE; clypeus only moderately lobed in the middle of the ventral border. Chelicerae, maxillae and lip: all apparently typical of males of the genus from the regions under study. Sternum: also essentially typical of the genus in this general region; sternal grooves less intricate than in several other species; sternal suture procurved; fourth coxae separated by about four-thirds of their width. Legs: 42=13 in order of length; tibial index of first leg 11, of fourth leg 10; as far as observed, claws and trichobothria essentially as described for *D. seclusa* Chickering (1951). Leg spines also essentially as described for *D. seclusa.* Palp: all segments except tarsus simple and without special modifications; tarsus with distinctive embolus and associated structures (Figs. 40-41). Abdomen: in general typical of the genus; dorsal and ventral scuta cover nearly the entire surface; spinnerets retracted and nearly invisible; genital aperture typical of the genus. Color in alcohol:

carapace, sternum and abdominal scuta all a rich reddish brown; body of palpal tarsus light yellowish.

Records. One poorly preserved male paratype accompanies the holotype. No date of collection is given. The female is unknown.

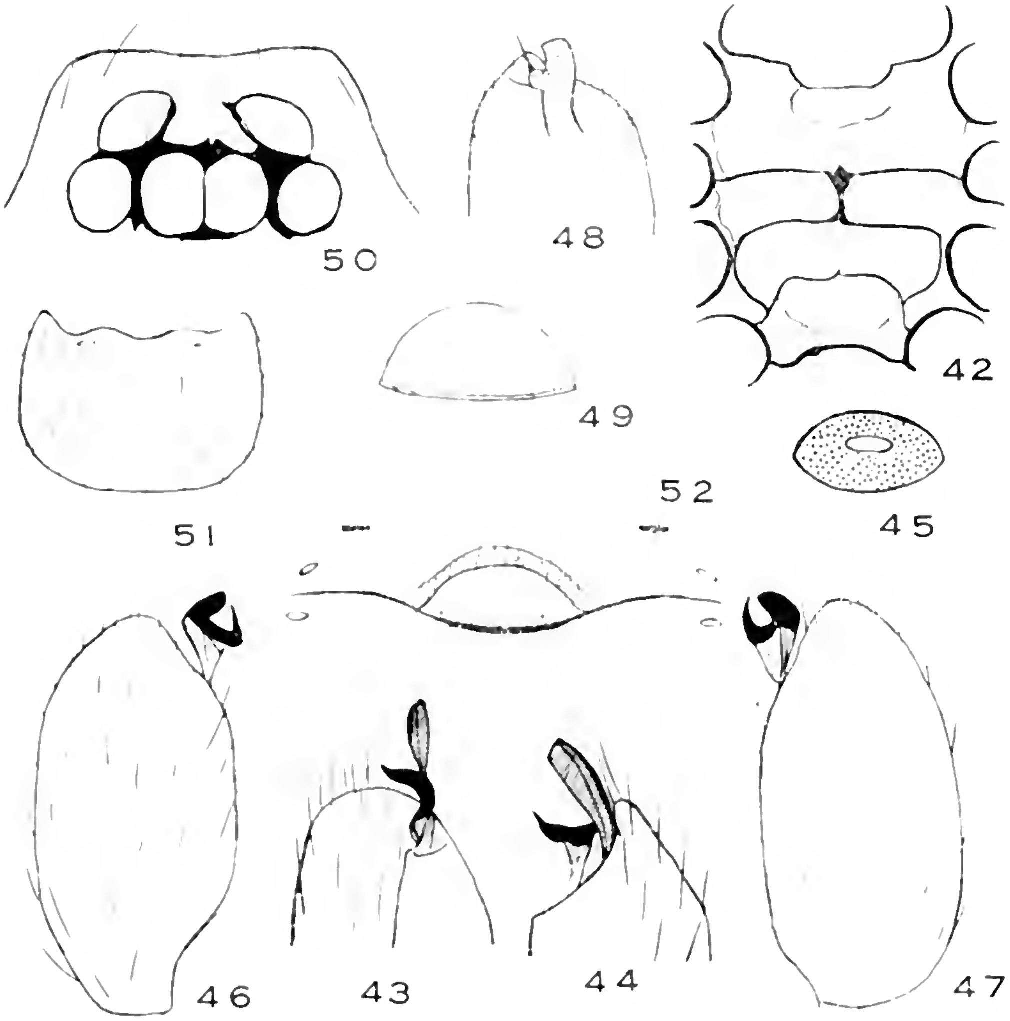
DYSDERINA OBTINA sp. nov.

Figures 42-45

Holotype. The male holotype is from El Volcan, Panama, August, 1950. The name of the species is an arbitrary combination of letters.

Description. Total length 2.54 mm, including extended spinnerets. Carapace 1.1 mm long; 0.88 mm wide opposite second coxae where it is widest; 0.52 mm tall; otherwise essentially typical of males of the genus. Eyes: posterior row occupies about two-thirds of width of carapace at that level; only slightly recurved as seen from above. Ratio of eyes ALE : PME : PLE = 9 : 8.5 : 8. ALE separated from one another by five-ninths of their greatest diameter; separated from PLE by about two-ninths of their diameter and from PME by one-third of their diameter. PME contiguous for about one-sixth of their circumference; separated from PLE by about one-eighth of the diameter of the latter. Posterior row of eyes wider than anterior row in ratio of about 5 : 4. Height of clypeus equal to about eleven-ninths of the diameter of ALE. Chelicerae, maxillae and lip essentially as described for *D. abdita* sp. nov. Sternum: only slightly longer than wide between second coxae; grooved in a distinct manner closely similar to the pattern shown by *D. abdita* sp. nov. and *D. recondita* Chickering (Fig. 42). Fourth coxae separated by nearly five-thirds of their width. Legs: 4123 in order of length; tibial index of first leg 10, of fourth leg 9; trichobothria observed on first femora and tibiae but number and placement not accurately determined. Leg spines: first femur with ventral spines 0-0-2-2-0 unevenly placed; first tibia with five pairs of ventral spines and a pair of distal bristles; first metatarsus with three pairs of ventral spines; second femur with two small ventral spines on promargin; second tibia with four pairs of ventral spines; second metatarsus as in first. Third and fourth legs devoid of true spines. Palp: general features as usual in males of the genus; specific tarsal features shown in Figures 43-44. Abdomen 1.32 mm long exclusive of extended spinnerets; 0.92 mm wide slightly behind the middle; pedicel, scutta, etc., essentially as described for *D. abdita* sp. nov.; genital aperture as shown in Figure 45. Color in alcohol: also essentially as described for *D. abdita* sp. nov. with minor variations.

Records. No paratypes have appeared in my collection and the female is unknown. For some time the holotype was regarded as a deviate of *D. recondita* Chickering but careful attention to the male palp has convinced me that it must be considered to represent a new species as presented here.



Figs. 42-45. *Dysderina obtina* sp. nov. Fig. 42. Sternum from below. Figs. 43-44. Distal end of left male palpal tarsus; nearly prolateral and retrolateral views, respectively. Fig. 45. Genital aperture from below. Figs. 46-49. *Dysderina plena* O. P.-Cambridge. Figs. 46-47. Left male palpal tarsus; nearly prolateral and retrolateral views, respectively. Fig. 48. Distal end of male palpal tarsus; nearly ventral view. Fig. 49. Epigynal area from below. Figs. 50-52. *Dysderina potena* sp. nov. Fig. 50. Eyes from above. Fig. 51. Ventral scutum from below. Fig. 52. Epigynal area from below.

DYSDERINA PLENA O. P.-Cambridge

Figures 46-49

Dysderina plena O. P.-Cambridge, 1894: 143; 1896: 192, pl. 17, fig. 7; pl. 24, fig. 4. Male and female syntypes from Teapa, Mexico, are in the British Museum (Natural History). F. P.-Cambridge, 1899: 44; Banks, 1909: 196; Petrunkevitch, 1911: 125; Roewer, 1933: 185; 1942: 283; Chickering, 1951: 211; Bonnet, 1956: 1638.

As pointed out in 1951, the specimens reported from Panama by Banks (1929) and referred to this species really belong to other genera and species. The specimens reported by Williams (1941) and identified by Dr. W. J. Gertsch as *Dysderina plena* O. P.-Cambridge appear to be *Dysderina silvatica* Chickering (1951).

The female from Teapa, Mexico, on loan from the British Museum (Natural History), has an epigynal area (Fig. 49) very similar to that of *D. silvatica* Chickering. The intricate grooves on the sternum are somewhat different from those on *D. silvatica* Chickering but the two seem to be closely related.

Male. From the British Museum (Natural History). Total length about 2.1 mm. Carapace 0.98 mm long. 0.78 mm wide opposite second coxae where it is widest; about 0.52 mm tall opposite interval between second and third coxae where it is tallest; descent nearly precipitous from highest point to posterior border; surface finely granulate; without a median thoracic groove or pit. Eyes: posterior row occupies a little more than three-fourths of width of cephalic region at this level; gently recurved as seen from above. Ratio of eyes ALE : PME : PLE = 10 : 9.5 : 10. All eyes are somewhat irregular in outline; PME and PLE are more oval than ALE. ALE separated from one another by nearly one-third of their diameter. PME contiguous for about one-fourth of their circumference; PLE nearly contiguous to PME posteriorly but separated anteriorly; PLE and ALE nearly contiguous; posterior row longer than anterior row in ratio of about 5 : 4; viewed from in front, posterior row procurved. Height of clypeus a little more than two-thirds of the diameter of ALE; border of clypeus strongly chitinized. Sternum finely granulate and intricately grooved about as usual in the genus. Genital aperture a narrow slit surrounded by a broad margin. Important features of the palp shown in Figures 46-48. Other features essentially typical of males of the genus.

DYSDERINA POTENA sp. nov.

Figures 50-52

Holotype. The female holotype is from El Volcan, Panama, August, 1950. The name of the species is an arbitrary combination of letters.

Description. Total length, including spinnerets, 2.8 mm. Carapace 1.08 mm long; 0.97 mm wide opposite second coxae where it is widest; 0.48 mm tall; gradually arched from PLE to posterior border; finely but irregularly granulate; without any visible thoracic groove or pit. Eyes: seen from above, posterior row straight if measured by posterior borders; posterior row occupies about two-thirds of width of carapace at that level; seen from in front, posterior row gently procurved. Ratio of eyes ALE : PME : PLE = 9.5 : 9 : 8. ALE separated from one another by a little more than their radius; barely separated from PLE (Fig. 50). Height of clypeus equal to a little more than the diameter of ALE. Chelicerae, maxillae and lip; essentially typical of females of the genus as observed in this study. Sternum only slightly longer than wide; with the usual intricate grooves; quite convex; fourth coxae separated by about 1.5 times their width. Legs: 4123 in order of length; tibial index of first and fourth legs 9; spines on legs essentially as described for *D. silvatica* Chickering (1951). Abdomen: essentially typical of females of the genus with minor variations; ventral scutum as shown in Figure 51. Epigynal area: appears to have certain obscure but distinctive features (Fig. 52). Color in alcohol: carapace irregularly darkened along posterior declivity and lateral sides; generally a rich reddish brown.

This species appears to be closely related to *D. plena* O. P.-Cambridge but differs from that species most conspicuously with respect to its epigynal area which is in the form of a modified oval opening (Fig. 52) with a distinct anterior border and a series of faintly indicated granules along the posterior border. The height of the clypeus is somewhat greater than usual in the genus.

Records. Two paratype females taken August, 1950, in vicinity of El Volcan, Panama. One female from Boquete, Panama, August, 1954 is somewhat doubtfully assigned to this species.

DYSDERINA PRINCEPS Simon

Figures 53-54

Dysderina princeps Simon, 1891, 557. The female holotype from St. Vincent, B. W. I., is in the British Museum (Natural History). Simon, 1893: 290, 304; Petrunkevitch, 1911: 125; Roewer, 1942: 283; Bonnet, 1956: 1638.

So far as I have been able to determine, the species has never been correctly reported since its first recognition. In 1893, however, Simon published his figure 260 which is a drawing of a male palp and it is labelled *D. princeps.* The figure closely resembles the original drawing (fig. 1) accompanying the brief description of *D. principalis* Simon.

The following facts are derived from the study of a female from St. Vincent, B. W. I. on loan from the British Museum (Natural History): Total length 2.66 mm (the author of the species gave the length as 4 mm). Carapace 1.17 mm long; 0.97 mm wide opposite second coxae where it is widest; otherwise essentially typical of females of the genus as seen during this study. Eyes in general as usual in the genus (Fig. 53); ratio of eyes ALE : PME : PLE = 9 : 8.5 : 9.5. Clypeus somewhat higher than that in *D. spinigera* Simon but otherwise closely similar. Sternum intricately but not deeply grooved. Legs 1 and 2 with the usual long ventral spines essentially typical of the genus. Abdomen with the typical scuta and related parts. Epigynal area more distinctive than usual (Fig. 54).

DYSDERINA PRINCIPALIS (Keyserling)

Figures 55-56

Oonops principalis Keyserling, 1882: 296, pl. 11, fig. 16. The male holotype from Colombia is in the British Museum (Natural History).

Dysderina principalis,-Simon, 1891, 557, pl. 42, fig. 1. Simon, 1893: 304; Petrunkevitch, 1911: 126; 1928: 87; Roewer, 1942: 283; Bonnet, 1956: 1638. (Not *D. principalis* Simon from St. Vincent, B. W. I.)

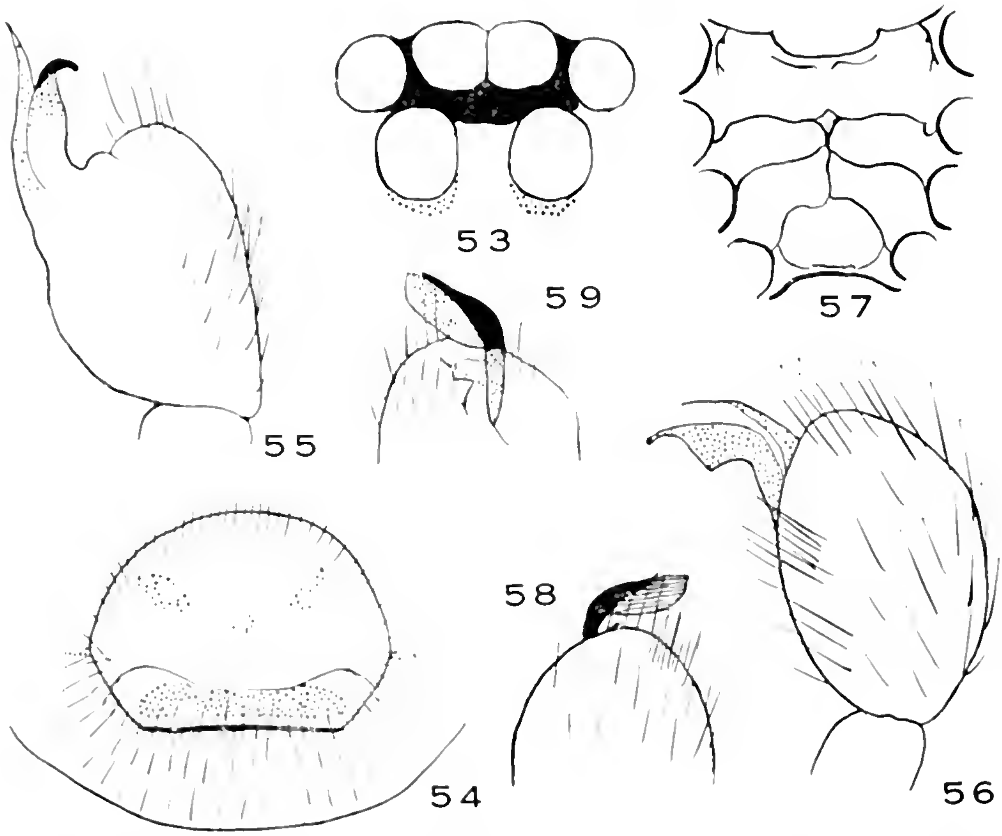
Simon was correct in transferring *Oonops principalis* Keyserling to his new genus *Dysderina* but he was in error when he identified a species of this new genus from St. Vincent, B. W. I., as being *D. principalis* described from Colombia. Apparently Keyserling had only the male upon which to base his species. This specimen has been on loan from the British Museum (Natural History). It is dismembered, but the right palp is in good condition and establishes Simon's error very clearly. In order to aid in clarifying this confusion I am offering two figures of the palpal tarsus (Figs. 55-56). Keyserling's small figure 16 closely resembles those I am providing.

DYSDERINA RECONDITA Chickering

Figures 57-59

Dysderina recondita Chickering, 1951: 217, fig. 4. The male holotype and two paratypes from Boquete, Panama, July, 1939, are in the Museum of Comparative Zoology.

During my brief visit to Boquete, Panama, in August, 1954, I collected eleven additional males. The female is unknown but it seems probable that it is among the different females now recognized from the mountainous regions of Panama. Figures 58-59 are added to the original drawing of the male palp; Figure 57 shows the essential features of the sternal grooves.



Figs. 53-54. *Dysderina princeps* Simon. Fig. 53. Eyes from in front. Fig. 54. Epigynal area from below. Figs. 55-56. *Dysderina principalis* (Keyserling). Two views of right male palpal tarsus. Figs. 57-59. *Dysderina recondita* Chickering. Fig. 57. Sternum from below. Figs. 58-59. Two views of distal end of left male palpal tarsus.

DYSDERINA RIGIDA sp. nov.

Figures 60-61

Holotype. The female holotype is from El Volcan, Panama, August, 1950. The name of the species is a Latin adjective referring to its strongly chitinized scuta, pedicel and other outer parts.

Description. Total length 2.49 mm. Carapace 1.05 mm long; 0.88 mm wide opposite second coxae where it is widest; 0.44 mm tall; other features essentially as described for *D. silvatica* Chickering (1951). Eyes: posterior row gently recurved, seen from above; occupies about five-sevenths of width of carapace at that level. Ratio of eyes ALE : PME : PLE = 9 : 9 : 8. ALE separated from one another by slightly more than their radius; only slightly separated from PLE and from PME by about one-fourth of their diameter. PME contiguous along about one-fourth of their circumference and longer than wide in ratio of about 9 : 7.5; separated from PLE by one-sixth of their long diameter. Posterior row wider than anterior row in ratio of about 13 : 11. Height of clypeus slightly greater than the diameter of ALE. Chelicerae: vertical, essentially parallel; outer margin with a shallow groove at end of upper third and a slight swelling near middle; a single tooth along margin of fang groove appears to be definitely promarginal (observed on paratype); otherwise essentially as reported for *D. silvatica* (1951). Maxillae, lip and sternum also essentially as reported for *D. silvatica* (1951) except for the system of grooves on sternum (Fig. 60). Legs: 4123 in order of length; tibial index of first and fourth legs 9; trichobothria observed on palpal tibia and tarsus but number and placement not accurately determined. Leg spines: first femur with five ventral spines not evenly paired; first tibia with five pairs of ventral spines; first metatarsus with three pairs of ventral spines. Second leg with ventral spines nearly as on first leg; with only minor differences. Abdomen: spinnerets with a lightly chitinized ventral semicircular sclerite partially surrounding these organs; other features essentially typical of females of the genus. Epigynal area: simple as usual but apparently with obscure distinctive features (Fig. 61). Color in alcohol: essentially typical of the genus with minor variations.

This species is also regarded as being rather closely related to *D. plena* O. P.–Cambridge. It differs from that species most conspicuously with respect to its epigynal area which is in the shape of a modified oval region with a narrow, transverse area along its posterior border (Fig. 61). The pattern of grooves on its sternum also appears to be somewhat distinctive (Fig. 60).

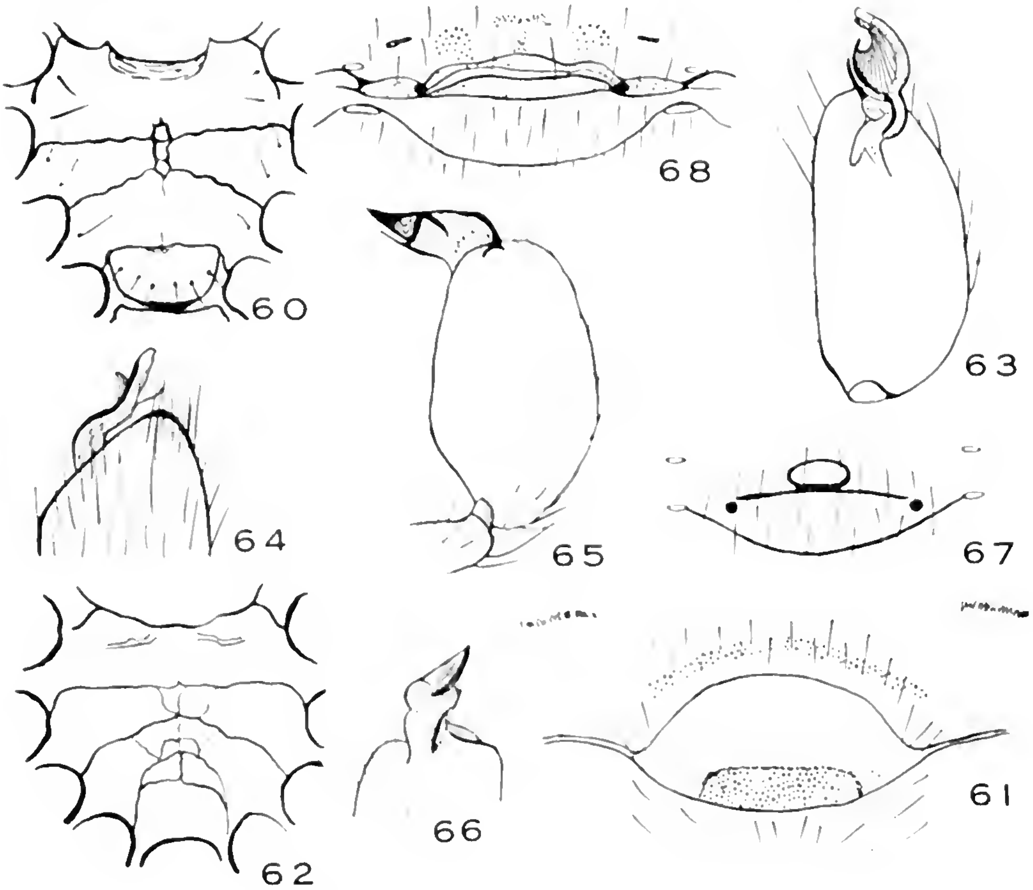
Records. Several female paratypes taken with the holotype, El Volcan, Panama, August, 1950.

DYSDERINA SECLUSA Chickering

Figures 62-64

Dysderina seclusa Chickering, 1951: 213, fig. 5. The male holotype and five male paratypes from Barro Colorado Island, Panama Canal Zone, are in the Museum of Comparative Zoology. All of these were taken in a Berlese funnel by Dr. Zetek, July, 1943-March, 1944, and June-October, 1946.

Since the original description was written, I have added four males to the collection as follows: June-October, 1946 (Zetek); June-August, 1949 (Zetek); August, 1954. I have been unable to match these males with females in any satisfactory manner. With the hope of further clarifying the status of the species three additional figures are offered.



Figs. 60-61. *Dysderina rigida* sp. nov. Fig. 60. Sternum from below. Fig. 61. Epigynal area from below. Figs. 62-64. *Dysderina seclusa* Chickering. Fig. 62. Sternum from below. Fig. 63. Left male palpal tarsus; ventral view. Fig. 64. Distal end of left male palpal tarsus; nearly dorsal view. Figs. 65-68. *Dysderina simla* sp. nov. Fig. 65. Left male palpal tarsus; retrolateral view. Fig. 66. Distal end of left male palpal tarsus; nearly ventral view. Fig. 67. Genital area of male holotype. Fig. 68. Epigynal area of female paratype.

DYSDERINA SILVATICA Chickering

Dysderina silvatica Chickering, 1951: 217, fig. 6. The female holotype and numerous paratypes from several localities in the Panama Canal Zone and El Valle, Panama, are in the Museum of Comparative Zoology.

Since my report in 1951 I have added numerous females of this species to the collection from the following localities: Barro Colorado Island, Canal Zone Forest Preserve and Summit Gardens all in Panama Canal Zone. Although the evidence is not conclusive, I think it probable that these females belong with *D. dura* Chickering.

DYSDERINA SIMLA sp. nov.

Figures 65-68

Holotype. The male holotype is from Simla, Arima Valley, Trinidad, W. I., April 5, 1964. The name of the species is a noun used in apposition after the type locality.

Description. Total length 1.69 mm. Carapace 0.88 mm long; 0.75 mm wide opposite second coxae where it is widest; 0.47 mm tall; median thoracic groove lacking; smooth along broad, median area from PLE to beginning of posterior declivity; irregularly granulate along lateral sides and much of posterior declivity; fits closely to anterior end of abdomen which is unusual in this genus. Eyes: six as usual in a compact group which occupies nearly three-fourths of width of carapace at level of PE; viewed from above, posterior row slightly recurved. Ratio of eyes ALE : PME : PLE = 8 : 9 : 9. ALE separated from one another by slightly more than their radius; other relationships of eyes typical of the genus in the region under study. Height of clypeus equal to about three-fourths of diameter of ALE. Chelicerae, maxillae and lip all appear to be typical of the genus. Sternum: granulate; intricately but not deeply grooved and lobed; the usual anterior, transverse groove is complete, conspicuous and only slightly behind procurved sternal suture; only slightly longer than wide just behind second coxae; fourth coxae separated by nearly twice their width. Legs: 4123 in order of length; tibial index of first leg 10, of fourth leg 11. Spines on legs about as usual in males of the genus. Palp: all segments simple and without special modifications except the tarsus which has distinctive features (Figs. 65-66). Abdomen: typical of the genus in general; with dorsal and ventral scuta less strongly chitinized than usual (all paratypes appear to be the same in this respect); genital region quite clear and rather distinctive (Fig. 67). Color in alcohol: carapace essentially as described for *D. craneae* sp. nov.; legs and mouth parts a variable yellowish; sternum a deeper yellowish; abdomen with dorsal and ventral scuta a light yellowish in contrast to the usual much darker coloration; epigastric scutum somewhat darker; the free areas not covered by scuta are whitish.

Female paratype. Total length 1.98 mm. Carapace 0.9 mm long; 0.84 mm wide opposite interval between second and third coxae where it is widest; 0.36 mm tall; surface granulate essentially as in male. Cephalothorax closely contiguous to abdomen as in male. Eyes essentially as in male. Chelicerae, maxillae and lip: all essentially typical of females of the genus. Sternum: essentially as in male but with granulation more extensive; fourth coxae separated by nearly twice their width. Legs: 41 = 23 in order of length; tibial index of first and fourth legs 11; spines essentially typical of the genus. Abdomen: general appearance as usual in the genus; dorsal scutum somewhat less extensive than usual; epigastric scutum about as usual; ventral scutum much smaller than usual and reaches slightly less than half way from genital groove to spinnerets; a narrow, ventral, semicircular sclerite partly surrounds the spinnerets. Epigynal area: quite distinctive but difficult to represent accurately in a drawing (Fig. 68). Color in alcohol: all parts except the abdomen as in male; because of the smaller scuta much more of the abdomen appears nearly white than in the male; posterior to the ventral scutum are several vague darker spots which in some paratypes are quite distinct brownish, irregular spots.

Records. The described female paratype was taken with the holotype. Three male and seven female paratypes are in the collection from Simla, Arima Valley, and along the side of the road from Simla to Blanchesseuse, Trinidad, W. I., March 31-April 25, 1964.

DYSDERINA SOLTINA sp. nov.

Figures 69-75

Dysderina principalis,-Simon, 1891: 557, pl. 42, fig. 1. Male and female syntypes from St. Vincent B. W. I. are in the British Museum (Natural History). (Not *D. principalis* (Keyserling) from Colombia.)

In his study of the genus *Dysderina* from St. Vincent, B. W. I., Simon selected what he considered to be a male and a female of *D. principalis* (Keyserling), gave a brief description and furnished a figure of the male palp. As a result of a study of these specimens together with an example of Keyserling's species from Colombia on loan from the British Museum (Natural History), I am obliged to disagree completely on the identification of these specimens. They seem to me to represent a new species which is described below.

Holotype. The male holotype is from St. Vincent, B. W. I., and will be returned to the British Museum (Natural History). The name of the species is an arbitrary combination of letters.

Description. Total length 1.91 mm (recorded as 3.5 mm in Simon's description). Carapace 0.92 mm long; 0.73 mm wide opposite second coxae; 0.35 mm tall; only gradually narrowed behind eyes; surface irregularly granulate as usual; otherwise typical of the genus. Eyes: six as usual; seen from above, posterior row gently recurved; ratio of eyes ALE : PME : PLE = 8 : 7 : 7 (outlines poorly defined). ALE separated from one another by their radius. PME contiguous for about one-fourth of their circumference; barely separated from PLE. Height of clypeus equal to about five-eighths of the diameter of ALE. Chelicerae, maxillae and lip typical of the genus as far as observed. Sternum: typical of the genus in general; major and minor grooves and depressions moderately complex; extended as usual between fourth coxae and articulated with pedicel; fourth coxae separated by five-thirds of their width. Legs: 4123 in order of length; tibial index of first leg 10, of fourth leg 9; ventral spines on first leg as shown in Figures 71-73; fewer ventral spines on second leg. Palp: all segments except tarsus simple and unmodified as usual; tarsus considerably inflated and with distinctive terminal structures difficult to observe clearly (Figs. 69-70). Abdomen: all parts in general typical of males of the genus; scuta cover nearly the entire surface. Color in alcohol: also typical of the genus with few minor variations.

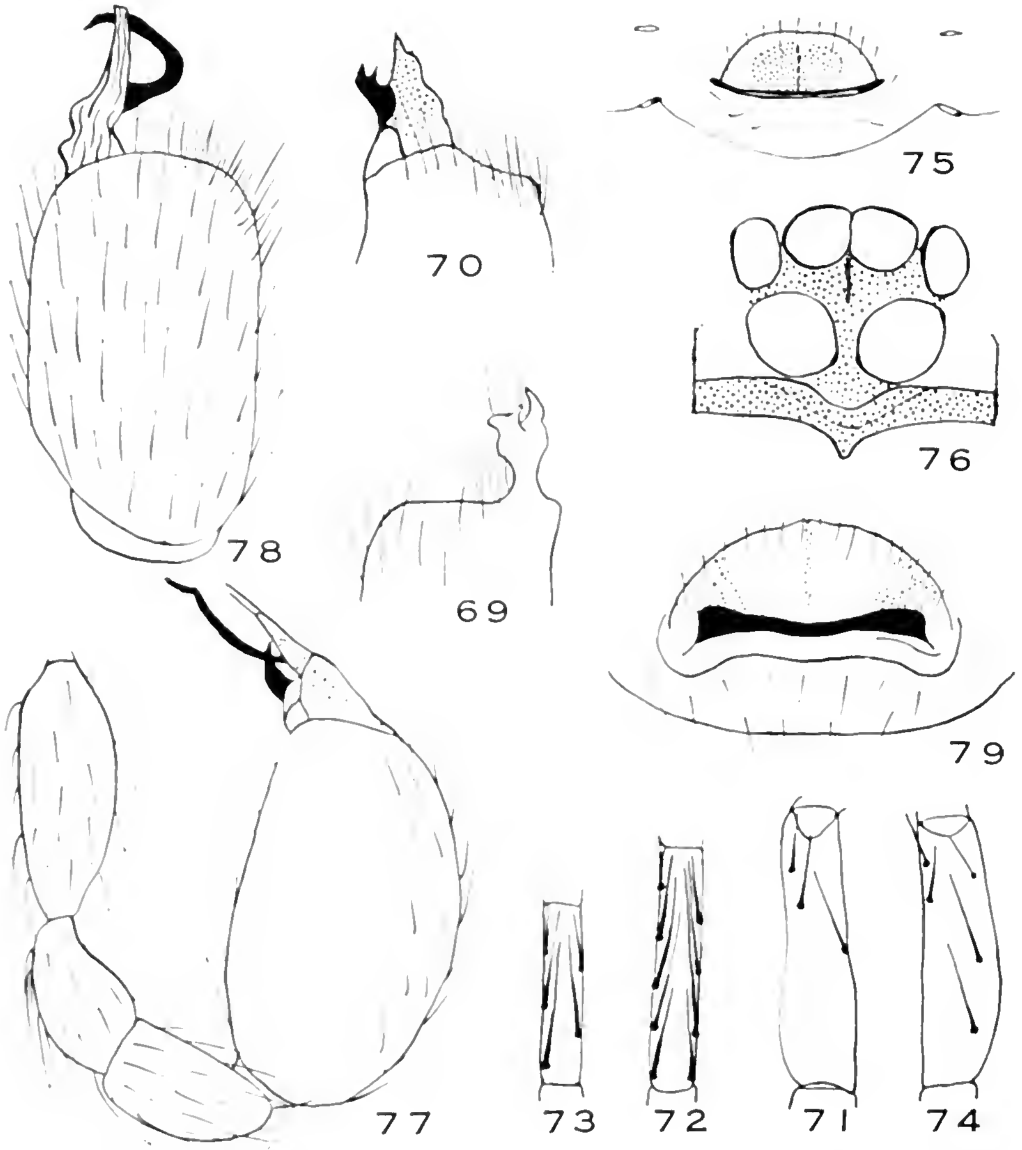
Female paratype. This is apparently the specimen which Simon regarded as the female of *D. principalis* (Keyserling). For the present I am regarding it as the female of the new species *D. soltina.* Total length 1.98 mm (Simon gave length as 4 mm). Carapace 0.9 mm long; 0.73 mm wide; 0.4 mm tall; general features typical of females of the genus. Leg spines: the first femur has five ventral spines, two on promargin and three on retromargin (Fig. 74); other segments with spines much as in male. Abdomen with scuta and other parts essentially typical of the genus. Epigynal area: obscurely distinctive as usual (Fig. 75).

Records. As far as I have been able to determine the two specimens described here are the only members of the species known at present.

DYSDERINA SPINIGERA Simon

Figures 76-79

Dysderina spinigera Simon, 1891, pl. 42, figs. 2-3. Male and female syntypes from St. Vincent, B. W. I., are in the British Museum (Natural History). Simon, 1893: 304; Petrunkevitch, 1911: 126; Roewer, 1942: 283; Bonnet, 1956: 1639.



Figs. 69-75. *Dysderina soltina* sp. nov. Fig. 69. Left male palpal tarsus; nearly dorsal view. Fig. 70. Distal end of left male palpal tarsus; retrolateral view (more enlarged). Figs. 71-73. Ventral spines on first left femur, tibia and metatarsus, respectively. Fig. 74. Ventral spines on first left femur of female paratype. Fig. 75. Epigynal area of female paratype from below. Figs. 76-79. *Dysderina spinigera* Simon. Fig. 76. Eyes from in front. Fig. 77. Left male palp; retrolateral view. Fig. 78. Left male palpal tarsus; dorsal view. Fig. 79. Epigynal area from below.

Simon reported both sexes of this species from St. Vincent and Venezuela where he regarded it as widespread. I have not seen the specimens from Venezuela but, on the basis of my study of this genus, I consider it unlikely that they are the same as these from St. Vincent. I was disappointed in my failure to collect any specimens of the genus *Dysderina* during my brief visit to this island in October, 1966.

The following facts relating to this species have been recorded as a result of my study of a male and two females on loan from the British Museum (Natural History).

Male. Total length 1.61 mm (Simon gave length of male as 4 mm). Carapace 0.86 mm long; 0.66 mm wide opposite second coxae where it is widest; otherwise essentially typical of the genus as observed in this study. Eyes: essentially as shown in Figure 76; ratio of eyes ALE : PME : PLE = 10 : 9 : 9 (outlines irregular); ALE closer together than usual in the genus; clypeus with strongly chitinized ventral border and conspicuously lobed ventrally in front (Fig. 76). Sternum moderately grooved in fairly typical manner. Legs essentially typical in respect to spination and relative lengths; trichobothria observed but exact distribution undetermined. Palp: quite distinctive; appearance very different from Simon's figure 3, 1891; essentials shown in Figures 77-78. Abdomen: with typical dorsal and ventral scuta; genital aperture a simple, minute slit.

Female. Total length, exclusive of projecting spinnerets and slightly exposed chelicerae 2.09 mm; including posterior spinnerets and slightly exposed chelicerae, length is 2.2 mm (Simon gave length as 4.5 mm). General form and external features essentially like those of male. Abdomen: with dorsal and ventral scuta somewhat less extensive than in male; epigynal area very distinctive; unlike that seen in other species (Fig. 79).

DYSDERINA WATINA sp. nov.

Figures 80-84

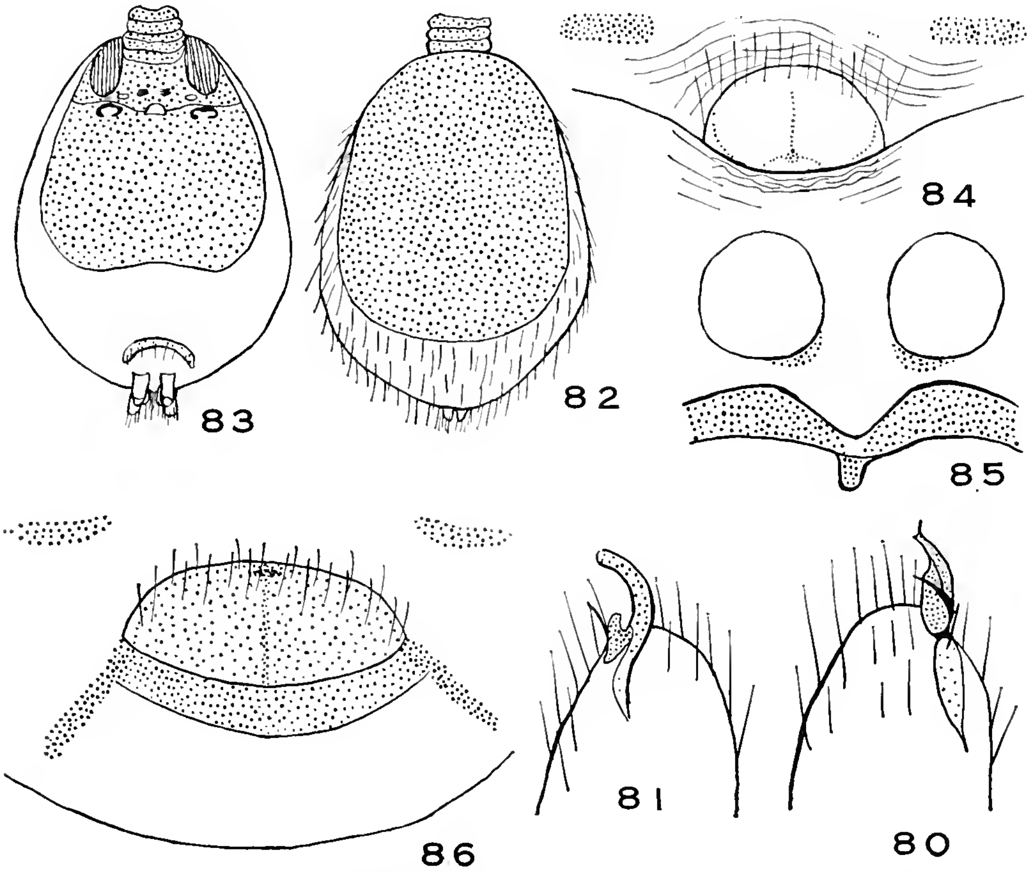
Holotype. The male holotype is from Turrialba, Costa Rica, July 25-Aug. 15, 1965. The name of the species is an arbitrary combination of letters.

Description. Total length 2.24 mm. Carapace 1.03 mm long; 0.86 mm wide opposite second coxae where it is widest; 0.45 mm tall opposite second coxae; moderately grooved immediately behind PE; regularly arched from groove to beginning of moderately steep posterior declivity; surface irregularly granulate; otherwise essentially typical of the genus. Eyes: six in two rows as usual; posterior row gently recurved, seen from above; posterior row occupies about seven-ninths of width of carapace at that level.

Ratio of eyes ALE : PME : PLE = 10 : 8 : 9. ALE separated from one another by about their radius, from PLE by nearly one-fifth of their diameter and from PME by about three-tenths of their diameter. PME barely separated from one another and from PLE by about three-sixteenths of their diameter. Height of clypeus nearly equal to long diameter of ALE. Chelicerae, maxillae and lip typical of the genus as far as observed. Sternum: clearly but less intricately grooved than in several other species; posterior coxae separated from one another by about 1.5 times their width; otherwise essentially typical of the genus. Legs: 4123 in order of length; tibial index of first leg 8, of fourth leg 7; spines conspicuously long and slender but otherwise essentially typical of males of the genus. Palp: all segments except tarsus simple and unmodified; tarsus with distinctive distal features as shown in Figures 80-81. Abdomen: essentially typical of males of the genus. Color in alcohol: lighter than usual in the genus; carapace, pedicel and sternum a medium yellowish brown; abdomen and legs yellowish with variations.

Female paratype. Total length 2.75 mm exclusive of slightly projecting spinnerets and chelicerae; including these parts total length is 2.9 mm. Carapace 1.1 mm long; 0.92 mm wide opposite interval between second and third coxae; about 0.44 mm tall; rather deeply grooved immediately behind PE and then gently arched to posterior declivity; otherwise typical of the genus. Eyes: PME contiguous for nearly one-fourth of their circumference; ratio of eyes ALE : PME : PLE = 10 : 10 : 9.5; other features essentially as in male. Height of clypeus immediately below ALE equal to slightly less than the diameter of these eyes; clypeus conspicuously lobed in middle between bases of chelicerae. Chelicerae, maxillae and lip essentially typical of females of the genus. Sternum: with the usual pattern of major grooves and other inconspicuous irregularities; fourth coxae separated by five-thirds of their width. Legs: 4123 in order of length; tibial index of first leg 9, of fourth leg 10; spines of first and second legs conspicuously long but essentially typical of females of the genus with minor variations. Abdomen: scuta, pedicel, spiracles, etc. nearly typical of females of the genus (Figs. 82-83); a very clear narrow sclerite partially surrounds spinnerets on ventral side; what appears to be a chitinous dot marks the position of the reduced colulus. Epigynal area: obscurely distinctive (Fig. 84). Color in alcohol: much more colorful than in male; carapace, sternum and abdominal scuta all a rich reddish brown with lateral sides of carapace irregularly darkened by granulations; areas of abdomen not covered by scuta clear white; legs brownish yellow with variations.

Records. The described female paratype together with three other females were all taken from weed and hay debris in the same general locality from which the male holotype was taken, Turrialba, Costa Rica, July 25-August 15, 1965. It seems reasonable to assume that the male holotype and females belong together but there can be no absolute certainty.



Figs. 80-84. *Dysderina watina* sp. nov. Figs. 80-81. Distal end of left male palpal tarsus; prolateral and retrolateral views, respectively. Figs. 82-83. Dorsal and ventral views of abdomen of female paratype. Fig. 84. Epigynal area of female paratype, from below. Figs. 85-86. *Dysderina zinona* sp. nov. Fig. 85. ALE and clypeus from in front. Fig. 86. Epigynal area from below.

DYSDERINA ZINONA sp. nov.

Figures 85-86

Holotype. The female holotype is from St. Vincent, B. W. I., Mt. Soufriere, June 1, 1965 (R. T. Bell). The name of the species is an arbitrary combination of letters. The specimen serving here as the holotype of a new species is somewhat damaged but its most important features are still in good condition.

Description. Total length about 2.28 mm. Carapace 1.08 mm long; 0.86 mm wide opposite second coxae where it is widest; 0.54 mm tall; irregularly granulate as usual; otherwise essentially typical of females of the genus. Eyes: in general, as usual in the genus; viewed from above, posterior row gently recurved and occupies about seven-tenths of width of carapace at that level. Ratio of eyes ALE : PME : PLE = 9 : 8.5 : 8. ALE separated from one another by nearly their radius; from PLE by nearly one-half their radius and by slightly more than this from PME, which are contiguous for about one-fourth of their circumference and barely separated from PLE. Clypeus conspicuously lobed in front (Fig. 85); height immediately below ALE equal to nearly two-thirds of the diameter of these eyes. Chelicerae, maxillae and lip typical of females of the genus as far as observed. Sternum: fairly typical also; major grooves and secondary depressions make a rather intricate pattern; fourth coxae separated by a little more than their width. Legs: 4123 in order of length; tibial index of first leg 10, of fourth leg 9; first leg with five ventral spines on femur as in Figure 74; first tibia with five ventral spines on promargin and four on retromargin; first metatarsus with three ventral spines on promargin and two on retromargin. Second leg with somewhat fewer ventral spines than occur on first leg. Third and fourth legs without true spines. Abdomen: considerably damaged but apparently quite typical of females of the genus. Epigynal area: undamaged; rather distinctive (Fig. 86). Color in alcohol: carapace a rich reddish brown; sternum somewhat lighter; legs yellowish brown with variations; abdominal scuta probably much like carapace but somewhat lighter like the sternum.

D. zinona sp. nov. is regarded as closely related to *D. princeps* Simon. The epigynal area (Fig. 86) is quite different from that region in *D. princeps* Simon (Fig. 54) and much simpler. The clypeus is also conspicuously lobed in front (Fig. 85).

Records. No paratypes have appeared in the collection.

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POPULATION STRUCTURE OF THE *ASTHENES FLAMMULATA* SUPERSPECIES (AVES: FURNARIIDAE)

François Vuilleumier[1]

INTRODUCTION

While conducting a survey of speciation phenomena in twenty-five genera of Andean birds, I found that the existing classifications of these birds were often insufficient for my purposes. I had to undertake systematic studies in each genus before I could proceed to an analysis of species formation. In view of the groundwork already laid by Hellmayr, Chapman, Zimmer, Peters, and others, it may seem surprising that a student of speciation should find it necessary to do so much systematic work. However, these earlier systematists were primarily concerned with the purely formal aspects of assigning samples to species and subspecies, rather than interested in the process of speciation; their works contain little information on population structure (in the sense of Mayr, 1959:294) or species relationships. My own taxonomic work on Andean birds was designed to fill this gap.

This is the first in a proposed series of papers on these Andean birds. My purpose has been to gain an understanding of the process of speciation in each genus sampled through study of population structure and interspecies relationships, and then to synthesize this information, arriving at a general picture of speciation phenomena in Andean birds. In the present paper, an effort has been made to uncover the evolutionary relationships of the component members of the *Asthenes flammulata* superspecies by means of an analysis of the distribution and geographical variation of these spinetails.

This study was undertaken at the Museum of Comparatize Zoology of Harvard University. My investigations were based largely on

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the collections of this institution, but I have also examined specimens from other museums. When referring to individual specimens, the following abbreviations are used: MCZ = Museum of Comparative Zoology; ANSP = Academy of Natural Sciences of Philadelphia; CM = Carnegie Museum, Pittsburgh; FMNH = Field Museum of Natural History, Chicago; MVZ = Museum of Vertebrate Zoology, Berkeley; MP = Muséum National d'Histoire Naturelle, Paris.

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THE *ASTHENES FLAMMULATA* SPECIES GROUP

The genus *Asthenes* Reichenbach, 1853, consists of about 18 species of small spinetails (Furnariidae) living in western and southern South America. At least four species groups can be recognized in *Asthenes.* Since this arrangement of the genus will be published elsewhere, it is sufficient to mention here that what I call the *Asthenes flammulata* species group comprises four nominal species: *Asthenes flammulata* (Jardine), *A. virgata* (Sclater), *A. maculicauda* (Berlepsch), and *A. urubambensis* (Chapman).

These four forms were considered full species by Hellmayr (1925), Peters (1951), and de Schauensee (1966). They all have a diagnostic pattern of streaking — a narrow stripe along the feather shaft contrasting with the remainder of the feather.

Within the *A. flammulata* species group, *A. urubambensis* can be diagnosed by the combination of a lack of streaking on the dorsum and a lack of rufescent color on the forehead and crown. Furthermore, *A. urubambensis* is sympatric with two of the three other nominal species of the *flammulata* species group: with *A. flammulata* in Peru (see Zimmer, 1930:345) and with *A. maculicauda* in Bolivia (see Bond and de Schauensee, 1942:334). There is therefore no doubt that *A. urubambensis* is a good biological species.

THE *ASTHENES FLAMMULATA* COMPLEX

The other three nominal species of the *A. flammulata* species group can be described collectively as the *A. flammulata* complex. They are morphologically rather similar to one another, and are largely allopatric, although there are two apparent exceptions: (1) in southern Peru ("contact" between *virgata* and *maculicauda*) and (2) in central Peru (alleged sympatry between *flammulata* and *virgata*).

SYMPATRY

Asthenes virgata was described by Sclater, in 1874, on the basis of one specimen collected by Jelski in "Junin," in the Andes of central Peru. In 1930, M. A. Carriker, Jr., secured five specimens of *A. virgata* in the Rock Forest area west of Lake Junín (Bond, 1945:33; 1956:245). Although Jelski did not give precise locality data, it is possible that "Junin" refers to the village of that name situated southeast of the lake at the edge of the flat depression forming the present-day Lake Junín and adjoining marshes (see Fig. 1). Junín and Rock Forest are about 50 km apart.

These are the only published localities where *A. virgata* has been taken, at least to my knowledge. However, C. Koford collected a single female *Asthenes* in the Department of Puno, southern Peru, in 1951 (MVZ 124302). This bird is morphologically much closer

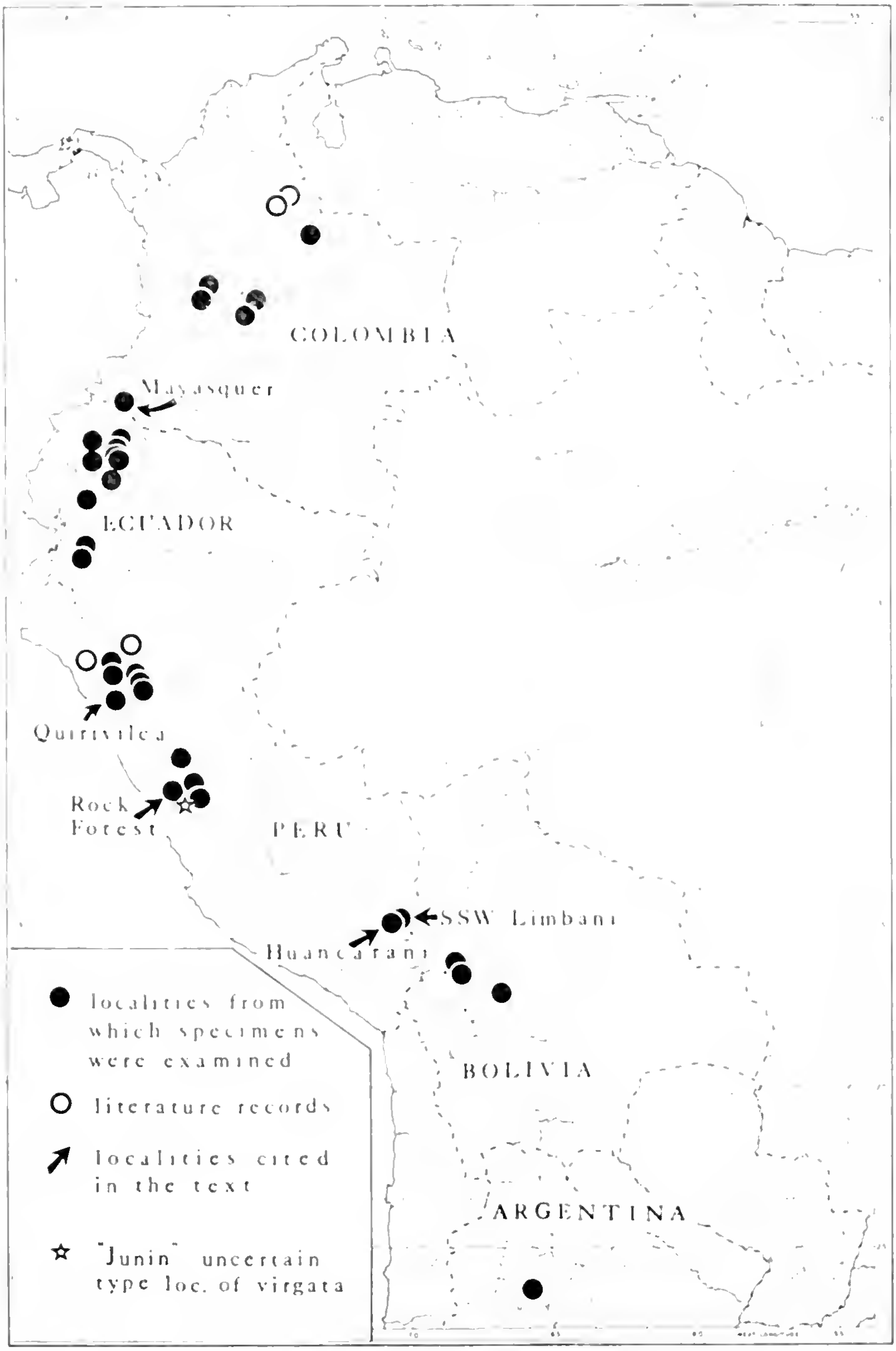

FIG. 1. Collecting localities of the *Asthenes flammulata* complex.

to the geographically distant *A. virgata* from central Peru than to its nearest neighbor, *A. maculicauda*. As far as I know, this specimen has not been previously reported in the literature, although it was known to Zimmer, who identified it as *A. virgata* (pencilled comment on the label).

"Contact" between *A. virgata* and *A. maculicauda* appears possible when the collecting localities of Koford's specimen of *virgata* and of the northernmost record of *maculicauda* are examined. Koford's bird was collected eight miles SSW of Limbani at 15,250 feet (label data). The northernmost specimen of *maculicauda* appears to be a bird collected by Carriker at Huancarani, 13,000 feet (ANSP 103442). According to Bond (1945:19), Huancarani is "about ten miles above Limbani." Limbani is a village on the left (west) bank of the valley, and is accessible by only one road or trail from the southwest. Thus it is likely that "above Limbani" and "SSW Limbani" are very close to each other (Fig. 1). However, even if these two localities are not separated by a significant linear distance, they are separated by an altitudinal gap of 2250 feet (about 700 m). There is thus no direct evidence for sympatry between *A. virgata* and *A. maculicauda,* but in view of their morphological differences, their sympatry in southern Peru would not be surprising.

Sympatry between *A. virgata* and *A. flammulata* in central Peru was made apparent by the mention of four specimens of *A. flammulata taczanowskii* collected at Rock Forest by Dorst (1956: 268). But as I shall show below, Dorst's specimens are actually referable to *virgata;* sympatry is therefore non-existent, since only one taxon occurs at Rock Forest.

GEOGRAPHICAL VARIATION

Altogether about 140 specimens have been examined from localities covering the entire range of the three nominal species of the *A. flammulata* complex (Fig. 1). Specimens were grouped into "populations," which are mapped on Figure 2. The grouping was based on several considerations, primarily (a) whether or not certain localities appeared to be isolated from others, thus representing potential interruptions in gene flow, and (b) whether or not the birds from several more or less adjacent localities were morphologically uniform. Thus specimens from the widely-spaced collecting locatities of the Eastern Andes of northern and central Peru were considered as one "population" (H) because of their considerable

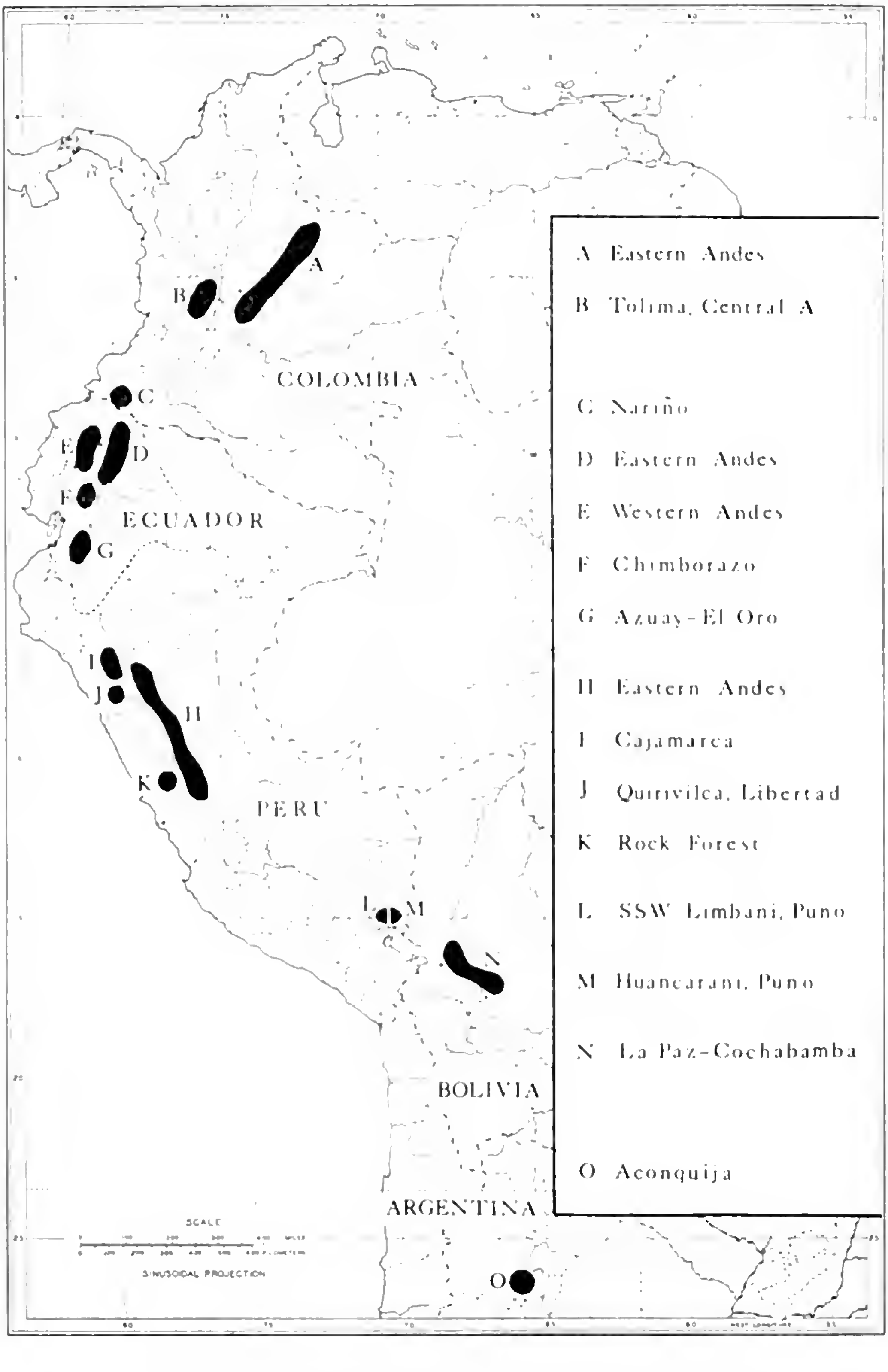

FIG. 2. The populations of the *Asthenes flammulata* complex.

morphological uniformity; on the other hand, those from the Western Andes of northern Peru were placed in two "populations" (I and J) because of geographical variation in some characters.

Despite this grouping into populations, the samples available were small. Under these circumstances, statistical treatment of the mensural characters was not attempted.

TABLE 1

Geographical variation of bill length in the *Asthenes flammulata* complex

Populations	Range of mean bill length (in mm)	
	Males	Females
Colombia, Ecuador northern Peru (A-L)	17.0-17.9	16.0-19.0
Southern Peru, Bolivia, northern Argentina (M-O)	15.0-16.5	15.3-15.5

TABLE 2

Geographical variation of tarsus length in the *Asthenes flammulata* complex

Population	Tarsus length of males (in mm)			Tarsus length of females (in mm)		
	Range	(Mean)	N	Range	(Mean)	N
A	24.0-27.0	(25.3)	3	23.0-24.0	(23.7)	3
B	25.0-27.0	(25.9)	11	23.5-26.0	(24.7)	6
C						
D	24.0-27.0	(25.8)	12	25.0-25.5	(25.1)	4
E	25.0-26.0	(25.6)	9	23.0-26.0	(24.8)	14
F	25.0-25.5	(25.2)	3		24.0	1
G	24.5-26.0	(25.3)	2	24.0-25.0	(24.5)	2
H	23.0-24.0	(23.9)	7	23.0-24.0	(23.8)	4
I	23.0-24.0	(23.0)	2		25.0	1
J	24.0-25.0	(24.3)	3			
K	23.0-27.0	(24.6)	7	23.0-24.0	(23.5)	2
L					26.0	1
M		23.0	1			
N	22.0-24.0	(22.8)	4	22.0-22.0	(22.0)	2
O	22.0-23.5	(22.8)	3	20.0-21.5	(20.8)	2

Mensural characters. Geographical variation in bill length, tarsus length, and wing length, respectively, is summarized in Tables 1 and 2 and in Figure 3. Populations M, N, and O (from southern Peru to northern Argentina) are distinguishable from their neighboring populations by a gap (step) in either absolute size or in mean length of all three characters. By contrast, steps between any two of the populations from A through L (Colombia to southern Peru) are much less significant (see especially Fig. 3).

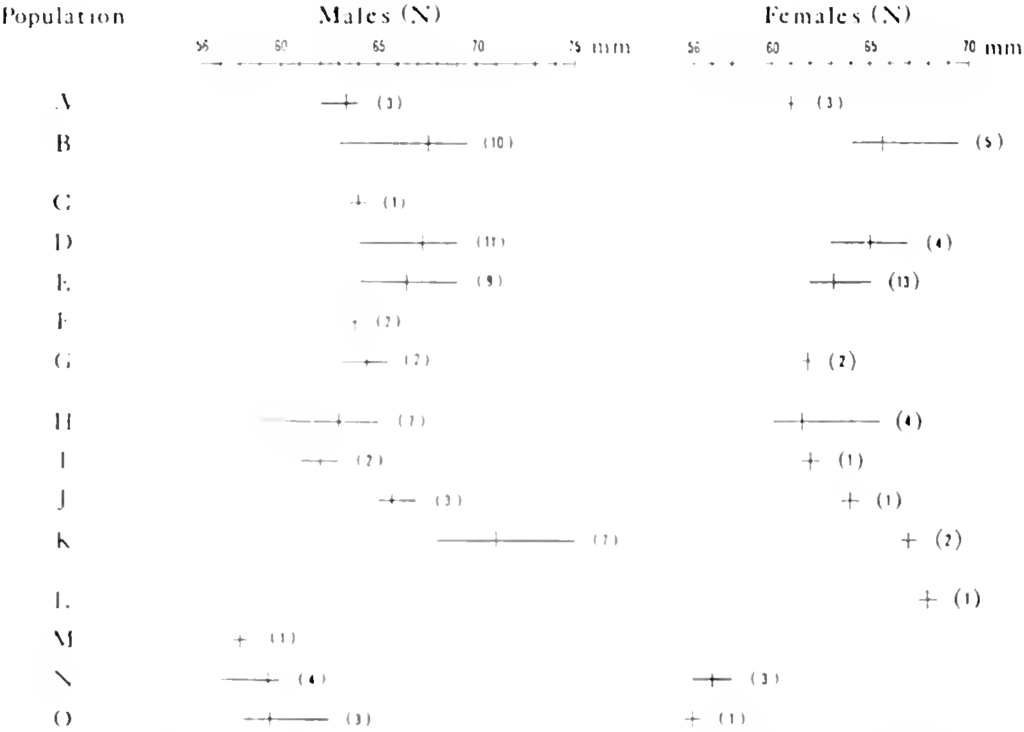

FIG. 3. Geographical variation of wing length in the *Asthenes flammulata* complex.

From the variation in mensural characters, one might conclude that the *A. flammulata* complex consists of two units, each an interbreeding species. The first would include populations A through L (nominal species *A. flammulata* and *A. virgata*), and the second populations M through O (nominal species *A. maculicauda*).

Color characters. Geographical variation in the color of the gular patch, the color of the forehead, the amount of streaking on the abdomen and crissum, the color of the rump and upper tail coverts, and the markings of the median pair of rectrices is summarized in Table 3. Variation in wing pattern is illustrated in Figure 4. Detailed notes on variation in these characters are included in Appendix I; only the major trends will be discussed here.

TABLE 3

Geographical variation of some color characters in the *Asthenes flammulata* complex

Character	Population														
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O
Gular patch	RO	RO	PO	PO	PO	PO	PO	Y	Y	Y	RO	RO	A	A	A
Forehead	Ru	Ru	Sr	Sr	Sr	Sr	Sr	Sy	Sy	Sy	Sy	Sy	Ru	Ru	Ru
Crissum	St	St	St	St	St	St	St	St	St	St	Bu	Bu	Bu	Bu	Bu
Rump	HS	HS	HS	HS	HS	HS	HS	HS	HS	HS	U	U	HS	HS	HS
Central pair rectrices	Un	Un	Un	Un	Un	Un	Un	Un	Un	Un	Un	M?	M	M	M

Symbols:

Gular patch: RO = Rich ochraceous; PO = Pale ochraceous; Y = Yellowish; A = Gular patch undifferentiated

Forehead: Ru = Rufous; Sr = Streaked with rufescent; Sy = Streaked with yellowish

Crissum: St = Streaked; Bu = Buffy, unstreaked, or with obsolescent streaks only

Rump: HS = Heavily streaked; U = Unstreaked

Central pair rectrices: Un = Unmarked; M = With irregular markings

Characters such as the color of the gular patch, the color of the forehead, and the intensity of streaking on the underparts vary rather gradually. There is a trend, from north to south, toward a decrease both in saturation of pigmentation and in the amount of streaking. Exceptions to this trend are provided by populations K and L (gular patch color) and populations M, N, and O (forehead color).

The other characters seem to vary more discontinuously. These patterns of discontinuous variation permit one to distinguish morphologically several populations or groups of populations within the *A. flammulata* complex. The best-marked group includes populations from southern Peru to northern Argentina (M, N, O). These birds are differentiated from their neighboring populations by gular patch color, forehead color, and streaking on the rump. The steps observed in the variation of these color characters correspond to those noted in the mensural characters.

Other groups of populations can also be separated morphologically, but on the basis of fewer characters. Thus the birds of populations A and B (Colombia) can be distinguished by the color of the gular patch and the color of the forehead. Similarly, birds from populations K and L (Rock Forest and SSW Limbani) are separable from others by the color of the gular patch and the general absence of streaks on the rump and upper tail coverts (if these streaks are present, they are obsolescent).

However, it must be pointed out that such a neat separation of populations cannot be done using some other characters. For example, populations K and L are not distinguishable from populations M, N, and O on the basis of color or streaking of the underparts. Also, populations K and L are indistinguishable from populations H through J in forehead color.

When variation in color characters (as in mensural characters) is considered as a whole, the *A. flammulata* complex appears to comprise two units. Geographical variation within populations A through L, and within M through O, could be interpreted as that normally to be found in an interbeeding species. However, unlike what is found in mensural characters, the gap in color characters separating populations A-L and M-O does not seem to be as well marked as the gap separating some populations within A-L.

POPULATION STRUCTURE

The dual type of geographical variation (gradual and discontinuous) exhibited by the *A. flammulata* complex is often found in a single polytypic species with a partially continuous and partially discontinuous range.

Although the number of specimens examined is not large enough to reach definite conclusions, it seems probable that the gradual size trends (especially in tarsus and wing length) detected are positively correlated with altitude. Thus the largest birds seem to live at slightly higher elevations (in north-central Ecuador and central to southern Peru) than the smallest birds (in southern Ecuador and northern Peru. Altitudinal variation in Andean birds has been demonstrated by Traylor (1950) and myself (unpublished). However, the correlation of increase in size with increase in altitude is not the only possible one. In Peruvian birds, for example, the north-south size increase along the Western Andes could be due to latitude or aridity (Hamilton, 1961), rather than to altitude.

The decrease in the intensity of pigmentation from north to south cited earlier is also detectable in several species belonging to other Andean genera (unpublished). Such variation may be correlated positively with the decrease in rainfall along the Andes from north to south (see, e.g., Troll, 1959); thus it corresponds to Gloger's rule.

The apparent trends of gradual geographical variation are clearest in populations A through L, which have the earmarks of representing a single species, as already noted. It is, therefore, of interest that populations M-O, which are separated from populations A-L by a marked morphological gap in some characters, have a very different type of population structure. Although populations M, N, and O are apparently disjunct (see Fig. 2), the birds I have examined are all remarkably uniform and display only slight geographical variation — in wing length, for example (see Fig. 3). This lack of significant geographical variation can be explained either by free gene flow, or by recency of occupation of the vast geographical range, or possibly by both. Whatever the reason, the differences in population structure would tend to confirm the previous impression of specific distinctness between populations A-L (*flammulata-virgata*) and M-O (*maculicauda*). Since, as noted previously, there is no apparent barrier between the two groups of populations in southern Peru, I would conclude that their differentiation does not reflect the result of evolution *in situ* (unless, of course, a barrier once present has subsequently been removed). This question cannot yet be answered, but the problem will be taken up in a later paper in this series.

To study the possible correlation between discontinuous variation and geographical barriers in the *A. flammulata* complex, we must turn to populations A-L, ranging from Colombia to southern Peru.

Discontinuous Variation and Geographical Barriers

The presence of a geographical barrier between avian populations does not *ipso facto* mean that gene flow between the isolates is interrupted. Similarly, the fact that geographical isolates are not differentiated morphologically, or are so only slightly, does not necessarily mean that gene flow takes place between them. Consequently, statements made in the following paragraphs about differentiation and gene flow across barriers must be taken, not as expositions of known facts, but as cautious expressions of probabilities.

The correlations between morphological differentiation and geographical barriers in populations A-L of the *A. flammulata* complex will be mentioned in geographic sequence from north to south.

(1) In Colombia, the birds from the Eastern Andes (*multostriata*) are separated from those of the Central Andes (*quindiana*) by the Magdalena Valley (Fig. 5). Morphological differences between these two isolated populations (A and B on Fig. 2) include wing length, the width of the streaks on the underparts, the presence or absence of a slight buffy wash on the undertail coverts, the extent of the gular patch, and the intensity of the coloration of the forehead. The two populations are certainly sufficiently differentiated to be recognized taxonomically, although they are more similar to each other than they are (either as a group or separately) to populations farther south in Colombia and Ecuador (C-G).

(2) Between the Eastern or the Central Andes of Colombia and the Andes of Nariño in southern Colombia is an apparent distribution gap (Fig. 5). The only specimen from Nariño (C) I have seen (Mayasquer, ANSP 149893) appears somewhat intermediate in both postocular stripe and cheek color between Colombian birds (A-B) and Ecuadorian specimens (D-G). However, since these differences are slight, it is not possible to assess the real extent of intermediacy. In other characters, furthermore, the Nariño specimen falls fully within the range of variation of Ecuadorian specimens. The vast geographical gap between Colombian populations A-B and southern Colombian-Ecuadorian populations C-G is therefore correlated with a relatively well-marked morphological gap. Taxonomic recognition of populations C-G (subspecies *flammulata*) is thus warranted.

(3) The Interandean Depression of Ecuador (Fig. 5) is a low and relatively dry region separating the Eastern from the Western Andes. Only a slight difference in wing length and tarsus length

between birds of the Eastern (D) and Western (E) Andes was detected, suggesting only a slight restriction in gene flow; taxonomic subdivision within populations C-G (*flammulata*) would be unjustified.

(4) There is a gap between the northern Peruvian populations of the Eastern (H: *taczanowskii*) and Western (I: *pallida*) Andes and those of southern Ecuador (G). For population H, the gap corresponds to the eastward bend of the Marañon River; for population I it corresponds to the generally low altitude and small area of suitable habitat of the Andes of northwestern Peru (Northern Peruvian Low: Fig. 5). The morphological differences between Ecuadorian and Peruvian birds are not large. They include the intensity of streaking on the underparts and the extent of rufous on tail feathers. The lack of major differences suggests either some gene flow over the gap, or that the separation of Ecuadorian from Peruvian birds is of recent origin.

(5) The Upper Marañon Basin (Fig. 5) separates the northern Peruvian populations of the Eastern Andes (H: *taczanowskii*) from those of the Western Andes (I and J: *pallida*). Only slight morphological differences can be noted between them, however: these include characters such as tarsus length, wing length, and intensity of streaking of the rump and upper tail coverts. I could find no differences in the other characters examined. In view of this minor morphological differentiation, subspecific separation of the two populations may not be warranted; *pallida* may be considered a synonym of *taczanowskii.* As Bond (1945:32) has remarked, *pallida* "is not a very well-marked race."

(6) The specimens collected in the Rock Forest area of central Peru (K: *virgata*) are distinguishable morphologically from the birds living in both the Eastern (H) and Western (I, J) Andes. The differences are in wing length, color of gular patch, color of central pair of rectrices, amount of streaking on rump and upper tail coverts, wing pattern, and color of the lower abdomen and crissum. These differences are better marked between Rock Forest specimens (K) and birds from the Eastern Andes (H), than between Rock Forest birds and specimens from the Western Andes (I, J). An approach to Rock Forest birds is clearly seen in Western Andean birds (especially population J) in size (Fig. 3) and in wing pattern (compare nos. 5 and 6 on Fig. 4).

Geographical isolation between Rock Forest birds (*virgata*) and Eastern Andean birds (*taczanowskii*) is apparently provided by the Lake Junín Basin (Fig. 5). But since the first specimen of *virgata* may have come from "Junin" in the center of the basin, a more

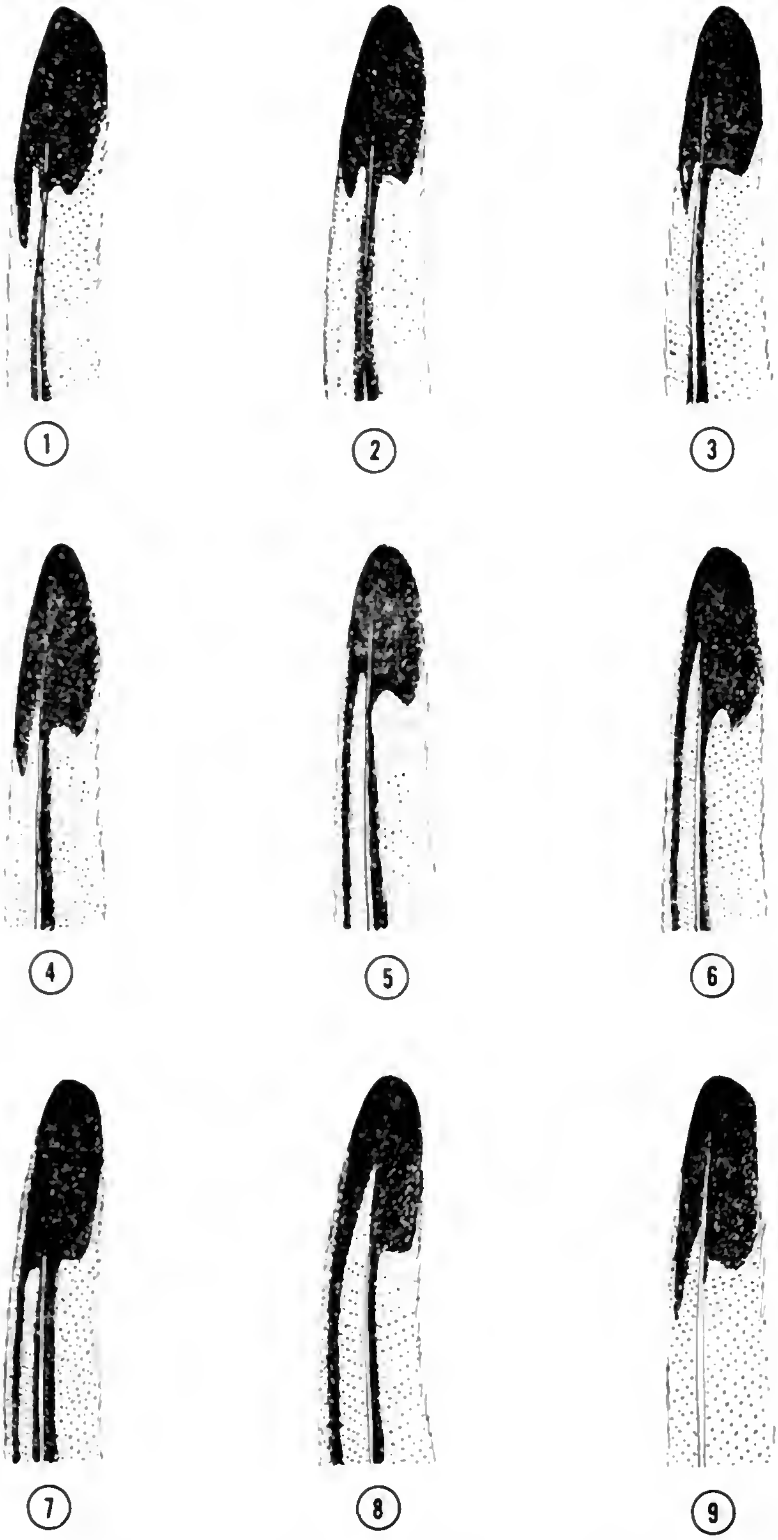

FIG. 4. Geographical variation of wing pattern in the *Asthenes flammulata* complex. The feather illustrated is the sixth outer primary.

Key: 1 = Volcán Pichincha, Ecuador; 2 = Huánuco, northern Peru; 3 = Maraynioc, central Peru; 4 and 5 = Quirivilca, Libertad, northern Peru; 6 = Rock Forest, central Peru; 7 = SSW Limbani, southern Peru; 8 and 9 = Incachaca, Cochabamba, Bolivia likely barrier may be the high Andes farther east. In any event, although the barrier is not clear-cut at present, morphological differentiation is fairly sharp.

Isolation between Rock Forest birds (*virgata*) and populations found farther north along the Western Andes (J: *"pallida"*) is not clear. The closest specimens come from Quirivilca, Libertad, about 375 km from Rock Forest. No specimens are known to me from the intervening area, although apparently suitable habitats occur there. A possible barrier might be the Santa River Canyon, which makes a cut across the Andes between the Cordillera Blanca and the Andes of Libertad.

(7) The vast Andean area between central and southern Peru (about 800 km) seems to represent a distribution gap in the range of the *A. flammulata* complex. However, suitable habitat occurs there, and further collecting might reveal the presence of the complex there (? on Fig. 5). The specimen from SSW of Limbani is practically identical with Rock Forest specimens (*virgata*), except in the pattern of the central pair of rectrices.

TAXONOMIC CONCLUSIONS

The classification of Hellmayr (1925), Peters (1951), and de Schauensee (1966) is as follows. Colombian, Ecuadorian, and northern Peruvian populations (A-J) are treated as one species, *Asthenes flammulata.* The two disjunct populations from central and southern Peru (K and L) would constitute a second species, *A. virgata.* Finally, the populations from southern Peru to northern Argentina (M, N, O) make up a third species, *A. maculicauda.* A slight modification of this classification was made by Bond and de Schauensee (1942:334), who considered *maculicauda* a subspecies of *flammulata.* (Later, however, Bond, 1945:32, cited *maculicauda* as a full species without any comment.) This classification finds justification in the fact that there is a morphological and partial geographical gap between *flammulata* and *virgata* (see (6) above), and because there is a morphological gap between *flammulata-virgata* and *maculicauda.*

I believe, however, that the evidence presented in this paper allows one to construct a classification of the *A. flammulata* complex which is at the same time a simplification and an improvement over the older scheme.

The *Asthenes flammulata* complex constitutes a superspecies (*sensu* Mayr, 1963:501) having two component species. The first

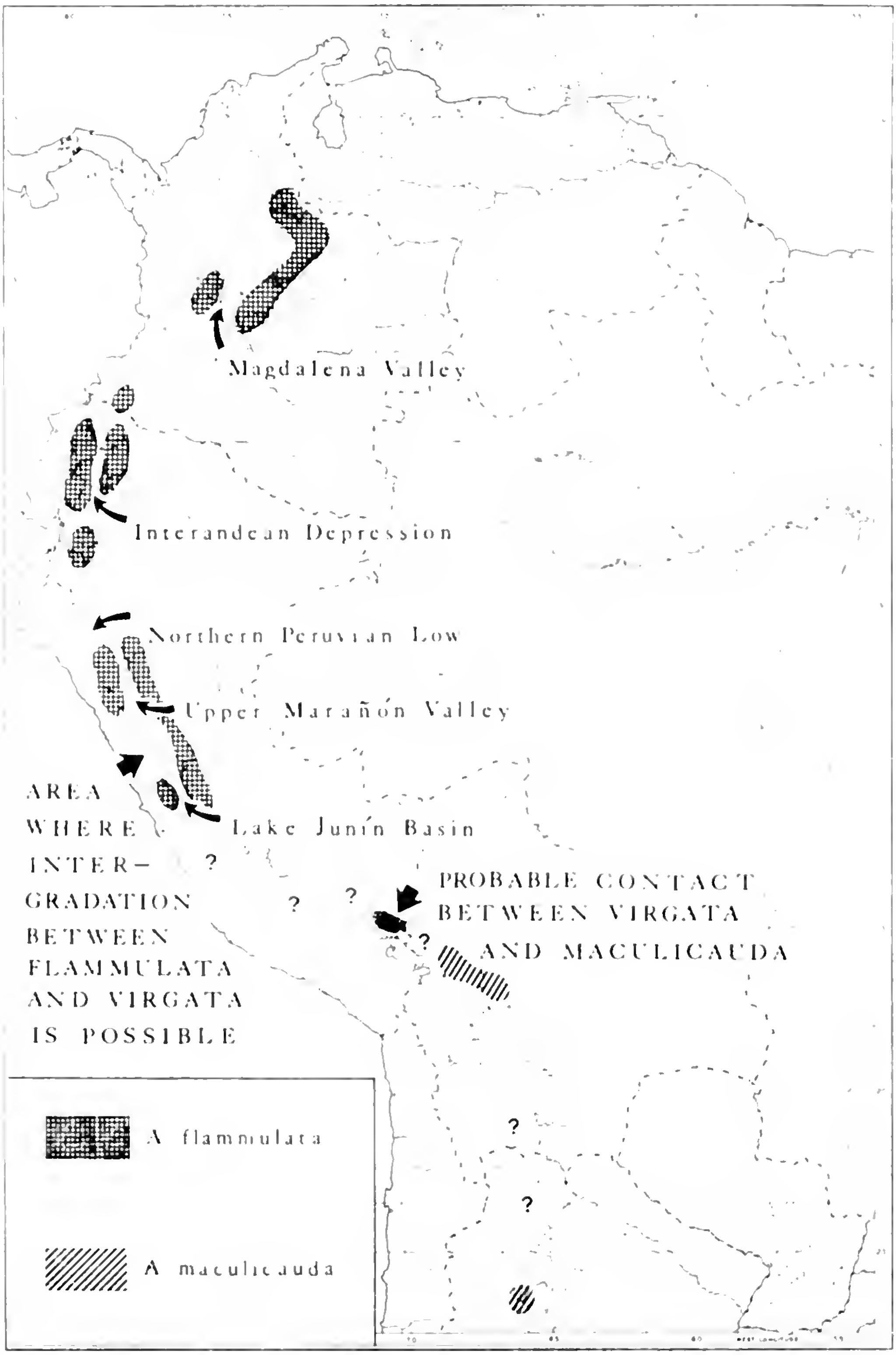

FIG. 5. Taxonomic and evolutionary interpretation of distribution and geographic variation in the *Asthenes flammulata* superspecies.

species is composed of several isolated and semi-isolated populations ranging from Colombia to southern Peru (*Asthenes flammulata*). Fully isolated populations of *A. flammulata* which have reached a moderate to marked degree of differentiation (incipient species) are the Colombian *multostriata* and *quindiana*. These two isolates are perhaps best considered as a subspecies group with two subspecies. The specimens from Rock Forest and SSW Limbani fall within the range of variation of a single taxon (*virgata*).[1] Some gene exchange between Rock Forest birds and birds farther north in the Western Peruvian Andes is suggested by the variation of characters such as wing length (Fig. 3). I consequently recommend that *virgata* be treated as a subspecies of *A. flammulata*.

The second component species of the *A. flammulata* superspecies, *Asthenes maculicauda*, is composed of three apparent isolates (M, N, O), but it does not exhibit much geographical variation.

The taxa of the *A. flammulata* superspecies and their relationships can be listed as follows:

Asthenes flammulata superspecies (two component species which may have achieved reproductive isolation)
- (1) *Asthenes flammulata* (Jardine, 1850)
  - (a) Colombian subspecies group (one or two incipient species): *A. flammulata multostriata* (Sclater, 1858), *A. flammulata quindiana* (Chapman, 1915)
  - (b) Ecuadorian-Peruvian subspecies group (two or three incipient species): *A. flammulata flammulata* (Jardine, 1850); *A. flammulata taczanowskii* (Berlepsch and Stolzmann, 1894; includes *A. f. pallida* Carriker, 1933); *A. flammulata virgata* (Sclater, 1874)
- (2) *Asthenes maculicauda* (Berlepsch, 1901)
  Shows insignificant geographical variation

SUMMARY

The Andean spinetails of the *Asthenes flammulata* complex include three nominal species, *flammulata, virgata,* and *maculicauda,* which, together with a fourth, *A. urubambensis,* constitute the *A. flammulata* species group.

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[1] The specimens reported by Dorst (1956) as *A. flammulata taczanowskii* from Rock Forest are therefore referable to *virgata*.

Specific status of *A. urubambensis* is shown by sympatry with two nominal species of the *A. flammulata* complex and by morphological distinctness.

The evolutionary relationships of the three nominal species of the *A. flammulata* complex were analyzed by a study of geographical variation and its correlation with geographical barriers. Geographical variation is largely discontinuous in populations ranging from Colombia to southern Peru (nominal species *flammulata* and *virgata*). By contrast, populations from southern Peru to northern Argentina show great morphological uniformity (nominal species *maculicauda*).

It is concluded that the *Asthenes flammulata* complex is best considered as a superspecies with two component species. The first species, *A. flammulata*, contains several isolated groups of populations (incipient species) showing various degrees of morphological differentiation across barriers. *A. virgata* should be included as a subspecies of *A. flammulata*. The second species, *A. maculicauda*, may come in contact with *A. flammulata virgata* in southern Peru. Gene exchange between the two species is not suggested, but there are only two specimens on which to base a decision.

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APPENDIX I: NOTES ON GEOGRAPHICAL VARIATION IN NON-MENSURAL CHARACTERS

Gular patch. The gular patch varies in color intensity from whitish and yellowish to rich ochraceous, and in extent from a small, roughly triangular patch more or less restricted to the chin, to a wider patch comprising also the throat and upper chest.

Colombian specimens (populations A and B) have a richly ochraceous gular patch. Central Andean birds (B) have a rather broad patch, while in Eastern Andean birds (A) it is more restricted.

Ecuadorian specimens and the Nariño specimen from Mayasquer (populations C-G) have relatively narrow and more or less triangular gular patches, varying from whitish-yellow to pale ochraceous.

Peruvian specimens (populations H-J) have a broad, ill-defined gular patch merging into the upper chest. The patch varies in color from dirty white to yellowish-cream. Usually the chin area is somewhat paler than the throat. Some specimens of Ecuadorian birds (e.g. MCZ 199104, female, and MCZ 199099, male) have a more ill-defined gular patch than do most other Ecuadorian specimens, thus showing an approach to Peruvian specimens.

Peruvian specimens from Rock Forest and SSW Limbani (K and L) have a relatively small, well-defined gular patch, usually of a rich ochraceous color.

Specimens from southern Peru to northern Argentina (M, N, O) lack a buffy-ochraceous gular patch: the gular area is of about the same color as the chest.

Forehead color. In Colombian specimens from both the Eastern and Central Andes (A and B) the forehead is an almost solid rufous, especially in males. The forehead of most Ecuadorian specimens (C-G) is streaked with rufescent, although in some birds (e.g. MCZ 138553) it is a solid rufous. In Peruvian birds from populations H, I, and J the forehead streaks are less rufescent, more yellowish, but here again at least one specimen (FMNH 65849, male) has a rufous forehead, where the streaks almost join to form a solid color. In Peruvian specimens from Rock Forest and SSW Limbani (K-L) the streaks are relatively yellowish, not very rufescent. Finally, specimens from southern Peru, Bolivia, and northern Argentina (M, N, O) have rufescent foreheads, distinctly more pigmented than those of Peruvian birds in general, and of Rock Forest-SSW Limbani birds in particular.

Coloration of underparts. Colombian specimens are the most heavily streaked; Bolivian and Argentine specimens are almost unstreaked. The birds from Rock Forest, SSW Limbani, Huancarani, Bolivia, and northern Argentina (K-O) are the least streaked of all populations within the *Asthenes flammulata* complex. The additional fact that in the birds from these same populations the lower abdomen and crissum are buffy with obsolescent streaks, rather than whitish with rather conspicuous streaks, permits one to distinguish them immediately from all other populations (A-J). There is, in particular, a rather well marked difference in streaking intensity between the crissum of Peruvian birds from the Eastern (H) and Western Andes (I, J), and that of birds from Rock Forest (K).

Specimens from southern Peru to northern Argentina (M, N, O) have, alone among the populations of the *A. flammulata* complex, a series of ill-marked streaks on the chest converging toward the center to form a ring.

Color of rump and upper tail coverts. The birds from Rock Forest and SSW Limbani (K and L) have slight or obsolescent streaking on the rump and upper tail coverts. (This was already noticed by Bond [1956: 245] for Rock Forest specimens.) By contrast, specimens from all other populations have generally much heavier streaking on the rump and upper tail coverts. These streaks are relatively well marked in Peruvian populations H, I, and J, as well as in Peruvian, Bolivian, and Argentine populations M, N, and O. Rock Forest and SSW Limbani (K-L) specimens are thus distinguishable as a group from neighboring populations.

Wing pattern. The primaries of birds in all populations are more or less rufous with a dark brown to blackish tip. I have studied interpopulation variation in pattern by comparing the patterns of the sixth outer primary, which was chosen arbitrarily.

Except for a few Colombian specimens, which have only a relatively narrow rufous edge to both vanes of the sixth primary, in most other specimens (including those from Colombia) the tip of the feather is more or less wholly dark brown, while its base is rufous (see Fig. 4, Nos. 1, 2, 3, 4, and 9).

The most significant population variation is in the presence or absence of a thin dark brown stripe along the outer vane of the primary (compare Nos. 4 and 5 of Fig. 4, for example). This pattern is seen in some specimens from Quirivilca, Libertad (population J), every specimen from Rock Forest (K), the single specimen from SSW Limbani (L), and most specimens from southern Peru to northern Argentina (M, N, O). The presence of the two major patterns in the Libertad and Cochabamba populations is illustrated in Fig. 4 (Nos. 4 and 5, and Nos. 8 and 9, respectively).

Marking of rectrices. Analysis of variation in this character is difficult because a rather large number of specimens have one or several rectrices in molt or missing and because many specimens have extremely worn rectrices. Nevertheless, the detectable variation appears as follows.

There is a tendency for Peruvian specimens (including the specimen from SSW Limbani, but excluding Rock Forest specimens) to have more rufous on outer tail feathers than do Ecuadorian or Colombian specimens.

Rock Forest specimens lack entirely or almost entirely the narrow rufescent or pale brownish outer edge to the outer vane of the central pair of rectrices, which is present in specimens from all other Peruvian localities including SSW Limbani.

In birds from southern Peru to northern Argentina (M, N, O), the central pair of rectrices is marked with irregular dark brown designs on a rufous or rufescent background. No other specimen from anywhere in the range of the *Asthenes flammulata* complex has similar markings on the median rectrices, with one exception: in the central pair of rectrices of the specimen from SSW Limbani, the outer part of the outer vane is rufescent, with a thin and irregular dark brown line running alongside the rufescent color. This pattern, although reminiscent of that found in birds from populations M, N, and O, is not really similar to it.

In rectrices other than the central pair, a pattern reminiscent of the one found in specimens from southern Peru to northern Argentina (M, N, O) is noticeable in specimens from Rock Forest (ANSP 92428, ANSP 92427, MP CG1956 No. 942, MP CG1956 No. 940), as well as in other populations. But the number of specimens in which this pattern occurs tends to become smaller north of central Peru.

B R E V I O R A

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MONOGRAPH OF THE CUBAN GENUS *VIANA* (MOLLUSCA: ARCHAEOGASTROPODA: HELICINIDAE)

William J. Clench and Morris K. Jacobson

Abstract. The genus *Viana* in the family Helicinidae is limited in its distribution to the Sierra de los Organos in Pinar del Río, the westernmost province of Cuba. All members are found only on limestone substrate. The genus consists of one species, *regina* Morelet, with two subspecies, *laevigata* Pfeiffer and *subunguiculata* Poey, that form many races which are not clearly discrete morphologically and which show no coherent geographical distribution.

INTRODUCTION

This study of the genus *Viana* is based upon specimens housed in the Museum of Comparative Zoology which include the very large collections made by Carlos de la Torre, Pedro Bermúdez and Julio Armenteros. Much additional material was contributed by Thomas Barbour, William J. Clench, Paul Bartsch, Carlos G. Aguayo, Miguel L. Jaume, Morris K. Jacobson, and numerous other Cuban and American collectors.

The strikingly handsome shells of the helicinid genus *Viana* are confined to the Sierra de los Organos, Pinar del Río Province, in the western end of Cuba. Their range is limited in the west by the sierras and mogotes[1] about Mendoza, and in the east by the Sierra Rangel, about 75 miles away. The species of *Viana* are purely calciphilous, living exclusively on the limestone mogotes and sierras which emerge from the surrounding red, iron-bearing soil. In such locations during the rainy season they can be collected as readily as littorinids on rocky sea coasts. Unlike the related genus *Emoda,* they are found in no other part of the island.

Within their range they inhabit practically every outcrop of limestone of any size which enjoys sufficient moisture and shade.

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[1] In western Cuba a mogote is any isolated limestone block separated from the main sierra.

Thus they are common on high sierras like those of Guane, Paso Real, Viñales, San Carlos, San Andrés, Guajaibón, and Rangel, and on the small mogotes in the valley of Viñales, the Laguna de la Piedra, and around Luis Lazo, Isabel María, and between the Estrechura of San Carlos and Guane (Tenería, Punta de la Sierra, La Muralla, and Los Portales).

Map 1. Showing the greater part of the Province of Pinar del Río, Cuba, outlining the areas containing the sierras and mogotes which are occupied by the three subspecies of *Viana regina* Morelet.

A. *Viana regina subunguiculata* (Poey). B. *V. r. laevigata* (Pfeiffer). C. *V. r. regina* (Morelet).

Cities and towns
1. Guanajay
2. Artemisa
3. Consolación del Norte
4. Viñales
5. Consolación del Sur
6. Pinar del Río
7. Guane

Sierras and Mogotes
8. Sierra Rangel
9. Pan de Guajaibón
10. Sierra San Andrés
11. Sierra Viñales
12. Mogotes at "Km. 14"
13. Sierra del Quemado
14. Sierra Paso Real

The genus *Viana* appears in a series of differentiated forms. These vary in sculpture from smooth and shining to dull and spirally grooved; in color from yellow to reddish and purple, ornamented at times with red, yellow, or diaphanous bands, or with whitish mottling; and in size from the large forms of Sierra Rangel, (29.5 mm in width) to the small forms (18.2 mm in width) which inhabit small mogotes such as those at Kilometer 14, Viñales. In most cases, specimens o*f Viana* collected on small mogotes are dwarf forms about one-half the size of typical specimens. It is apparent that the size of individual specimens is a function of the area of the habitat and may very well be of selective value for survival, based upon the supply of food. In addition to other variations, the margin of the peristome may be simple and unreflected as in *V. regina regina* and *V. regina laevigata*, or more or less strongly reflected as in *V. regina subunguiculata*.

From the scant field notes we assembled we find that vianas are largely satisfied with the presence of limestone, shade, and moisture. We have never collected a live specimen other than on limestone rock. Nothing has been published about their food, but they probably eat the lichens found on the rocks on which they live.

They have an enemy in the larval form of the large Cuban firefly, *Alecton* sp.; pictures have been taken of such a larva devouring a *Viana* through the aperture (Pl. 1). Probably the firefly larva

PLATE 1

Viana regina (Morelet)

Viana regina Morelet being attacked by a lampyrid beetle larva (*Alecton* sp.). Photo by F. de Zayas (about 6 X).

attacks its prey when the snail is relaxed. The predator may wait for the *Viana* to relax the operculum and then attack, much like the marine predators of the genus *Melongena,* among others.

Baker described the radula of *Viana* (1922) and its anatomy (1926). We could find nothing in print regarding its natural history. The following notes are translated from a personal communication from Oscar Alcalde Ledón who, until he left the country in 1963, was in charge of the Division of Malacology in the newly formed Academia de Ciencias de la República de Cuba. Alcalde tells us that he unfortunately left his notes behind and writes from recollection only.

> "[The eggs] are subglobular in shape, the size of a capital letter 'O' in normal typewriter print, or perhaps a bit larger. I found them under a slab of rock and they were covered with the reddish soil on which the rock rested. After being washed, they proved to be wax colored [whitish]. I did not know at first that they were *Viana* eggs, but later upon breaking them, I found the nepionic whorls of a snail which under microscopic examination proved to be identical to the nepionic whorls of *Viana.* The operculum was very small and thin."

According to Thiele (1929:81), all helicinids lack a male copulatory organ, and the manner of transfer of sperm from male to female is unknown.

Several of the forms of *Viana* mentioned above were given names by the late Dr. Carlos de la Torre, but almost all remain in manuscript. Under these manuscript names they have been widely distributed by Cuban collectors, and one of the purposes of the present study was to examine the validity of these forms. After carefully localizing a large number of *Viana* specimens on an enlarged map of the Sierra de los Organos region, we find that we are amply justified in rejecting these names *in toto.*

The confusion in this genus is very much like that of *Polymita* and *Liguus.* That is, unless the localities of the various forms are carefully plotted, the worker would find it easy to attach names to the many color forms and forms with only minor morphological differences. A review of the literature covering *Polymita* and *Liguus* has demonstrated amply the confusion which results from such a proliferation of names. We choose to follow a more conservative course and to refer to striking varieties, which blend into one another, by vernacular names such as marbled, lirate, smooth, banded, roseate, yellow, dwarf, shining, dull, etc., instead of using Latin infraspecific taxa which might be misunderstood as taxonomic designations.

In doing so we follow the procedure generally adopted for such a variable species as the intertidal marine mollusk from the northeast coast of North America, *Thais lapillus* (Linnaeus). The analogy between the two groups mentioned is quite close, since in both cases we are dealing with prosobranch mollusks living in more or less isolated colonies on rocks, and hence displaying a rich variety of sculpture, size, and color. The common practice today is to designate all the *lapillus* varieties under the simple name *Thais lapillus*. We propose to do the same for *Viana regina* (Morelet). The distribution of the various populations as revealed on our maps nevertheless seems to justify the recognition of *subunguiculata* Poey and *laevigata* Pfeiffer as valid subspecies.

V. subunguiculata extends southwestward from a line running between Sierra del Quemado–Sierra Viñales (with a very strong salient reaching into the Sierra Celadas branch of the Sierra Viñales complex) and Sierra Cabezas. Southwestward from this line, *subunguiculata* is found reaching to the extreme western limit of the distribution of the genus *Viana* at Sierra de Guane and Sierra Paso Real near Guane. This range includes the sierras around Luis Lazo (San Carlos, Los Acostas), at Isabel María and Cabezas, and at the isolated mogotes between Luis Lazo and Guane.

The subspecies *laevigata* is centered about the complex of mountain ranges which go under the name of Sierra de Viñales,[1] with disconnected outrunners at the Cayos de San Felipe, Lagunillas, Matahambre, Pan de Azúcar, Cabezas, Isabel María, and some colonies on the Sierra del Quemado. The line separating *laevigata* from *regina, sensu stricto,* appears to run south between the Baños de San Vicente on the west and the Sierra San Andrés (with La Jagua) to the east. East of this line, and reaching to the eastern limit of the range of the genus at Rangel, the nominate subspecies *regina regina* can be found. The mogotes at Kilometer 14 and El Guamá also are inhabited by *regina regina,* as are many mogotes in the Viñales valley (Dos Hermanos, Mogote La Vega, Hoyo de los Santos, Mogote de los Muertos), whereas others in the same area (Mogote Pequeño, Mogote Alto, Hato Morales, El Cuajaní) have populations of *laevigata.*

We realize, of course, that certain populations are sufficiently distinct to enable the student to recognize the locality from which

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[1] Sierra del Infierno, Sierra Penitencia, Sierra Pan de Azúcar, Sierra Martillo, and others.

they come. Nevertheless, there are many specimens for which this is not possible, nor did we find it easy to establish fixed dividing lines between the various characteristics, with the exceptions noted below. Throughout the range of the genus there is much duplication of the characteristics upon which de la Torre based his manuscript names.

This separation of the genus into three subspecies and numerous, if not clearly defined, races presupposes an early continuous limestone area which, by subsequent lifting and corrosion, was broken up into a series of discontinuous ranges (sierras) and isolated blocks (mogotes). There is a small amount of territory at the southwestern end of Sierra de Viñales and at Sierra del Quemado where *laevigata* and *subunguiculata* overlap with very little fusion of characters. However, more collecting is needed in these two areas. This is also true of the small territorial overlap in Viñales at El Queque between *laevigata* and *regina*. Mechanical dispersal may be responsible for this overlap. Gene flow, however, between members of the same subspecies must be vary rare, particularly between isolated populations, such as those of Pan de Guajaibón and Sierra Rangel. Hurricanes could be the means of such mechanical dispersal, carrying specimens or their eggs.

Writing about a large mogote near Viñales, called previously El Tumbadero but now El Queque, Henderson (1916:234) states:

> "The rock is discolored and considerably altered by metamorphic process. It is just possible that the limestone of this southern range of the Organos Mountains is a shade older than that of the northern system (the Costanera), but the folding upward of the two was certainly contemporaneous. All the mogotes of the Viñales valley, including the large Tumbadero, the Dos Hermanos, and the many smaller ones scattered about the valley floor are clearly but fragments of the main sierra now wholly detached and isolated by erosion [corrosion]. The ammonites, which Dr. Torre has been collecting for several years, come principally from the rocks of this southern range and indicate probably Jurassic origin of the limestone.[1] As heretofore noted, the mogotes about 'Kilometer 14' do not belong to the Viñales range, but together with the Cerro de Cabras hills farther west, represent either remnants of a third line of Jurassic sierra that once followed a course parallel with the existing ranges, or possibly a later Tertiary deposit upon the flanks of the older mountains."

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[1] According to Weyl (1966: 42-47), the Viñales limestone (Kalk) is of Upper Jurassic age and has come by three overthrusts from the north.

Some of the localities cited here must be taken provisionally. There are no reliable detailed maps of the Sierra de los Organos region. Even the map composed by the Cuban army engineers in 1933-1941 is too general, not always accurate, and in several instances illegible. Coupled with this difficulty is the haphazard way in which the Cuban peasant assigns names to the various features of his local geography. Many mogotes, cerros, vegas, hoyos, and arroyos have the same name, but on the other hand, many of these features have several. Frequently the name of a mogote is that of the farmer near or on whose land it stands; hence, when this land changes hands, these names frequently change. There is no certainty that such names were ever officially recognized or published, or even that they appear on local land records. A final difficulty lies in the matter of spelling. The unique Cuban pronunciation of Castillian is reflected at times in the orthography. Thus, AYÚA, the local name of a tree (*Fagara* sp.), which is also associated with the name of a hill and cove in the Sierra San Andrés, appears as AYÚDA, ALLÚA and ALLÚDA on field labels. In one instance a mogote called MUELA DE LA VIEJA (Old Woman's Tooth) also appears on a collecting label as COLMILLO DE LA VIEJA (Old Woman's Fang).

The most useful local maps where those published by de la Torre and Bartsch (1938) and field maps prepared by Oscar Alcalde Ledón and Julio Armenteros. The gazetteer on Cuba published by the United States Board on Geographic Names (1957) was also very useful. In some cases, however, we have had to be satisfied with reporting localities as they appear on the collection labels. We do so in the hope that local inquiry at a later date will enable the collector to find these localities.

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SYSTEMATIC DESCRIPTION

Genus VIANA H. and A. Adams

Viana H. and A. Adams, March 1854, The Genera of Recent Mollusca, **2**: 305 [as subgenus of *Trochatella* Swainson] (type-species, *Helicina regina* Morelet 1849, subsequent designation, Pilsbry and Brown 1910, Proc. Acad. Nat. Sci. Philadelphia, **62**: 525); *non* Walker 1869 [Lepidoptera]

Hapata Gray, November 1856, Ann. Mag. Nat. Hist., (2) **18**: 414 (type-species, *Trochatella regina* (Pfeiffer) [*sic*, Morelet], original designation).

Rhynchocheila Shuttleworth 1877, Notitiae Malacologicae, **2**: 15 (type-species, *Helicina regina* Morelet 1849, monotypic).

Fitzia Guppy 1895, Proc. Victoria Inst. Trinidad, **1**, pt. 2: 74 (type-species, *Helicina regina* Morelet 1849, monotypic).

Description. Shell large, reaching 29 mm in diameter, imperforate, trochiform, generally solid, faintly to rather strongly sculptured, and lacking periostracum in adult specimens. Shells unicolored, or ornamented with bands of varying width, or with a marbled or mottled design; a thin reddish subsutural line is present in some specimens. Lip simple and occasionally sinuous or flaring, male shell with a notch midway between the outer lip and its insertion in the parietal area. Protoconch 1½ whorls, smooth or irregularly pitted, sharply raised above the succeeding whorls as in *Eutrochatella*, generally lighter in color than the rest of the shell except the base.

Operculum calcareous, auriculate, white externally with a thin, light brown, internal corneous layer and darker at the periphery. The outer margin is widely rounded, the columellar margin concave above, generally straight and descending almost vertically below. It is rounded at the base, generally on a single plane, but sharply raised basally and less so along the columellar margin. There is a long, rounded, low, more or less vertical protuberance along the inner margin, thickest centrally. Outer margin very slightly thickened; a thin, opaque, transverse area reaches internally across the mid-line. Nucleus lateral and central near the columellar margin, with concentric lines of growth which follow the outline of the shell.

Remarks. The notch on the peristome of the male, which we hereafter call the peristome notch, was one cause of the repeated renaming which this genus underwent. Morelet (1849: 19) writes "Peristomo supero. . . profunde emarginato." Gray (1856: 414) likewise thought the notch was characteristic of the entire group and created his genus *Hapata*. H. and A. Adams (1854: 305) also thought this to be true of their genus *Viana*. Fischer (1885: 796), citing Pfeiffer, says "les coquilles d'une même espèce ont leur labre tantôt échancré, tantôt à peine sinueux et cette différence serait en rapport avec la sexe." Arango (1878: 41) took the notched shells to be females. Wagner (1908: 129) correctly stated that it was the male which possessed the notch, but then changed his opinion (1910: 185). He was corrected by

Baker (1926: 52), and the dissections performed for this study by Turner[1] support Baker's contention that the notched shells are male. Athough Thiele (1929: 83), correctly describes the situation, Wenz (1938: 438) and Keen (1960: 288) state that the entire genus is characterized by the notch. Wagner (1910: 184) noted other features of sexual dimorphism in the shell which our examinations did not seem to justify.

Baker (1922: 62) considered *Ampullina* De Blainville a synonym of *Eutrochatella sensu stricto,* a Jamaican group. However, the only helicinids of Jamaica that compare in size with De Blainville's figure of the type, *A. striata* (1827: pl. 35, fig. 4a-c), are *Eutrochatella tankervillei* (Gray) and *Alcadia major* (Gray). But neither the description (1824: 441) nor the rather poor figure indicate either of these. There is no mention of the strong sculpture of *tankervillei,* and the aperture of *Alcadia major* is quite different.

Ampullina striata De Blainville (1824: 567) (locality unknown) has been considered to be in the genus *Viana,* but a re-examination of the figure published by De Blainville in his Manuel de Malacologie (1827, pl. 35, fig. 4a-c) indicates that it is not a member of this genus. The operculum figured (4b-c) is quite different from that of *Viana.* De Blainville shows a strong ridge on the inner face from the center margin at the parietal area and extending horizontally to the opposite margin. This morphological structure does not appear in any of several hundred opercula examined in the three subspecies of *Viana.* The whereabouts of the figured specimen (type) is unknown to us.

The range of *Viana* extends in a broad arc from the Sierra Rangel near San Cristóbal, west and south to the immediate vicinity of Guane, all within the Province of Pinar del Río, Cuba.

VIANA REGINA REGINA (Morelet)

Plate 2, figures 1-4

Helicina virginea d'Orbigny 1842 [*in*] Sagra, Hist. l'Ile de Cuba, Mollusques, 1: 241 (Intérieur de l'Ile de Cuba); *non* Lea 1834.

Helicina regina Morelet 1849, Testacea Novissima Insulae Cubanae et Americae Centralis, Paris, 1: 19 (Ad Montes Guajaibón, Insulae Cuba). [Paratypes, MCZ 146706, ex Putzey's collection.]

Helicina maculosa 'Newcomb' Jay 1850, A Catalogue of the Shells Contained in the Collection of John C. Jay, 4th ed., New York, p. 261 [*nomen nudum*].

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[1] Dr. Ruth D. Turner is in the process of preparing a detailed anatomical investigation of *Viana,* which will appear later in this series of reports.

Helicina multistriata 'Velasquez' Jay 1850 *ibid.*, p. 261 [*nomen nudum*].

Eutrochatella (*Hapata*) *regina* Morelet. Wagner 1908, [*in*] Conchylien-Cabinet, (2) 1, Sect. 18, pt. 2: 130, pl. 25, figs. 12, 13, 18, 19.

Viana regina (Morelet). Baker 1922, Proc. Acad. Nat. Sci. Philadelphia, **74**: 63, pl. 7, figs. 34-36.

Viana regina marmorata (Torre MS) Webb 1948, Foreign Land and Fresh Water Shells, St. Petersburg, Florida, p. 143, pl. 65, fig. 6.

Description. Shell moderately large, turbinate, sculptured with spiral cords of varying degrees of strength, from deeply lirate to quite smooth, crossed by weak, oblique, irregular growth lines. Color basically yellow, whitish, or light reddish purple, at times with faintly outlined spiral bands. Shell with some degree of mottling, occasionally covering the entire surface or else being confined to the spire. When such a shell is held to the light, the whitish or yellowish markings are seen to be more opaque than the base color of the shell, and they apparently constitute an added layer of shell matter on the surface. These markings, however, are so closely bound to the rest of the shell that they cannot be removed even by the most diligent scraping. Whorls 6½, moderately inflated, regularly widening; body whorl rounded. Aperture widely lunate, white near the edge, yellowish or light reddish purple internally. Outer lip entire, not reflected and not flaring, except very weakly near the insertion with the columella, and deflected downward at the base of the aperture. Peristome notch rather deep, V-shaped, narrowly rounded at the base. Parietal lip smooth, without folds, gently convex above, sharply and almost vertically descending below, barely rounded at the juncture with the basal part of the lip. Columella without a fold but with a low, oblique, rounded and slightly raised margin at the umbilical area, appearing as a slight tubercle on the outer basal edge. Shell imperforate, but with a shallow excavation just above the base of the columella. Sutures moderately impressed, faintly and irregularly scalloped by the edges of the growth lines. Operculum as in the generic description.

Height mm	Width mm		
20.5	23.0	♀	Pan de Guajaibón. Syntype.
24.5	29.5	♂	Sierra Rangel.
21.5	23.5	♂	Pico Grande, Sierra San Andrés.
23.0	25.0	♀	Sierra de Guacamaya, San Andrés.
15.5	18.2	♂	Kilometer 14, Viñales.
15.2	17.5	♂	" " "
16.5	18.5	♀	" " "

Remarks. There are many intergrading forms throughout the range of this subspecies. Some populations are composed largely of a single variety, while others are a mixture of several forms. At Guajaibón, the type locality, there exists a pale yellow form, occasionally ornamented with a more or less distinct reddish subsutural line. The shell here is moderately lirate, dull, and rather coarse to the touch. The characteristic marbling is confined to the upper whorls. At San Andrés a rather spectacular form is found. The early whorls are pale yellow but this soon gives way to a light reddish purple or roseate ground color, variously ornamented with irregular white or pale yellow marbling. This marbling is occasionally arranged in broad spiral bands distinguished by the differing nature of the spots. The ground color, as well as the marbling designs, becomes obsolete near the aperture and at the base, both of which are white. The lirations are very faint, not perceptible to the touch and barely visible under a magnifying glass, but the shell, though smooth, does not possess the brilliant sheen which occurs in some of the populations of the subspecies *laevigata.* In some colonies in the San Andrés region (e.g., El Aserradero near Caiguanabo and Puerto Escondido), yellow shells occur together with purplish ones, as well as some that have varying mixtures of purple and yellow. The marbling in both color forms covers practically the entire shell. The bands sometimes consist of a solid color and hence resemble the prominent spiral bands of the subspecies *laevigata.* Occasional populations, as at La Sierra, have both the yellow and purple colors, which, however, are very pale and appear faded, and the marbling is widely scattered over the surface. At some isolated mogotes (Bella María and Talavera near La Palma, Hoyo de los Mogotes near Viñales, La Catalina near San Diego de los Baños, Mogote del Rojero between Cayo San Felipe and Isabel María, and some of the mogotes about Kilometer 14) a dwarf form occurs, generally in some shade of yellow.

These remarks are not to be construed as having at all exhausted the range of variations of *regina.* Variations of all sorts occur, in sculpture, color, and size, sometimes in localities quite close to one another (as near Isabel María), sometimes even on a single mogote (as El Queque). It is not the purpose of this study to give a full account of all the forms in which *regina* or either of the other two subspecies occurs, or to give a detailed description of each population. Such an undertaking would lead us far beyond our original purpose.

Specimens examined. CUBA: PINAR DEL RÍO. *Viñales:* Mogote W of Kilometer 14; Mogote E of Kilometer 14; Abra de la Colmena;

Arroyo Melindre; Encinar Alto; La Laguna, Potrero Constancia; Mogote de José María García; Hoyo de la Sierra; Hato Morales; Hoyo de los Mogotes; Hoyo de los Santos; Mogote la Cañona; Constancia; Mogote Capón; Mogote Dos Hermanos. *Viñales* (*Palmarito*): Ensenada de Antonio Miranda; Vega de Lorenzo Martínez; Hoyo de Majá; Vegas de Palmarito; Ensenada Martín Miranda; El Grillo; Vega de Lorenzo. *Viñales* (*El Queque* [*Tumbadero*]): Ensenada del Valle; lower part of El Queque; Ensenada del Río; Hoyo de los Muertos; Ensenada de la Bandera. *San Andrés:* Ensenada de la Ayúa; Pasada de la Ayúa; Colmillo (or Muela) de la Vieja; Mogote La Paloma, NW of La Paloma; entrada a la Ayúa; Sitio de la Sierra; Mogote de la Tumba, Puerto Escondido; Ensenada del Corojal, Puerto Escondido; Mogote del Puerto Escondido; La Pastora, Puerto Escondido; Ensenada del Cafetal; Mogote Simón; Mogote del Indio; Pico Grande; Pico Chico; Los Caracoles; Hoyo del Infierno; Mogote Luis Diaz, Falda de Pico Chico; Mogote las Cuevitas; Hoyo Largo de San Antonio. *San Andrés* (*Canalete*): Los Hoyos; Mogote del Abra de Canalete; Ensenada de Borges; Ensenada de los Colorados; Mogote de Abraham; Ensenada de Canalete. *San Andres* (*Caiguanabo*): El Aserradero; Mogote Largo; Mogote Puertecitas; Mogote Andrés Diaz; Mogote de Caiguanabo; Abra de Caiguanabo. *San Andrés* (*Consolación del Norte* or *La Palma*): Sierra de Guacamaya; Río de la Puerta, Guacamaya; Las Vulicas; Farallón de las Avispas; Mogote de la Palma; Mogote Bella María. *San Andrés* (*Galalón*): Mogote Colmena de Piedra; Cueva del Chino; Pinalito; Las Calabazas; Mogote de Galalón; Mogote Fuerte, SW of Sierra de Galalón; Mogote Campamento; Mogote Delicias. *San Diego de los Baños:* Cueva del Indio; La Cumbre; Mogote de los Portales de San Diego; Mogote Colorado; Los Cayitos, Catalina; Mogote de los Indios; Bermejales, Sierra de la Güira; La Catalina, N of San Diego; Lagunita, Sierra la Güira; Hoyo de la Jutía, 1 km E of San Diego; Mogote el Bosque; Camino de Galalón, Sierra de la Cumbre; Soroa. *Pan de Guajaibón:* San José de Sagua, Pan de Guajaibón and Sierra Chica, S of Pan de Guajaibón. *Rangel:* Rancho Mundito; El Retiro; El Taco; La Plata; about 2 km S of Rancho Mundito, San Cristóbal; Loma Sabicú; El Aspiro; Guanibadro; about 3 km N of Santa Cruz de los Pinos.

VIANA REGINA LAEVIGATA (Pfeiffer)

Plate 3, figures 1-4

Trochatella regina Morelet, *var.* Pfeiffer 1864, Malakozoologische Blätter, 11: 106 (Cayos de San Felipe [Charles Wright]; Pan de Azúcar [Rafael Arango] [both Viñales, Pinar del Río], Cuba); Pfeiffer 1865, Novitates Conchologicae, **2**: 253, pl. 44, figs. 4, 5. [Holotype probably destroyed.] We here limit the type locality to the Cayos de San Felipe close to the town of Viñales.

Trochatella regina laevigata Pfeiffer 1865, Monographia Pneumonopomorum Viventium, **3**: 211 (Cuba).

Eutrochatella regina lyrata Torre. Hand 1927, Nautilus, **40**: 89 [*nomen nudum*].

Description. Shell similar to *regina regina*, but lacking mottling or marbling. It differs from *regina subunguiculata* in having the lip of both male and female specimens simple and not flaring.

Height mm	Width mm		
21.5	25.5	♀	Sitio del Infierno, Viñales.
22.0	23.0	♂	La Chorrera, San Vicente, Viñales.
21.0	24.0	♂	Cayos de San Felipe, Viñales.
21.0	23.0	♀	Sierra Celadas, Viñales.

Remarks. As is the case with the other subspecies, *laevigata* is variable in size, sculpture, and color pattern. This subspecies seems to have more populations in which pronounced, and occasionally quite spectacular, banding occurs, as for example the populations in several of the sierras of the Sierra del Infierno complex, at the Sitio del Infierno and at Cayos de San Felipe. The last two localities have some of the most beautiful shells in the genus. They are gleaming roseate, purplish, or bright lemon-yellow and generally have three rather broad alternate whitish bands. Many of the lemon-colored shells have a thin, dark-reddish subsutural line. As is the case with the other two subspecies, some populations consist of shells differing in color, ornamentation, and sculpture, whereas others are more or less uniform.

At Sierra del Quemado and Sierra Celadas there are populations of *subunguiculata* as well as *laevigata.* At El Queque, besides *laevigata,* populations of *regina* also occur. See remarks under *subunguiculata.*

Specimens examined. CUBA: PINAR DEL RÍO. *Viñales:* Sitio del Infierno; Mogote del Cejanal, El Abra, Sierra de Viñales; La Penitencia; Pan de Azúcar; Sierra de Pan de Azúcar; Sierra de Viñales; Cayos de San Felipe; Sierra Derrumbada; El Cuajaní; Hoyo del Majagual; Sierra Serrucha; Hoyo de la Jutía; Mogote de los Muertos; Mogote de la Vega; Mogote Pequeño; Potrero de Manuel Sánchez (near Capón). *Viñales (San Vicente):* Las Cuevitas, Finca Ancón; Llana Manacas; Mogote La Cañona (between Laguna de la Piedra and Constancia); La Guasasa; Ensenada de los Baños; San Vicente de los Baños; Puerta del Ancón; Costanera de San Vicente (*or* Ancón); Valle de Delicias; Finca Ancón; La Chorrera; Cejanal, El Abra; Punta de la Costanera; Ensenada de los Baños; Mogote Pequeño, Costanera de San Vicente (or Ancón); Cueva de José Miguel Gómez; Hoyo de Magdalena, Costanera de San Vicente; Mogote del Cao, Laguna de la Piedra; Mogote de Justo; Cueva del Río San Vicente; Sierra Gorda, Ancón; Sierra del Ancón. *Isabel María:* Mogote Isabel María; boundary between Isabel María and Cabezas.

VIANA REGINA SUBUNGUICULATA (Poey)

Plate 4, figures 1-4

Helicina subunguiculata Poey 1857, Memorias sobre la Historia Natural de la Isla de Cuba, Habana, 2: 34 (Sierra de Guane). [Lectotype, here selected, MCZ 73672.]

Description. Shell similar to the typical form but differing in the nature of the lip, which in the female is expanded and slightly reflected, in the male is extended into a claw-like structure which is sometimes expanded, especially at the base where it joins the columellar margin.

Height mm	Width mm	
24.0	24.5	Sierra de Guane. Syntype.
22.0	24.0	Punta de Sierra de Guane.
23.5	26.5	Sierra San Carlos, Luis Lazo.
25.0	28.5	Sierra Celadas, Viñales.

Remarks. In size, the shells vary from the medium-sized ones found at the type locality and near Mendoza to the rather large ones from Luis Lazo and especially on the Sierra Celadas of the Sierra Viñales complex. The shells at the type locality are white or pale yellow in color, and sculptured with spiral lirations of moderate strength so that they are moderately rough to the touch. At La Muralla on the road to Luis Lazo the shells are larger, quite smooth, although with very faint, widely spaced lirations, pale lemon-yellow, and frequently ornamented with a red subsutural band. These shells also display some degree of whitish banding and mottling on the spire as in some populations of *regina,* but their large size, and especially the flaring lip in the female, and the strong and at times flaring ungulation in the male, reveal their true subspecific standing. At Luis Lazo the shells are similar, the lirations somewhat stronger, and many purplish or roseate specimens appear. At Gramales and especially on the Sierra Celadas a population of large, heavy, smooth, generally pale yellow shells occurs, with a strongly flaring lip and white bands that vary from moderately broad to quite narrow. Occasionally a purplish specimen occurs. This population seems to share the Sierra Celadas with a typical broadly banded, purplish colony of *laevigata*. In all likelihood the two subspecies, as at Sierra del Quemado, live in isolated areas in the sierra. It must be borne in mind that the sierras of the Sierra Viñales complex do not necessarily constitute a continuity of ecological conditions. Isolation of populations sometimes occurs as the result, among other things, of gaping chasms or hoyos that present effective barriers even to calciphiles like *Viana*. A population of stenomorphs, light purplish in color, of this subspecies lives on a mogote at the border between Isabel María and Luis Lazo.

Specimens examined. CUBA: PINAR DEL RÍO. *Guane:* Sierra Paso Real; Sierra de Guane; Mogote 1 km N of Mogote Punta de la Sierra; Punta de la Sierra; Mogote near Punta de la Sierra. *Luis Lazo (Sumidero):* Entrada a Sumidero; Ensenada de los Barrios; La Picapica; Ojo de la Palma, Finca "La Güira." *Luis Lazo:* La Estrechura; Valle de San Carlos; Sabanas Llanas; Sierra Los Acostas; Valle de Luis Lazo (Valle de San Carlos [El Potrerito]); La Claraboya; La Güira; Mogote Central; El Junco. *Isabel María (Guamá):* El Guamá; Hoyo El Guamá; Mina El Guamá. *Isabel María (Cabezas):* Ensenada Chica; Valle Cabezas; Mogote del Cementerio; Ensenada los Burros.

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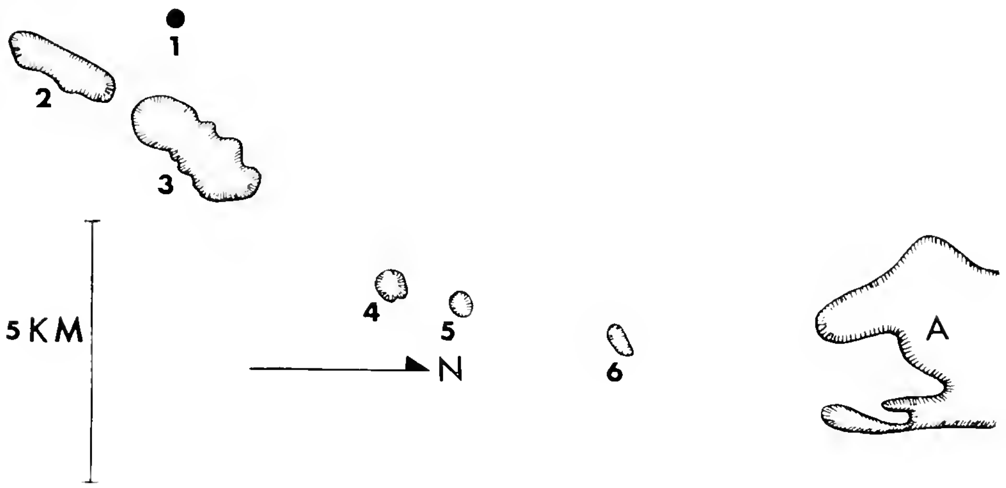

Map 2. Sierra Paso Real to Sierra San Carlos.[1]
1, Guane (town); 2, Sierra Paso Real; 3, Sierra de Guane; 4, Los Portales; 5, La Muralla; 6, Tenería.
A. Sierra San Carlos.

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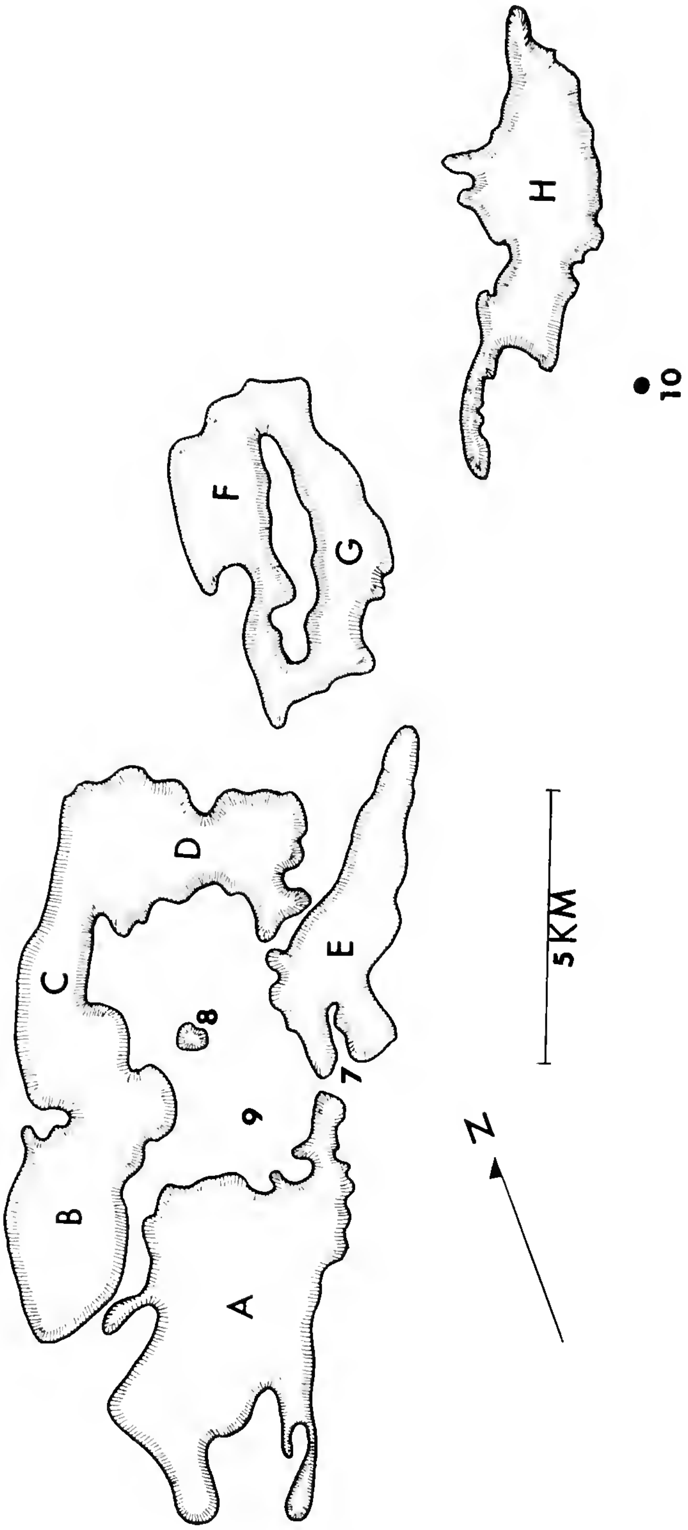
[1] Maps 2 to 5 were redrawn from those given by Torre and Bartsch (1938) and the military (topographic) maps of Cuba (1933-1934).

Map 3. Sierra de San Carlos to Sierra del Quemado.
A, Sierra de San Carlos. B, Sierra de los Acostas. C, Sierra de Francisco. D, Sierra Resolladero. E, Sierra Sumidero; 7, La Estrechura; 8, Mogote Central; 9, Potrero de Luis Lazo. F, Sierra Gramales. G, Sierra Cabezas. H, Sierra del Quemado; 10, Isabel María (town).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Map 4. Sierra del Quemado to Sierra Guacamaya.

H, Sierra del Quemado. I, Sierra Celadas; 11, Santo Tomás (town). J, Sierra Pan de Azúcar. K, Sierra Martillo. L, Sierra del Infierno; 12, Cayos de San Felipe[1]; 13, El Guamá; 14, Mogotes de Km 14. M, Sierra Penitencia. N, Sierra El Abra. O, Sierra Viñales; 24, Mogote Palmarito; 25, Hoyo Magdalena. P, El Queque; 17, Mogote Vigil; 18, Mogote Rojas; 19, Abascal; 20, Dos Hermanos; 21, Viñales (town); 22, Hoyo de los Santos; 23, Ensenada Miranda; 26, Puertecites; 27, Mogote Capón. Q, La Chorrera; 28, Hoyo de Jaruca; 29, Laguna de la Piedra; 30, Mogote Jutía; 31, Fogón de los Negros; 32, West ridge of the Sierra San Vicente; 33, East ridge of the Sierra San Vicente; 34, Baños de San Vicente. R, Sierra Galeras; 15, Pan de Azúcar. S. Sierra Ancón; 61, San Cayetano (town). T, Sierra San Andrés; 35, Mogote Mina; 36, Rinconada; 37, La Jagua; 38, Asiento de la Jagua; 39, Mogote de la Jagua; 40, Hoyo Corto de San Antonio; 41, Canalete (town); 42, San Andrés (town); 43, Mogote Fonte; 44, Mogote de Canalete; 45, Mogotes de Canalete; 46, Ensenada de la Ayúa; 47, Pasada de las Escaleras; 48, Puerto de San Andrés; 50, Pico Grande; 51, Colmillo de la Vieja; 53, Sitio de la Sierra; 54, Mogote Bella María. U, Sierra Gaucamaya; 55, Mogote Grande; 56, Caiguanabo; 57, Pinalito; 58, Mogote Largo; 59, Mogote Angelena; 60, Mogote Mamey.

Localities numbered 49 and 52 represent place names that could not be located on any maps available to us.

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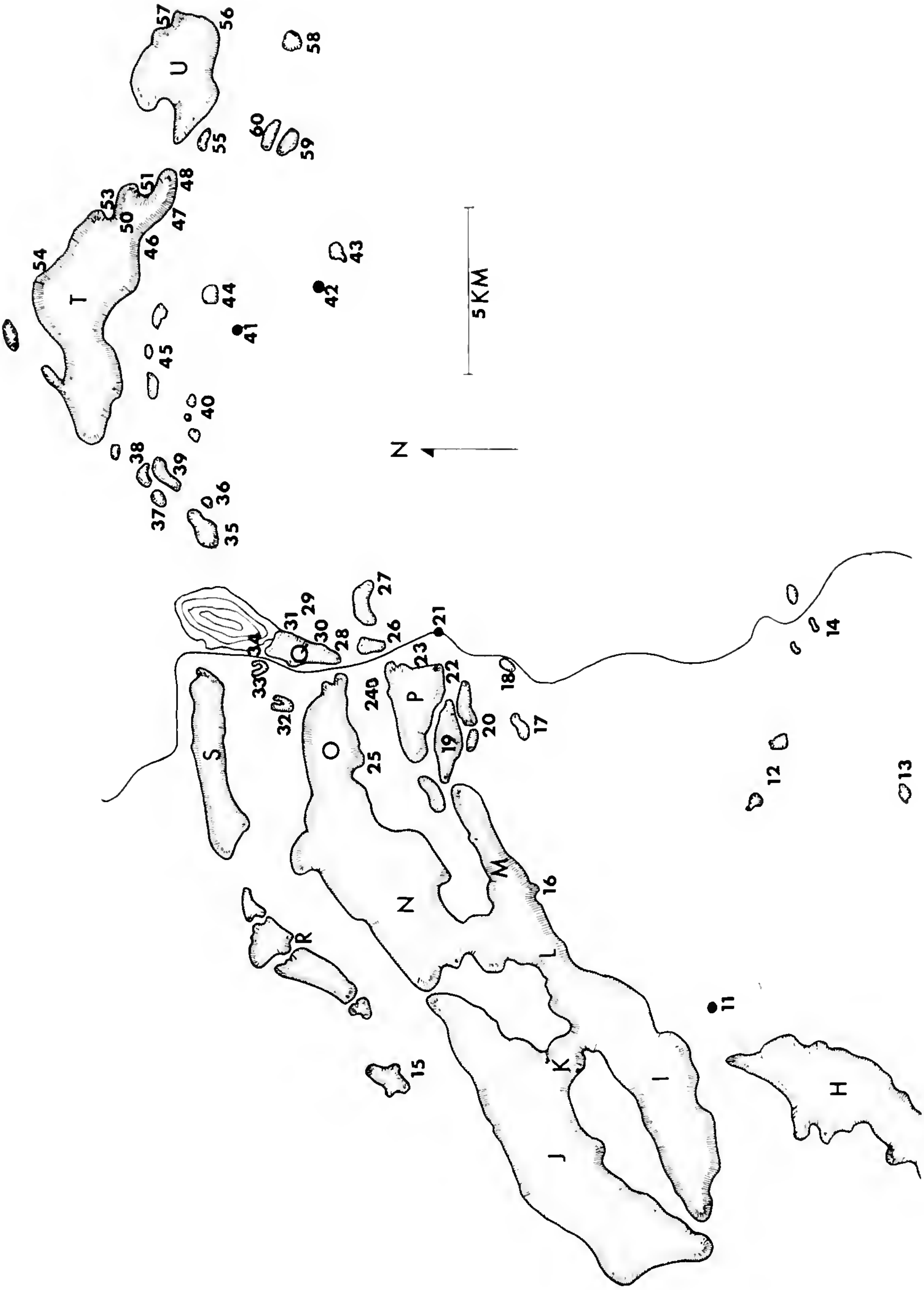
[1] Not to be confused with the small islands "Cayos de San Felipe" off the northwest coast of the Isla de Pinos.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Map 5. Sierra Guacamaya to Sierra Rangel.
U, Sierra Guacamaya. V, Sierra Galalón; 61, Caracoles; 62, Mogote Colmena de Piedra; 63, Los Portales. W, Sierra La Güira; 64, San Diego de los Baños (town); 65, Los Cayitos de Catalina; 66, Mogote Bosque; 67, La Cumbre. X, Pan de Guajaibon. Y, Sierra Rangel.

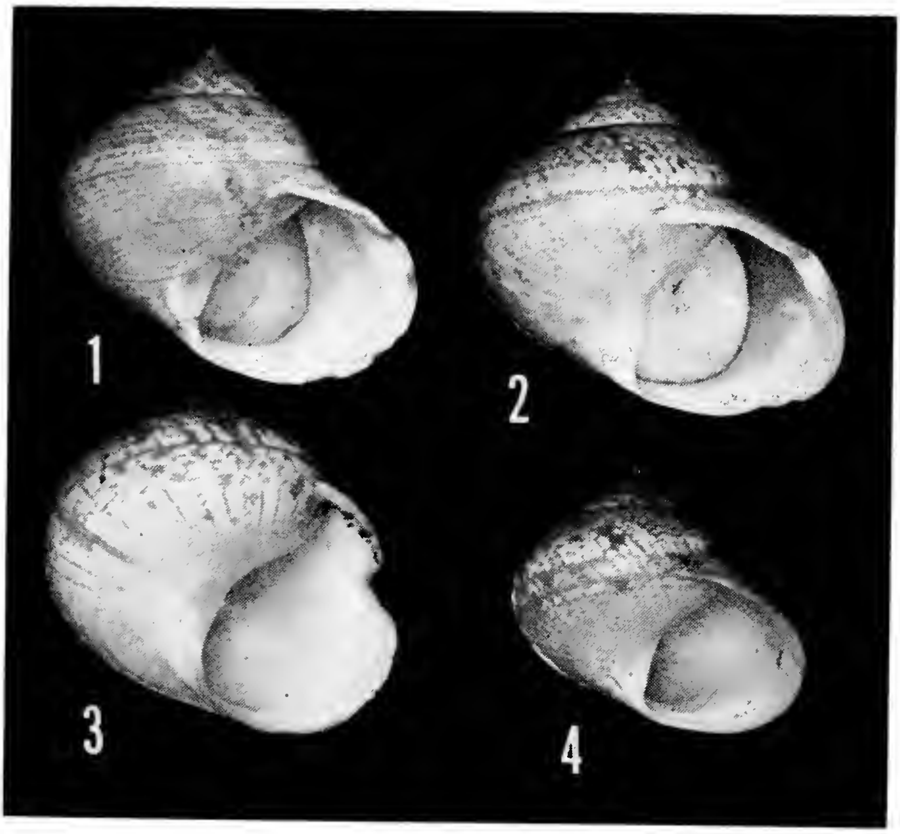

PLATE 2

Viana regina regina (Morelet)

Fig. 1. Pan de Guajaibón, Consolación del Norte, Pinar del Río (paratype, MCZ 146706♀).

Figs. 2, 3. Pico Grande, Sierra de San Andrés, Consolación del Norte, Pinar del Río (MCZ 256282♂).

Fig. 4. La Catalina, San Diego de los Baños, Consolación del Sur, Pinar del Río (MCZ 126684♀) (all 2 X).

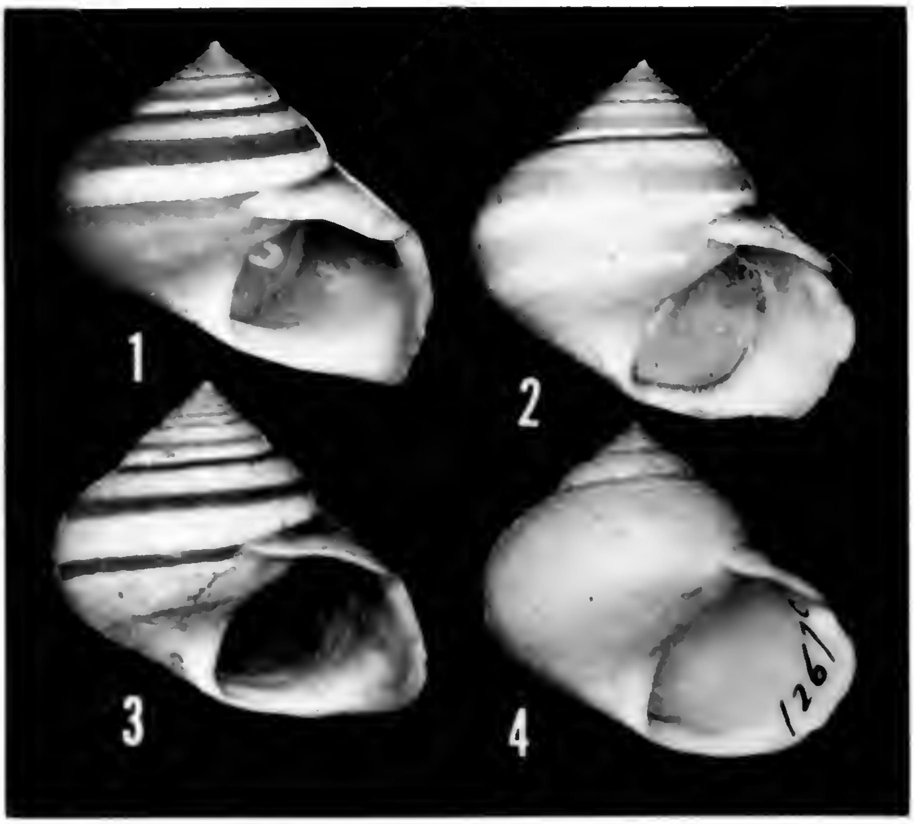

PLATE 3

Viana regina laevigata (Pfeiffer)

Figs. 1, 2. Cayos de San Felipe, Viñales, Pinar del Río (Topotypes, MCZ 126716 ♂).

Fig. 3. Sierra Celadas, Viñales, Pinar del Río (MCZ 256173 ♂).

Fig. 4. Pan de Azúcar, Viñales, Pinar del Río (MCZ 126703 ♂) (all 2 X).

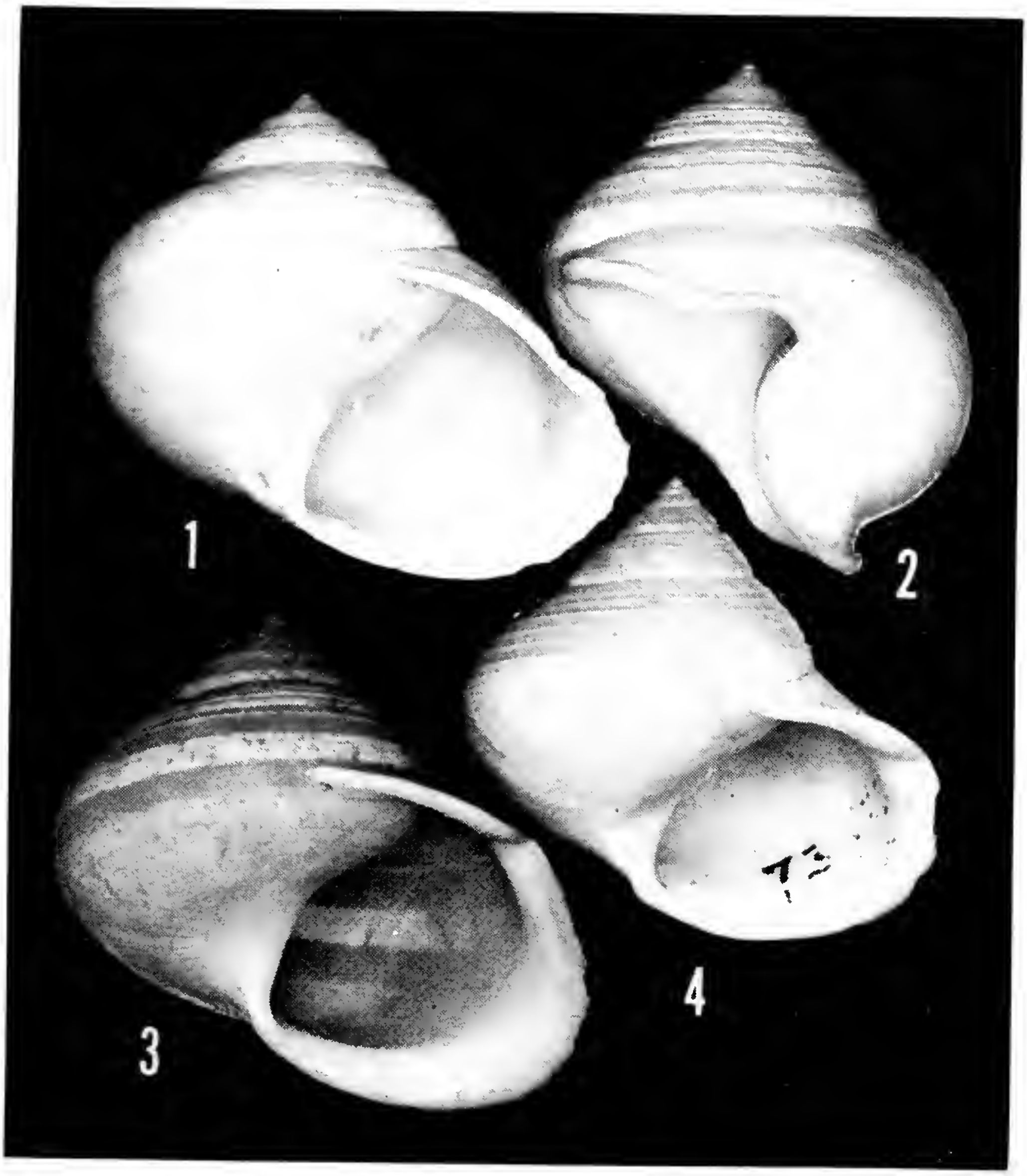

PLATE 4

Viana regina subunguiculata (Poey)

Fig. 1. Sierra Celadas, Santo Tomás, Viñales, Pinar del Río (MCZ 256342 ♂).

Fig. 2. Sierra Celadas, Santo Tomás, Viñales, Pinar del Río (MCZ 256342 ♂), to show the outer peristome notch in the male.

Fig. 3. Valle San Carlos, Luis Lazo, San Juan y Martínez, Pinar del Río (MCZ 256335 ♂).

Fig. 4. Sierra de Guane, Guane, Pinar del Río (Lectotype MCZ 73672 ♂) (all 2 X).

B R E V I O R A

Museum of Comparative Zoology

Cambridge, Mass. 11 October, 1968 Number 299

WHAT IS *LUMBRICUS EISENI* LEVINSEN, 1884 (LUMBRICIDAE, OLIGOCHAETA)?[1]

G. E. Gates[2]

Abstract. Levinsen's species, *eiseni*, after being in the synonymy of an unrelated form and in three lumbricid genera, is excluded from *Bimastos*, as defined by characters less liable to rapid evolutionary modification than those of the genitalia on which the classical system of the Oligochaeta (Michaelsen, 1900 — Stephenson, 1930) was mainly based. The species, now more adequately characterized, cannot go into any other lumbricid genus because of current ignorance of somatic anatomy in their type species. Relationships suggested by available anatomical data are with *Allolobophora chlorotica* and, less closely, with *Dendrobaena rubida* and *Lumbricus* spp.

As the references below show, no agreement has been reached as to the status of Levinsen's species and as to its generic affiliations. The taxon, like other more or less widely spread lumbricid anthropochores as well as most endemics of the family, never was adequately characterized. Although much less material could be procured than was desired, study of new material has enabled the following contribution toward a solution of the problem.

"LUMBRICUS EISENI" Levinsen, 1884

Lumbricus eiseni Levinsen, 1884, Vidensk. Meddel. Naturhist. Forhandl. Copenhagen, (4) **5**:311, 241. (Type locality, Deer Garden, Copenhagen. Types, 5, in the Copenhagen Museum.)

Allolobophora (Dendrobaena) eiseni,-Friend, 1892, Jour. Linnean Soc. London, (Zool.), **24**:302.

Helodrilus (Bimastus) eiseni,-Michaelsen, 1900, Das Tierreich, **10**:503.

Bimastus eiseni, Friend, 1911, Zoologist, (4) **15**:145.

Eisenia parva f. *typica* (part) Pop, 1950, An. Acad. Romane, Sect. Sti. Geol. Geogr. Biol., (A) **1** (9):89.

Eisenia eiseni,-Graff, 1953, Regenwürmer Deutschlands, p. 27.

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[1] From research financed by the National Science Foundation.

[2] Zoology Department, University of Maine, Orono, Maine, U.S.A.

SPECIMENS EXAMINED

Channel Islands. Herm, under rock above tide mark, June 24, 1925, 1-0-0. G. E. Pickford.

South Africa. Cape Province. Cape Peninsula. Kirstenbosch, rotting stump, October 29, 1925, 5-0-4. Table Mountain, Window Gorge, rotting log at 400 feet, July 30, 1926, 0-0-9. Brockenhurst, Queen's Bower, April 2, 1925, 0-0-1. G. E. Pickford.

INTERCEPTIONS BY U.S. BUREAU OF PLANT QUARANTINE

Eire. From soil with twenty-nine narcissus bulbs and two bundles of lily plants, in baggage on plane, arriving at Boston, June 22, 1964, 0-0-1.

Scotland. From heather plants, in plane, arriving at New York, October 26, 1949, 0-0-1.

Germany. From cabbage, in ships stores on Norwegian M/S Lancing, arriving at Savannah, Georgia, October 29, 1964, 0-0-1.

Portugal. From soil with five azaleas, five ferns, two orchids, in baggage on plane, arriving at Boston, May 21, 1965, 1-0-0.

Azores. From soil with one begonia, in baggage on plane, arriving at Boston, June 18, 1965, 0-0-1.

From roots of plants of *Citrus* sp., in baggage on plane, arriving at Boston, June 18, 1965, 2-0-0.

DESCRIPTION

External characteristics. Segments, 79-112 (*cf.* Table 1). Color, brown, slate to almost black but never red, restricted to dorsum except in ii-vi or vii, most obvious anterior to the clitellum, usually lacking or very sparse in buccal and anal segments. Body subcircular in cross section posteriorly. Prostomium, tanylobous (all).

Setae, all present in ii, the *d* setae at or below mL anteriorly but posteriorly above that level. BC usually $< AA$ throughout postclitellar region where $DD < \frac{1}{2}C$.

Nephropores, obvious. On one South African worm they are above *B* on the left sides of x-xiii, xv, xvi, xix-xx, xxvi, on the right sides of ix-xi, xv, xxii-xxvi, xxix. Other pores of that worm, in the region of iv-xxix, are well above *D*. Pores of xv-xvi, except on one other worm (left pore of xv not found), were lateral to *B*. Pores may be at the same level on one side for three, four, or five consecutive segments, but on the opposite side asymmetry is occasional. Pores of xii have been seen (rarely) just below *C*. The arrangement throughout most of the axis can be characterized as: irregularly alternating, usually between two levels, one slightly lateral to *B* and another about midway between *D* and *mD*, with occasional intrasegmental asymmetry.

First dorsal pore, at 5/6 (21 specimens), occasionally smaller than the one at 6/7.

Female pores, slightly lateral to *B*, equatorial in xiv. Male pores, minute, at or median to m*BC*, each laterally in a small cleft at eq/xv. Male tumescences, confined to xv and to median half of *BC*.

Clitellum, red (formalin preservation), saddle-shaped, reaching ventrally to or nearly to *A*, or mostly annular, in xxiv-xxxii but restricted to *DD* in xxiv and xxxii (13), xxiv-xxxiii/n (1), xxv-xxxi (2, possibly not fully developed). Even at apparent maximal development the clitellum is thinner in *AA* than laterally and intersegmental furrows still are recognizable ventrally from m*BC*.

Genital tumescences, often conspicuous, without distinct boundaries, transversely elliptical, including *a,b,* in xvi (27), xxiv (2), xxiv-xxv (1), xxv (26).

Internal anatomy. Septa, none thickly muscular, 10/11 bulged anteriorly and 11/12 posteriorly by the calciferous gland, the coelomic cavity of xii, xiii and xiv quite small. Pigment, lacking in peritoneum, present anteriorly in the longitudinal muscle band at mD but disappearing behind the clitellum, associated with or in circular muscle layer, apparently brown, yellow brown, or dark brownish red. Pharyngeal glands to 8/9.

Brain, circumpharyngeal connectives and subpharyngeal ganglion all left in iv (19), sometimes well posteriorly, by a transverse section exactly along 3/4.

Ventral bundles of the longitudinal musculature, according to Prof. Harman (*in litt.*), can be characterized as fasciculate, the pinnate arrangement so characteristic of some species of *Lumbricus* being lacking. The cells form compact "Kastchen" ventrally and a compact band dorsally. Ventrally the bundles resemble those of *A. chlorotica.*

Calciferous sacs, in x, elongated horizontally rather than vertically, anteriorly or anterolaterally directed, reaching to or nearly to 9/10, apparently opening posteriorly into gut lumen at level of insertion of 10/11. Calciferous lamellae, extending nearly to anterior end of sac but in x small and of squarish shape. Gut much widened, rather bead-shaped and with vertically slit-like lumen in xi, narrower (half as thick as in xi) and of nearly uniform calibre through xii-xiv. A deep internal constriction (or vertical groove) on one or both sides at or slightly behind insertion of 11/12. Calciferous lamellae, large and rectangular in xi, but behind insertion of 11/12 quite small, not reaching 12/13 (if present posteriorly too small to be recognized in dissections). The inner lining of the gut was rotted away in slightly macerated specimens so as to reveal lamellae with diagrammatic clarity. Intestinal origin, in xv (20). Gizzard, in xvii (20), the layer with brilliant muscular sheen in horizontal sections narrowing behind insertion of 17/18 and not reaching 17/18. A postgizzard valve, if present, is relaxed in each worm but the gut is somewhat narrowed at 18/19 or in xix. Typhlosole, beginning gradually in region of xx-xxiv, at first a low horizontal band, then becoming vertically and rather thickly lamelliform. A slight longitudinal groove may be recognizable on the ventral face at mV, or, if not, a slight longitudinal flange may be visible on each side. (Condition does not allow a more precise characterization.) The typhlosole ends, abruptly in unamputated specimens, in xc-xcvii (Table 1), leaving 8-15 segments (proctodeal?) atyphlosolate.

Dorsal blood vessel, continued onto pharyngeal bulb. Subneural, adherent to nerve cord. Extra-oesophageal trunks, median to hearts, posteriorly in xii passing up to dorsal trunk (21). Hearts, present in viii-xi (22). Quite slender vessels at sites (in other species) of hearts of vii were traceable to ventral trunk only in three worms in each of which only the dorsalmost quarter is heart-like.

Nephridia, vesiculate. Bladders, each in shape of a long U-shaped loop, from *A* well into *DD*, both limbs of the loop of about the same length, posterior limb passing into parietes near *B*. The one other major loop is longer than the bladder loop.

Holandric. Testes, flattened horizontal discs sometimes rather fan-shaped or saccular and pyriform. Male funnels, crenellate, large. Male deferent ducts, rather slender, almost straight, slightly sinuous, with several, very short, u-shaped loops, once a single long hairpin-loop, or coiled into a ball, loops or coils up to a millimeter away from funnel septum. Ducts of a side, uniting posteriorly in xii, continued to eq/xv across top of atrial gland (latter developed after penetration of duct into parietes?) or disappearing from sight at edge of gland. Seminal vesicles, rather small to small but not vestigial, vertical or dorsal, soft, without obvious lobing, in xi-xii (15). Anterior vesicles, flattened in the space between septum 10/11 and the anterior face of the calciferous gland.

Ovaries, often large and then reaching up to level of dorsal face of gut, filled except in proximal quarter or so with large ova, each with a single egg string containing one to three ova. Ovisacs, with one to five ova which were easily released by teasing, especially those in a distal portion. Oviducts, rather thick passing into parietes lateral to *D*.

Atrial glands (14 clitellate worms), confined to median portion of *BC* or reaching nearly to *C*, flat or of a rather low dome-shape, usually with a cleft at eq/xv and another at insertion of 15/16, reaching to or well toward 16/17. TP glands, lacking (all). GS follicles, large, conspicuously protuberant into coelomic cavities, genital setae elongated and otherwise modified. Follicles of ventral couple of xv not as much enlarged as the others. Supraparietal glands around GS follicles, lacking (all). Follicles of all ventral couples, from the clitellum anteriorly, larger than those of the lateral setae.

Variant specimen. Clitellum, light pink rather than red, reaching little below *C*, but of near maximal thickness in region of m*D* except at intersegmental furrows which are still obvious even there. Male funnels, smaller than usual but crenellate, with very slight iridescence. Male deferent ducts pass into parietes at eq/xv. Atrial glands lacking (no rudiments recognizable in longitudinal musculature). GS follicles smaller than usual. Distal two-thirds of ovaries with apparently mature ova. No ova in ovisacs.

The clitellum probably had not attained full development. Absence of atrial glands does not, however, appear to be attributable to immaturity. Hence the worm may be of a strain (possibly with obligatory parthenogenesis and markedly reduced spermatogenesis) in which the atrial glands already have been lost and in which genital setae as well as tumescences are disappearing. Elimination of genital tumescences and genital setae would result in a state similar to that of *Bimastos* species.

Reproduction. Spermatophores were present externally in clitellar region of two worms but no iridescence was recognized in the opaque matter within the transparent cases. Spermatozoal iridescence was lacking on funnels of one worm but on those of other clitellate worms does not seem to be as brilliant as in species with obligatory cross-breeding, and was not recognized in male deferent ducts. Sparse maturation of sperm is associated, in some lumbricids, with parthenogenesis. Pyriform testes are unusually soft, much of the interior filled with a watery fluid in which there are many morulae but only a very few sperm. Uniparental reproduction has been demonstrated for this species by Evans and Guild (1948).

Bimastos eiseni is diploid, 2n = 32, according to Muldal (1952:61). Parthenogenesis is not, however, contraindicated by the diploidy, that method of uniparental reproduction being obligatory (*idem*:66) in diploid individuals of *Octolasion tyrtaeum* (Örley, 1881).

Remarks. Soil particles of any sort were completely absent from guts of each of these worms, the lumen being filled with brown organic matter.

Distribution. Ireland, Scotland, England, Channel Islands, Sweden, Denmark, Germany, Poland, Belgium, Czechoslovakia, France, Switzerland, Austria, Italy (including Sicily), Jugoslavia, Albania, Bulgaria, Portugal.

Azores, Madeira, Canary Islands, South Africa, St. Helena. India (Western Himalayas only), New Zealand (including Stewart Island).

The extra-European records show that the species has been frequently transported by man with many successful colonizations. Absence from the Americas where so many other lumbricid anthropochores are well established is puzzling. In Europe, presence above the southern limit of Quaternary glaciation may also be a result of unintentional human carriage. The original home of the species is unknown. It must have been somewhere in Eurasia but how much of the distribution in southern Europe is fortuitous, remains to be learned.

The species has been called cosmopolitan (Omodeo, 1950:5) and Euro-American (Omodeo, 1961, table). The first adjective hardly seems applicable to a species absent from all Americas, most of Africa and all of Asia except for a couple of localities in the western Himalayas. The second characterization is inapplicable.

Systematic relationships. The clitellum is shorter posteriorly than in English definitions (Cernosvitov and Evans, 1947; Gerard, 1964). Paucity of data about individual variation in *eiseni* at present obviates further discussion of the differences.

The species does not belong in *Bimastos* as that genus now (Gates, in press) is defined. The calciferous sacs of segment x suggest relationships with *Lumbricus, Dendrobaena rubida* and related species (but certainly not *D. octaedra* and related species), as well as *Allolobophora chlorotica.* Further evidence is provided by the similarity, in each taxon, of nephridial vesicles and nephropore locations. Many characters provided by those and other somatic systems now seem resistant to rapid evolutionary modification and so are of greater systematic importance than the more easily changed genitalia on which classical specialists so much relied.

The purple red pigment by which *Dendrobaena, Eisenia* and *Lumbricus* were defined (Pop, 1941) is lacking in *chlorotica* and *eiseni.* The longitudinal musculature of *Lumbricus* spp. and of *D. rubida* (also closely related species?) is pinnate in cross-section rather than fasciculate as in *eiseni* and *chlorotica.* Atrial glands (ignored by classical authorities) are indeed present in *D. rubida* and related species just as in *eiseni* and *chlorotica* but are lacking in all species of *Lumbricus* studied by the author. Those differences seem to suggest that *chlorotica* and *eiseni* may be more closely related to each other than either is to any of the other above-mentioned taxa.

Then, should *eiseni* be transferred to *Allolobophora* of which *chlorotica* recently was made the type species? If the two species do belong in the same genus, that is where *eiseni* seemingly should go. *A. chlorotica,* however, differs from every one of the common allolobophoras by its calciferous sacs, by the presence of well developed atrial glands (lacking in every one of the common allolobophoras), as well as by other characters. Information now available indicates that: 1) *Enterion chloroticum* Savigny, 1826, should not have been designated the type of *Allolobophora.* 2) All of the common allolobophoras, if that type designation in some way cannot be nullified, must go into another and possibly new genus.

The common species of the classical *Allolobophora* are now widely distributed throughout much of the world. They successfully colonized many areas to which they were introduced and even now are spreading, and being spread both accidentally and deliberately, through considerable areas of Australia and New Zealand. Those same species also have been widely used in experiments. *A. chlorotica* and *B. eiseni,* on the contrary, were much less often transported, have not colonized so extensively, are much less common, and only rarely have been studied experimentally.

Attention was directed on two previous occasions (Gates, 1958a, b) to the fact that *eiseni* does not belong in the American genus *Bimastos,* primarily in the hope that some interest in the problem would thereby be aroused on the part of those who have access to more plentiful material. Because of our ignorance of so much essential data for a large majority of lumbricid species, no nomenclatural changes are made herein.

The single North American anthropochore, *Bimastos parvus* (Eisen, 1874), is not of the same genus as *eiseni* and just as obviously does not belong in *Eisenia.* What *Eisenia parva* of sundry authors was, probably can only be determined from an examination of the specimens.

Parasites. Nematodes from coelomic cavities of the Scotch worm, according to Dr. S. Prudhoe of the British Museum, probably are *Dicelis filaria* Dujardin 1845. Nematodes from the ventral blood vessel in x-xiv of a Channel Islands juvenile were identified by Dr. Maybelle Chitwood as larvae of *Spiroptera turdi* Molin by Cori, 1898.

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TABLE 1

Typhlosole termination and segment number in "*Lumbricus eiseni*"

Serial Number	Typhlosole ends in	Atyphlo-solate segments	Number of Segments	Remarks
1	70	9	79	Posterior amputee*
2	74	7	81	Posterior amputee*
3	82-85	3	88	Posterior amputee*
4	80-86		86	Posterior amputee*
5	88	11	99	Channel Islands
6	90	9	99	
7	90	13	103	
8	91	13	104	
9	92	9	101	
10	92	12	104	Posterior amputee*
11	92	15	107	
12	93	12	105	
13	95	8	103	Posterior amputee*
14	96	13	109	
15	97	15	112	

Specimens from South Africa unless otherwise indicated.

* After loss of the posterior end, the presently terminal metamere had been reorganized and now looks much like a normal anal segment. Proof of its original, preterminal position is provided by vestiges of former apertures of setal follicles. The latter were lysed after dehiscence of their setae.

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CONTRIBUTIONS TO A REVISION OF THE LUMBRICIDAE. III. *EISENIA HORTENSIS* (MICHAELSEN) (1890).[1]

G. E. Gates[2]

Abstract. The classical system of the Oligochaeta (Michaelsen, 1900-Stephenson, 1930) and proposed neoclassical revisions, did not permit definitive conclusions as to disposition of a taxon variously known as var. or *f. hortensis* which has been in each of five lumbricid genera. Characters less liable to rapid evolutionary modification than those of the genitalia, on which previous systematics primarily had been based, allow inclusion of the taxon, as a distinct species, in a genus recently redefined in terms of formerly neglected somatic anatomy. Parthenogenesis may be facultative in some lines. Evolutionary developments now under way in *hortensis* parallel some of the degradations in genital anatomy associated, in *D. rubida,* with parthenogenesis and male sterility. Characteristics of an undegraded amphimictic morph are predicted. Abnormalities are characterized. To the distribution, as previously known, are added Ireland and Greece.

Disagreements as to systematic status and generic affiliations of various species (one example provided by the synonymy below) indicate a need for revision of lumbricid classification. Even widely spread anthropochores, that usually, though mistakenly, are believed to be adequately characterized systematically, need a searching reinvestigation.

A single Irish specimen that arrived on St. Patrick's day provided a clue to a possible solution of some of the problems hitherto associated with *"dendroidea."*

LUMBRICIDAE

EISENIA Malm, 1877

EISENIA HORTENSIS (Michaelsen, 1890)

Allolobophora subrubicunda f. *hortensis* Michaelsen, 1890, Jahrb. Hamburgischen Wiss. Anst., 7: 15. (Type locality, Hamburg. Types, originally in the Hamburg Museum.)

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Allolobophora (*Notogama*) *veneta* f. *hortensis* Michaelsen, 1900. Abhandl. Naturwiss. Ver. Hamburg, 16: 12.

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Allolobophora (*Eisenia*) *veneta dendroidea* Friend, 1909, Gardener's Chronicle, 46: 243 (Type locality, St. James Garden, Malvern, Worcestershire, England. Types, in the British Museum.)

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Eisenia veneta var. *hibernica* f. *dendroidea* + *E. v.* var. *hortensis* Cernosvitov and Evans, 1947, Linnean Soc. London, Synopses of the British Fauna, No. 6: 25.

Dendrobaena hortensis (part ?) + *D. h. dendroidea* Omodeo, 1955, Ann. Ist. Zool. Univ. Napoli, 7: 6, 8. (Excluding *D. hibernica*.)

Eisenia veneta var. *hibernica* f. *dendroidea* Gates, 1958, Ann. Mag. Nat. Hist., (13) 1: 34. (Name of the taxon should have been enclosed by quotation marks!)

Dendrobaena veneta var. *hibernica* f. *dendroidea* + *D. v.* var. *hortensis* Gerard, 1964, Linnean Soc. London, Synopses of the British Fauna, No. 6 (2d ed.): 39.

Bimastos veneta Causey, 1953, Proc. Arkansas Acad. Sci. 6: 47.

SPECIMENS EXAMINED

Oregon. Yamhill County. McMinnville, kitchen drain, August 11, 1944, 0-0-6. Backyard, March 12, 1945, 0-1-1. Backyard, brought out by wash water, October 31, 1945, 0-0-1. Chicken yard, under cow manure, November 14, 1945, 0-1-0, November 23, 1945, 0-4-10. Under wet paper carton on back porch, January 10, 1946, several specimens. Backyard, December 1, 1947, 0-1-7. D. McKey-Fender.

California. San Francisco County. Arboretum of Golden Gate Park, March 28, 1951, 0-0-2. H. B. Leech per D. McKey-Fender.

Ohio. Trumbull County. Masury, greenhouse, 0-0-2. W. R. Murchie.

Virginia. Giles County. Goldbond, sawdust, August 21, 1955, a number of specimens. W. A. Harman.

Italy. Naples, November 23, 1925, 0-0-2. Posillipo, October 7, 1925, 0-0-7. G. E. Hutchinson per G. E. Pickford.

India. Darjiling, Northpoint, at *ca*. 6250 feet, June 1945 0-1-38.

INTERCEPTIONS BY U.S. BUREAU OF PLANT QUARANTINE.

Ireland. From 25 pounds of wood duff with seeds of *Crataegus oxycanthus* in mail arriving at Hoboken, November 1, 1963, (?)-1-0.

Greece. From soil with 25 unidentified herbs in baggage on plane arriving at Boston, August 28, 1962, 6-0-0.

DESCRIPTION

External characteristics. Size, 26 by 1½ mm (Ireland), 26-32 by 2-2½ mm (Maine, New York), to 22 by 2½ mm (Greece), to 37 by 2+ mm (Ohio), 42-54 by 2½-3 mm (Naples), width measured in the clitellar region not always at maximal tumescence, thickness of adults near hind end 1½ mm. The body is dorsoventrally compressed behind the clitellum and almost oblong in transverse section, ventral and lateral sides flat, the dorsum slightly convex. The *b* and *d* setae are at the four corners of the body. Segments, 42, 50, 55, 56, 60 (2), 64 (2), 69 (2), 70 (2), 74, 76, 77, 81, 82, 83, 84 (2), 85, 86 (2), 88, 90 (3), 92 (3), 94 (3), 95 (7), 96 (4), 97 (5), 98 (4), 99 (2), 100 (3), 101 (2), 102 (3), 103 (4), 104 (2), 105, 108, 115 (2), 124, 126, 130. The mean number of segments for 69 of the specimens is 90.7536, with a standard deviation of 17.4266 and a standard deviation of the mean of 2.0979. A large majority of unamputated worms have segments in a range of 90-105 which may be more useful systematically than the computerized figures. Worms with 115-130 segments were from Maine greenhouses in which they might almost be said to have been force-fed. Color, unrecognizable after alcohol preservation, otherwise light to bright red, reddish, restricted to dorsum and lacking below *C* except in front of xv and near the hind end where the ventrum may also be colored. In some Greek worms, color is in discontinuous unpatterned areas. Prostomium, epilobous, tongue open (all).

Setae, present from ii where none usually are lacking though sometimes hard to recognize, not closely paired, width of *AB* and *CD* somewhat variable but *CD* slightly $<$ or $>$ $AB < BC <$ or $>$ $AA < DD$ which is of course $<$ ½C, the *c* setae often seeming to be about at mL. In some worms, *AB* is ca. $=$ ½*AA* and slightly $<$ *BC*. Nephropores, inconspicuous, in xv-xvi at or just above *B* (39 specimens), one pore of xv at *D* (1), one pore of xvi at *D* (1), both pores of xiv at *D* (4), at *B* (10), one of xiv at *B* the other at *D* (22), usually unrecognizable in iii-vi or vii. Nephropores, at *B* on left sides of 17th, 19th, 21st, 24th, 26th, 29th, 30th, 33d, 34th, and on the right sides of the 17th, 23d, 25th, 27th-29th, 31st-33d segments (No. 1), on left sides of 14th-20th, right sides of 15th-17th, 19th. 20th segments (No. 2). On the left side of No. 3 the following locations were noted, at *B*, 35th-40th, 52d, 57th, 60th, 61st, 64th, 65th, at *D* in the 34th, 42d-51st, 53d-56th, 58th-59th, 62d-63d. Pores on the opposite sides of those same segments more often than not were in the alternate location. Both pores of vi were in *CD*, one Italian worm on which the right pores of 7th, 8th, and 11th segments were near *B*, of 12th at *D*, but those of 13th-17th in *BC*. Nephropores, just above *B*, on left sides of 7th, 8th, 11th, 14th-16th, 18th-22nd, 24th-32d, on the right side of 8th, 9th, 12th-15th, 17th-34th (Naples, No. 4), on the left of 7th-10th, 12th, 13th, 15th-22d, 24th, 27th, right sides of 7th-8th, 10th-12th, 15th-19th, 22d, 24th, 26th (Naples, No. 5). At present, about the only seemingly feasible characterization is: pores usually alternate irregularly and with asymmetry between two major locations along most of the anteroposterior axis. First dorsal pore, at 5/6 (22 specimens), at 7/8 (2).

Spermathecal pores, minute, superficial, at 9/10-10/11, close to mD in an area where color often is faint or quite unrecognizable. Female pores, minute, superficial, equatorial in xiv and just lateral to *B*. Male pores, minute, not superficial, within a cleft laterally and seemingly about at *mBC*. Male tumescences, almost confined to median half of *BC* but obliterating 14/15-15/16 and reaching well into xv and xvi.

Clitellum, saddle-shaped, at maximal tumescence reaching to or nearly to *B*, dorsal pores occluded, intersegmental furrows obliterated, setae unrecognizable, xxvii-xxxii (15 specimens), xxvii-xxxiii (14), eq/xxvii-xxxiii/eq (2), eq/xxvii-xxxiii (2), xxviii-xxxii (29), xxviii-xxxiii (3), eq/xxviii-xxxiv/eq (9). Tubercula pubertatis, usually longitudinal bands of greyish translucence just lateral to *B*, with straight median margins but with lateral margins slightly convex, in xxx-xxxi but occasionally extending slightly into xxxii, rarely reaching eq/xxxii. A deep groove occasionally demarcates a tuberculum laterally. Even when a red coloration (post-preservation artifact) of the clitellum is best developed, none is recognizable in the tubercula.

Genital tumescences, often rather indistinct and especially so in relaxed material, include setal couples as follows: *a, b* of xi (1 specimen), xii (4), xvi (2), xxii (1), xxiii (7), xxiv (7), xxv (1), xxvi (1), xxix (26), xxx (35), xxxi (35), xxxii (9), *c,d* of x (1), xi (22). Condition obviated recording locations on a number of worms but dissections indicate that ventral setae of xxx and xxxi always were associated with tumescences. Follicles opening through tumescences are thickened and have slightly enlarged apertures. The *b,c* and *d* follicles project conspicuously into the coelomic cavities but *a* follicles obviously are shorter and protrude only slightly above the parietes.

Internal anatomy. Septa, 13/14-14/15 often thickest and quite muscular, 10/11 near the gut separated into two lamellae the anterior of which passes straight to the gut, the other inserted on it more posteriorly so as to leave a space filled by a watery fluid without corpuscles or other solid matter. This curious situation presumably arises as a result of an ontogenetically late elongation of a small section of the esophagus. The anterior lamella seems to be at the front end of the calciferous gland. Setal gaps in longitudinal musculature, obviously eight. Special longitudinal muscle band at mD, present from 5/6. Pigment, red, in circular muscle layer, lacking immediately under intersegmental furrows. Pigment also is visible on or in the coelomic face of the parietes, dorsally throughout but also ventrally in front of xv, in flecks, or spots or rarely even in larger patches. Location of the brain is variable, a section exactly along 3/4 sometimes left the brain anteriorly in iii, sometimes anteriorly in iv. Pharyngeal glands, through iv-v to 5/6.

Esophagus of x has the shape of a truncate cone, narrower anteriorly. The wall is dark (gorged with blood?) and unthickened (no sacs or lamellae). The calciferous gland, insofar as could be learned from dissection, is between 10/11 and 12/13, sometimes not reaching the latter, usually not constricted at 11/12 but of the same thickness through both segments. Rarely the portion in xi is moniliform. Intestinal origin, in xv (62). Gizzard, superficially appearing to extend through xvii-xix. Actually, the muscular layer becomes much thinner just behind apparent level of insertion on gut of 17/18. Gut often valvular in region of insertion of 19/20. Typhlosole, beginning rather abruptly in region of xxi-xxv, thickly lamelliform, height variable, when gut is empty sometimes reaching or nearly touching intestinal floor, ending abruptly, as shown in Table 1.

The typhlosole does not end abruptly in specimens 1-5, 8-9, and 33 (cf. Table 1) but becomes much lower or even vestigial in the indicated regions, i.e., in 1xi-1xv of No. 9. Posterior amputation had been involved in each of those cases. The typhlosole, in a very large majority of the unamputated individuals, ended in a region comprising lxxiv-xcv. The typhlosole of the abovementioned specimens, on the contrary, ends in a region comprising xxxix-xlv, leaving 1-10 intestinal segments atyphlosolate. Very probably, the typhlosole had completely disappeared in some segments of each of those worms. In unamputated worms with abrupt typhlosolar termination, 10-15 segments were atyphlosolate, 10 (3), 11 (5), 12 (7), 13 (13), 14 (6), 15 (2). If, as some have thought, the atyphlosolate portion of the gut is of proctodeal origin, then that part of the gut extends through more segments than the embryologists indicated.

Extra-esophageal trunk, passing up to dorsal vessel in xii, but often unrecognizable (because empty) behind 10/11. In xii (one specimen) the trunk bifurcated, the larger branch joining the dorsal vessel, the other branch passing ventrally and shortly disappearing. A branch from the trunk occasionally passes up to the dorsal trunk in x. When that connective is distended with blood and the posterior portion of the trunk is empty the extra-esophageal could be thought to end in x. The ventral trunk is complete, bifurcating over the subpharyngeal ganglion. The dorsal trunk is also complete, having been traced forward to the brain when blood is present. The subneural trunk probably always is complete but usually is not traceable throughout because of lack of blood. Hearts, present only in vii-xi (62 specimens).

Nephridia, present from iii (presence or absence in ii not determined), vesiculate. Bladders, sausage-shaped (ellipsoidal), transversely placed, reaching to or nearly to *C* or even beyond *C*, joined laterally by the tubular portion of the nephridium, passing into parietes at or near *B*.

Testes, fan-shaped. Male funnels, plicate, size normal with reference to that of the body. Sperm ducts, without epididymis. Seminal vesicles, in ix, xi and xii. Atrial glands, large, deeply cleft at eq/xv, extending through xiv as well as xvi.

TP and atrial glands, acinous, supraparietal. GS glands, acinous, each lobe narrowing to a slender thread-like duct that passes straight down in the parietes, associated only with the *a,b* follicles of xii (once), the *b* follicles of xxx and xxi but usually lacking even in those two segments.

Spermathecae, not sessile, ducts slender, coelomic portions shorter than, to longer than, the ampullae. Spermathecae, in ix, x (56 specimens) but the following divergences were recorded; all in x (twice), one of the anterior pair in x (once), one of the posterior pair in xi (twice), in x-xi (once).

Ovaries, in xiii, each with one egg string which may contain 1-6 ova. Oviducts, passing into parietes lateral to *B*. Ovisacs, small, lobed, always present.

The peritoneum frequently is blistered away from the musculature. Intervening spaces are occupied by a flocculent white material. The blistering seems not to be so rigidly localized as anteriorly in *D. octaedra*. Areas recorded (perhaps not the only ones) from median margin of TP glands to just median to *A* in xxxi-xxxii or xxxiii, the surface more or less deeply cross-hatched, in poor preservation not easily distinguishable from the TP glands. Blistering, continuous through *AA* from one side to the other (once, Italy), between *A* and *B* of each side through xxvi-xxxii (Naples), in *DD* through a region containing the spermathecal pores.

Reproduction. Iridescence on male funnels and in spermathecae, of some worms, was so brilliant as to suggest profuse maturation as well as massive copulatory transfer. Spermatophores, some of which contained sperm, also were noted, in *AB*/xxviii. As a result, until nearly at the end of the present study, laboratory records contained the following comment, "Reproduction presumably is biparental." Although copulation usually had taken place in worms of appropriate age and stage, there does now seem to be some reason for suspecting facultative parthenogenesis.

Number of choromosomes in *hortensis* is 36 (2n) according to Muldal (1952:59) as well as Omodeo (1952:188). The latter says spermatogenesis is normal. Neither author mentioned any evidence indicative of parthenogenesis. Nor was polyploidy detected.

Breeding, in favorable conditions, may be year round.

Biology. Feeding appears to be selective, as guts contained only humus. Shaking ingesta in water produced no turbidity.

Male tumescences and tubercula pubertatis are obvious before other epidermal modifications are recognizable in the clitellar region.

Many of the worms were posterior amputees. Tail regenerates of the usual epimorphic sort never were seen. Regeneration caudally appears to be restricted (at least usually) to reorganizing posterior segments so that external evidence of the amputation no longer is recognizable. In such cases, if lysis has not yet proceeded too far, the typhlosole sometimes can provide proof of the amputation.

Brown bodies, in No. 36, were present in segments xc-xciii, one to three on each side of each segment. Coelomic cavities of xc-xcviii in No. 39 were also filled with similar structures, but in this worm there was only one brown body on each side in a segment, though the coelomic cavities were thereby almost completely filled.

Similar brown matter was not found in coelomic cavities anteriorly. The bodies may then have been formed *in situ*.

Distribution. E. hortensis had not been recorded previously from Ireland and Greece.

The single record for Ohio is of a specimen found in a toilet bowl of a city building.

Commenting on the Nearctic distribution of *E. hortensis*, Mrs. D. McKey-Fender wrote (*in litt.*) "the paucity of North American records of this species may be due to the filthy places it inhabits. It takes some fortitude to collect it. The Oregon specimens are from friable black soil saturated with septic tank effluvium. They seem to be between the wettest zone, where *E. foetida* is even more numerous, and the wet, relatively uncontaminated soil where *E. rosea, A. chlorotica* and the *caliginosa* complex predominate."

Abnormality. Metameric abnormality, just behind clitellum (once), further posteriorly (two specimens); other instances seen during counting of segments not recorded.

No. 1. Right ovary, rudimentary (clitellate adult).

No. 2. Left anterior spermatheca, bifid entally. One ampulla is in ix and the other is in x (Naples).

No. 3. Left female pore, anterior to eq/xiv but not quite half way toward 13/14. Extra pair of male clefts, associated with small male tumescences, in xvi. No pores were found in the posterior clefts and no sperm ducts were found in their vicinity. Atrial glands of xvi, large, each with a deep equatorial cleft.

No. 4. (Ireland). Tubercula pubertatis, markedly protuberant, subcircular, two pairs, those of a side completely separated from each other by an uninterrupted intersegmental furrow, 30/31. Testes, one pair, in vertical testis sacs that reach up to level of dorsal face of gut in xi. Seminal vesicles, one pair, medium-sized, not filling coelomic cavity of xii. Spermathecae, lacking. Iridescence on male funnels, none. The worm obviously is male sterile.

Abnormalities in metamerism are common and their frequency indicates the ease with which development of normal segmentation can be influenced, in a single small region, in a much larger axial portion, in several more or less widely separated areas, or, occasionally, even throughout nearly all of the axis. Divergences from normal of specimens 1-3 appear to have resulted from a rarer sort of interference with development. So rare, in fact, that exact repetition is unknown.

The male sterility of No. 4, being known at the moment only from a single specimen of *hortensis,* can also be of fortuitous origin. However, the aberrations of that worm exactly parallel conditions characterizing some male sterile morphs of various other megadrile species. In such taxa, where reproduction necessarily is parthenogenetic, the associated anatomy is exactly repeated again and again, always without spermatogenesis or receipt from another individual of copulatory sperm. The male sterility is inherited.

Knowledge of the evolutionary changes associated with male sterility and parthenogenesis in other megadriles enables characterization not only of a probably amphimictic norm for *E. hortensis* but also of current evolutionary trends therein.

Polymorphism. The amphimictic norm now postulated for *E. hortensis* is as follows. Male tumescences, large, obliterating 14/15-15/16 and extending through xiv-xvi. Male cleft deep but confined to parietes. Seminal vesicles, three pairs, in ix, xi, xii, all functional. Atrial, TP and GS glands, large, supraparietal, acinous. The atrial glands reach 13/14 as well as 16/17 and are deeply cleft at eq/xv

The more common evolutionary trends now recognizable in sperm-maturing and sperm-exchanging individuals are as follows. Reduction in size of male tumescences, confinement to xv with furrows 14/15-15/16 no longer obliterated though one or the other or both may be slightly displaced, restriction to slight swellings of immediate margins of male pore clefts. Finally, there will be no tumescence at all and clefts will have disappeared leaving the male pores superficial as in certain species of *Lumbricus.* Correlated with that trend is decrease in size of the associated atrial glands, limitation to xv, representation only by a few filaments slightly protuberant into the coelom from gaps between bands of longitudinal musculature. Slight protuberances of body wall, without interruptions of the muscular layer, over sites of male pores, may indicate presence of last rudiments of the atrial glands. Similar trends involve the TP and GS glands, one or the other or both of which have disappeared in certain lines.

Seminal vesicles of ix and xi, but never of xii, seem to be disappearing, more especially in ix. There the vesicles no longer become as large as in xi, and may retain a juvenile texture through maturity or may even be unrecognizable on one side or the other.

Inclusion of testes in paired, vertical testis sacs is known today, in the Lumbricidae, only in association with male sterility. The metandric reduction (deletion of tests and gonoducts of x), on the contrary, has been acquired in various families by amphimictic taxa as well as by male sterile morphs. Associated therewith is loss of all vesicles in ix and xi. Many male sterile morphs, in various families, are athecal but spermathecae have been lost by individuals that still produce mature sperm.

Evolutionary trends in *hortensis* may parallel, in part, those of *D. rubida*. That species has male fertile morphs (usually called subspecies, variety or f. *subrubicunda*) as well as male sterile morphs with obligatory parthenogenesis. Degradation of genital structure may have progressed further in *hortensis* than in *rubida*. Even more drastically modified morphs than now known are anticipated for *hortensis*, especially if its parthenogenesis was acquired earlier.

Disappearance of atrial and TP glands results in a state that parallels conditions characterizing the genus *Lumbricus*.

Remarks. Relaxed material furnished by Mrs. McKey-Fender provided beautiful demonstrations of nephropore locations and of uncollapsed nephridial bladders. Such information often is unprocurable from contracted specimens. Nevertheless, on her worms, genital tumescences were unrecognizable and clitellar boundaries probably could have been determined accurately, if at all, only from microtome sections.

Generic relationships. The following characters were found to be invariant in all samples examined. Calciferous gland, without sacs, opening directly into esophageal lumen behind insertion of 10/11 through a circumferential circle of small pores. Intestinal origin, in xv. Gizzard, mostly in xvii. Hearts, in vii-xi. Excretory organs, holoic. Nephridial bladders, sausage-shaped (ellipsoidal), transversely placed. Nephropores, inconspicuous, alternating irregularly and with asymmetry between a level just above *B* and another above *D*. Setae, paired. Longitudinal musculature, pinnate (as seen in transverse section). Pigment, red. Ovaries, in xiii, each terminating distally in a single egg string. Ovisacs, present in xiv. Some of these characters are now expected to be definitive at the family level. Others require inclusion of Michaelsen's *hortensis* in the genus *Eisenia* (*cf.* Gates, in press).

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TABLE 1

Typhlosole termination and segment number in *Eisenia hortensis*

Serial Number	Typhlosole ends in Segments	Atyphlosolate Segments	Segment Numbers	Comments
1.	36-39	3	42	
2.	46-47	3	50	
3.	47-48	7	55	
4.	52-54	10	64	
5.	57-59	1	60	
6.	58	6	64	
7.	59	10	69	
8.	61-62	8	70	
9.	61-65	9	74	
10.	62	7	69	
11.	64	13	77	Greece, juvenile
12.	65	5	60	Posterior amputee
13.	68	8	76	Greece, juvenile
14.	71	10	81	Posterior amputee? Greece, juvenile
15.	72	11	83	
16.	74	8	82	
17.	76	9	85	Posterior amputee
18.	77	11	86	
19.	78	6	84	
20.	78	10	88	
21-22.	78	12	90	Ohio (1)
23.	80	14	94	
24.	80	15	95	
25.	81	13	94	Greece, juvenile
26.	82	14	96	
27.	83	12	95	
28.	83	13	96	
29.	83	14	97	

30-31.	84	11	95	San Francisco (1)
32.	84	12	96	Ohio
33.	80-84	8	92	
34-35.	85	13	98	
36.	86	8	94	
37-38.	86	12	98	Ohio (1)
39.40	86	13	99	Maine, Italy
41.	87	12	99	
42.	88	13	101	Great Britain
43.	88	14	102	
44.	89	11	100	
45.	89	13	102	
46-47.	89	14	103	
48.	89	15	104	
49-50.	90	13	103	Ohio (1)
51.	91	13	104	
52.	92	10	102	Posterior amputee?
53.	92	13	105	
54.	95	13	108	Naples

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NEW ECHIMYID RODENTS FROM THE OLIGOCENE OF PATAGONIA, AND A SYNOPSIS OF THE FAMILY

Bryan Patterson and Rosendo Pascual[1]

Abstract. The living and extinct echimyid rodents are briefly reviewed, and placed in five subfamilies: Echimyinae Murray, Dactylomyinae Tate, Heteropsomyinae Anthony, Myocastorinae Ameghino, and Adelphomyinae nov. *Prospaniomys* and *Spaniomys* are placed in the Myocastorinae. Two new genera and species, *Xylechimys obliquus,* Deseadan, and *Paradelphomys fissus,* Colhuehuapian, are described; both are referred to the Adelphomyinae.

A SYNOPSIS OF THE ECHIMYIDAE

Echimyids today form the largest of the numerous families comprising the suborder Caviomorpha. Fifteen living genera are currently recognized, all but one wholly tropical or subtropical in distribution. Extinct genera, including those described below, number only eighteen and of these four are Antillean. We are hence far from a really adequate understanding of the phylogeny of the group. The living forms have usually been divided into two subfamilies, Dactylomyinae and Echimyinae (e.g. Ellerman, 1940;[2]

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[1] Museo de la Plata, La Plata, Argentina.

[2] Ellerman, while recognizing these subfamilies, also included in his Echimyidae, with the rank of subfamily, the Octodontidae (with *Ctenomys*), Abrocomidae, Capromyidae, *Plagiodontia, Myocastor* and even the African Thryonomyidae and Petromuridae. As will appear below, we agree as to recognition and inclusion of the Myocastorinae. Further work may require that the brachyodont to hypsodont Echimyidae and the hypselodont Capromyidae be merged; in that case the subfamilies of each would become tribes. The octodontids surely had a common origin with the echimyids in pre-Deseadan time, but the two groups diverged thereafter and merit familial rank. Abrocomids and ctenomyids are derivatives of the Octodontidae, the *Ctenomys* group being only a subfamily of it. The African families have nothing to do with this assemblage, being descended from the Fayum Phiomyidae (Lavocat, 1963; Wood, in press).

Cabrera, 1960), with the extinct forms placed in the latter (e.g. Simpson, 1945). There can be little doubt that *Dactylomys* and its relatives constitute a single suprageneric group, but the same can hardly be claimed for the Echimyinae, particularly if the extinct forms are taken into account. Wood and Patterson (1959:301-2), on the basis of work in manuscript by Patterson and Kraglievich, divided the family into five groups: the *Proechimys-Eumysops*, the *Dactylomys*, the *Echimys*, the *Spaniomys* and the *Adelphomys*. The *Echimys* and *Dactylomys* groups are so far unrepresented, or at least unrecognized, in the fossil record. The largest group and the one with the most continuous record is the *Proechimys-Eumysops*, which can be traced back to the Colhuehuapian Oligocene *Protacaremys;* it includes almost half of the known genera. The *Echimys* group, the Echimyinae proper, comprises only three genera. Ellerman (1940:106-108) pointed out the distinctions between these three and the rest of his Echimyinae but did not separate them formally. The extinct West Indian *Heteropsomys*, *Homopsomys*, *Brotomys* and *Boromys* appear to be closer to the *Proechimys-Eumysops* group than to any other division of the family (Miller, 1930; Williams and Koopman, 1951), and Kraglievich (1957, 1965) has extended Anthony's subfamily Heteropsomyinae[1] (1917) to include the whole assemblage. As regards two other extinct Antillean genera, *Isolobodon* and *Aphaetreus*, that are often placed in the Echimyidae, we are inclined for the present to follow Miller and Kellogg (1955:644-5) and associate them with *Plagiodontia* as a subfamily of the Capromyidae.

Wood and Patterson placed *Spaniomys* and *Prospaniomys* in a separate group on the basis of cheek tooth structure, but did not comment as to possible relationships to later forms. We now offer the suggestion that *Myocastor* may be a survivor of this group. This rather specialized genus does not fit comfortably into the Capromyidae — otherwise a purely Antillean group so far as known[2] — with which it is frequently associated. It also stands somewhat apart from the later Echimyidae in such characters as the very long paroccipital process, the prominent lateral process of the supraoccipital, the greatly reduced coronoid process, the presence of four fully developed lophids in all lower molars and five

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[1] Proposed by Anthony on the supposition that he was defining a subfamily of the Dasyproctidae. This is the oldest available name, antedating Eumysopidae Rusconi 1935 (Eumysopinae Kraglievich 1945).

[2] The Venezuelan record of "*Procapromys*" was surely based on erroneous locality data.

lophids and a small anterior fossettid in dm_4. A tendency toward reduction and loss of the metalophid in the molars is characteristic of the family. Dactylomyines, echimyines and most later members of the *Adelphomys* group (see below) lack it, while heteropsomyines may retain a vestige of it, or, alternatively, acquire a neolophid, on anterior lower molars, in the form of a small crest, connecting anterolophid and hypolophid, that isolates a small anterointernal fossettid. The members of the *Spaniomys* group do not display this tendency to the same degree. In the Colhuehuapian *Prospaniomys* the metalophid is present in M_{1-2} and interrupted or absent in M_3; in the Santacruzian *Spaniomys* it is present in M_{1-2} and absent in M_3. The cheek teeth of *Spaniomys* are quite variable, however, and two specimens in the Ameghino Collection display a tendency toward reacquisition of a fourth lophid in M_3. In one of these there is a pronounced spur projecting posteriorly from near the center of the hypolophid, and in the other (the type of *Graphimys provectus* Ameghino, a synonym of *Spaniomys modestus* Ameghino) this spur is larger, extending to the posterointernal corner of the tooth. The end result of this, if continued, would have been an M_3 with four lophids, the third of which, while resembling the third (the metalophid) of M_{1-2}, would have been a neomorph.

Unworn and, especially, little worn upper and lower molars of *Myocastor* (there is much change in crown proportions and some in structure as wear proceeds) resemble the corresponding teeth of *Prospaniomys* and *Spaniomys* more closely than they do those of other echimyids. The fourth crest of M_3 could have been inherited either from ancestors like *Prospaniomys,* in which the crest was still present in certain individuals, even if somewhat reduced, or from ancestors resembling *Spaniomys,* in which the tendency toward a neomorph crest had become fixed. Dm^4 of *Myocastor* is fully molariform as is that of *Prospaniomys; Spaniomys* differs in having only three lophs. Dm_4 of *Myocastor* is a complex tooth with five lophids, the anterior two united lingually to isolate the small anterior fossettid. *Spaniomys* has four lophids, the anterior pair uniting lingually with wear to isolate one or two shallow fossettids; in *Prospaniomys* the two anterior lophids are united at or shortly following eruption. These crests correspond topographically to the anterolophid and metalophid of the molars. The small extra lophid of *Myocastor* (the second in the series) is an addition to the crown. Acquisition of this crest by the ancestors of the living form seems likely. In one species of the late Pliocene *Isomyopotamus* the rather large anterior fossettid is partially divided by a spur directed internally from the united anterolophid and metalophid (Reig, 1950:113, fig. 2c); this suggests a method of origin of the extra lophid. *Myocastor* is specialized as regards the progressive enlargement of the cheek teeth from dm $\frac{4}{4}$ backward and the progressive obliquity of the lophids in the lower series. In the late Pliocene *Isomyopotamus* and *Paramyocastor* (Ameghino, 1904:252) these tendencies are less marked.

An imperfect skull of *Spaniomys* is known (Scott, 1905:410-411). This displays certain resemblances to *Myocastor*. The rostrum is relatively long and its ventral border somewhat elevated above the bony palate, the tip of the upper incisor is approximately at the level of the cheek teeth, the paroccipital processes are longer and the lateral processes are freely projecting (*fide* Scott[1]). The coronoid process of the mandible is not reduced, but such reduction may have been a late event in the group. Ameghino describes the coronoid of *Paramyocastor* as being "mucho más larga que en

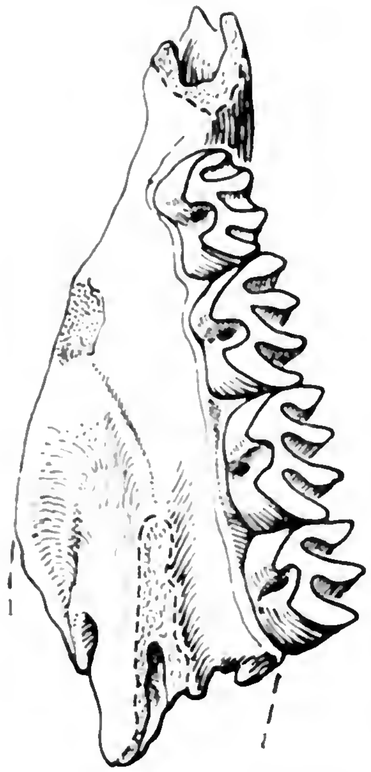

Fig. 1. *Spaniomys modestus* Ameghino. × 4. Princeton University No. 15577. Dorsal view of incomplete left mandible.

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[1] The specimen (American Museum No. 9529) does not now show these last two features clearly; possibly it has suffered some damage since 1905.

Myocastor." *Myocastor* has a very large, wide masseteric shelf that begins beneath M$_1$ and runs back to the angle. *Spaniomys* possesses a smaller but nevertheless rather comparable structure so far as preserved (Fig. 1). Both forms have a muscle scar running from the coronoid process to the front of the shelf; and in both the grinding surface of the upper cheek teeth faces somewhat outwardly, that of the lowers inwardly.

These resemblances in skull and dentition are collectively rather impressive. We believe a relationship to be possible and accordingly for the present include the *Spaniomys* group in the Myocastorinae. The test of this hypothesis will come with the discovery of late Miocene and earlier Pliocene forms ancestral to the later Pliocene myocastorines *Isomyopotamus* and *Paramyocastor.*

The *Adelphomys* group remains for consideration. It was the earliest of the several subdivisions to appear in the record and is the only one that, so far as can be judged on present evidence, has no surviving representatives. *Deseadomys* (Wood and Patterson, 1959:303-312) and *Xylechimys* gen. nov. of the early Oligocene are higher crowned than the late Oligocene *Protacaremys* and *Prospaniomys,* and are more advanced as regards obliquity of lophs and lophids and (in *Deseadomys*) reduction or loss of the metalophid in the lower molars. *Deseadomys* and *Xylechimys* differ from all later echimyids in the replacement of dm$^4_4$ by P$^4_4$. As pointed out by Wood and Patterson (1959:301), retention of the milk molars in the family presumably came about between Deseadan and Colhuehuapian time. There appears to have been an early dichotomy into the *Adelphomys* group, on one hand, and the ancestors of the rest of the family, on the other (Wood and Patterson, 1959, fig. 3), and it follows from this that retention of dm$^4_4$ has occurred more than once in echimyid history.[1] The group is distinct from the time of its earliest appearance, survived into the early Pliocene, and includes a third of the extinct genera. It is worthy of subfamilial rank and may be defined as follows:

ADELPHOMYINAE subfam. nov. Cheek teeth sub-mesodont to mesodont, no unilateral hypsodonty; lophs and lophids tending to become markedly oblique, sometimes lamellar; upper molars with metaloph and posteroloph uniting early to convert metaflexus

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[1] The selective advantage of retention of dm$^4_4$, especially in groups that retained brachyodont teeth throughout their subsequent history, is not too clear. A possible explanation might be that this afforded a simpler, more rapid means of attaining crown complexity than progressive molarization of P$^4_4$, dm$^4_4$ being of course more complex than the replacing tooth.

to metafossette, other flexi persistent; lower molars with marked tendency toward reduction and loss of metalophid.

Distribution: Early Oligocene to early Pliocene, South America.

Genera: Adelphomys, Stichomys, Santacruzean; *Paradelphomys* gen. nov., Colhuehuapian; *Xylechimys* gen. nov., *Deseadomys,* Deseadan. There is, in addition, an undescribed genus in the Chasicoan (Pascual, MS).

The distinctive characters of the cheek teeth of the other subfamilies may be summarized, with a listing of the included genera:

Echimyinae Murray 1866.[1] Mesodont, relatively long; lophs and lophids rather stout, tending to form transverse lamellae; flexi and flexids (or transverse valleys) fairly persistent. *Echimys, Diplomys,* Central and South America, *Isothrix,* South America, Recent.

Dactylomyinae Tate 1935. Brachyodont, wide, large relative to size of skull; lophs and lophids rather thin, sharp and with tendencies toward acquisition of lamellae; flexi and flexids persistent. *Dactylomys, Thrinacodus, Kannabateomys,* South America, Recent.

Heteropsomyinae Anthony 1917. Brachyodont to hypsodont, with some unilateral hypsodonty; upper cheek teeth tending to become subcircular to quadrate in outline; flexi and flexids not very persistent, converting to fossettes and fossettids after moderate wear; small anterointernal fossettid may be present in lower molars. *Proëchimys,* Central and South America, Recent, Puerto Rico, uncertain age; *Hoplomys,* Central and South America, Recent; *Euryzygomatomys, Clyomys, Mesomys, Lonchothrix,* South America, Recent; *Carterodon,* South America, Pleistocene to Recent; *Cercomys,* South America, Pliocene to Recent; *Heteropsomys, Homopsomys,* Puerto Rico, latest Pleistocene or early Recent; *Brotomys,* Hispaniola, latest Pleistocene or early Recent; *Boromys,* Cuba, latest Pleistocene or early Recent; *Eumysops,* South America, late Pliocene to Pleistocene; *Protacaremys,* South America, late Oligocene. *Protadelphomys,* South America, late Oligocene, is tentatively placed here, and there is an undescribed genus in the Santa Cruz Miocene of Patagonia.

Myocastorinae Ameghino 1904.[2] Brachyodont to hypsodont; labial flexi and lingual flexids of later forms converting to fossettes and fossettids after considerable wear; later forms showing an increase in size and in obliquity of lophs and lophids from front to

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[1] As Echimyina (= Echymyna Gray 1825, Echymidae Bonaparte 1845).

[2] Proposed as a family (= Myopotamini Tullberg 1900, Myiopotamyina Bonaparte 1850).

back; dm_4 with a small anterior fossettid, with five lophids in later forms; M_3 usually with four lophids, metalophid either retained or a third lophid reacquired. *Myocastor,* South America, Pliocene?, Pleistocene to Recent (and currently doing only too well in the feral state in Europe and North America); *Paramyocastor, Isomyopotamus,* South America, late Pliocene; *Spaniomys,* South America, early Miocene; *Prospaniomys,* South America, late Oligocene. *Tramyocastor* does not appear to be separable from *Myocastor.*

The new genera to be described, one of them Deseadan, the other Colhuehuapian, are both adelphomyines and appear to be more closely related to each other than to any of the previously known forms.

DESCRIPTION OF NEW FORMS

XYLECHIMYS[1] gen. nov.

Type species: X. obliquus[1] sp. nov.

Distribution: Deseadan, Patagonia.

Diagnosis: Reduced metalophid present on all molars, joined to metaconid to isolate antero-fossettid but continuing on into mesoflexid to define small anteroflexid, metalophid smallest in M_3, subequal in M_{1-2}; hypolophid and posterolophid very oblique, especially on M_{1-2}; posterolophid terminating lingually near median line of tooth row; principal flexids deep, all of nearly equal depth on M_{2-3}, metaflexid shallower on M_1; metaconid sharply angulate posteriorly.

XYLECHIMYS OBLIQUUS sp. nov.

Type: Museo de La Plata No. 59. II. 26. 81, portion of right ramus with M_{1-3}, base of I and alveoli of P_4.

Hypodigm: Type only.

Horizon and locality: Deseadan Oligocene; Laguna de los Machos, Campo Belisario Escobar, Departamento Paso de los Indios, Chubut, Argentina.[2]

Diagnosis: As for the genus.

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[1] ξύλοτ, wood, plus *Echimys.* Named for Professor Albert E. Wood in recognition of his contributions to our knowledge of the order. The specific name refers to the obliquity of the posterior lophids.

[2] This is a new locality that has yielded a small faunule. Found with *Xylechimys* were specimens of *Asteromys, Archaeohyrax, Plagiarthrus, Propachyrucos, Prohegetotherium,* Trachytheriinae indet., which are sufficient to reveal the age.

Description: The anterior cheek tooth is unfortunately represented only by its broken alveoli. X-rays reveal no trace of a tooth below these alveoli. It is virtually certain that the missing tooth was P_1, as in *Deseadomys.*

The molars are mesodont and exhibit no tendency toward unilateral hypsodonty. M_2 is the largest, and M_3 the smallest of the series, but the size differences are not great. All are broader relative to length than in *Deseadomys* and are wider anteriorly than posteriorly, most notably as regards M_3. The anterior portions of the molars are short anteroposteriorly.

The anterolophids are nearly transverse. A reduced metalophid is present on all teeth, that of M_3 being the shortest, those of $M_{1\text{-}2}$ subequal. Near the middle of its course each metalophid is united to the metaconid to isolate a small anterofossettid, and then continues lingually beyond this junction for a short distance. A short

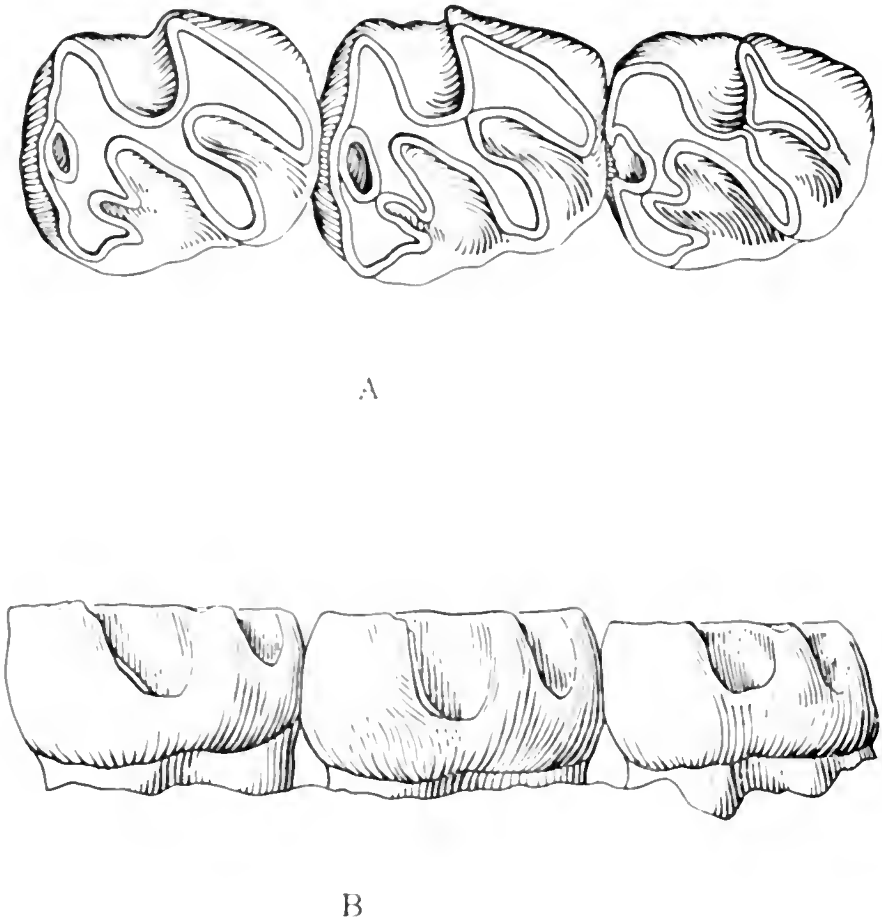

Fig. 2. *Xylechimys obliquus* gen. et sp. nov. × 10. Type. Museo de La Plata No. 59. II. 26. 81. *A*, $RM_{1\text{-}3}$, crown view; *B*, $RM_{1\text{-}3}$, lingual view.

and shallow anteroflexid is thus present in addition to the anterofossettid, a marked contrast to *Deseadomys arambourgi.* The hypolophid is decidedly oblique, being almost in a direct line with the ectolophid. On M_{1-2}, but not on M_3, this crest is slightly swollen lingually, the swelling marking the position of the entoconid. The posterolophid is essentially parallel to the hypolophid and terminates posteriorly a short distance lingual to the mid-line of each tooth. The metaconid is sharply angulate posteriorly. Hypoflexid and mesoflexid are of equal depth, extending nearly to the base of the enamel. The metaflexid progressively deepens posteriorly through the series until it is as deep as the hypoflexid and mesoflexid on M_3. The walls of these three valleys are steep. In M_{2-3}, especially in the latter, these flexids deepen toward the mid-line. The anterofossettid is shallower than the principal flexids, and the anteroflexid is little more than a conspicuous groove. The mesoflexid and anteroflexid together constitute the largest valley in M_{1-2}. On M_3 the connection between the posterolophid and the ectolophid had not yet been fully established by wear, which suggests that in the unworn state a gap existed between these lophids. On M_3 a slight notch in the anterior wall of the anterofossettid had not yet been obliterated by wear.

The base of the incisor is poorly preserved. All that can be said concerning it is that the enamel extends about half way around the lateral face.

The mandibular ramus, so far as preserved, is robust and deep, about as in *Deseadomys.* As in that form, the ascending ramus arises near the front of M_3. The masseteric crest begins, as a small shelf, at a point beneath the anterior portion of M_1.

PARADELPHOMYS[1] gen. nov.

Type species: Paradelphomys fissus[1] sp. nov.

Distribution: Colhuehuapian, Oligocene, Patagonia.

Diagnosis: Lophids very oblique, posterolophid forming an isolated lamella; metalophid vestigial on dm_4, absent on molars; anterofossettid of dm_4 elongate.

PARADELPHOMYS FISSUS sp. nov.

Type: Museo municipal de Mar del Plata No. 125, fragment of right mandible with dm_4 — M_1.

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[1] παρα, beside, plus *Adelphomys.* The specific name alludes to the isolation of the posterolophid.

Hypodigm: Type only.

Horizon and locality: Colhué-Huapí Formation; barranca south of Lake Colhué-Huapí, Chubut, Argentina.

Diagnosis: As for the genus.

Description: Dm$_1$ is nearly oval in outline and longer than M$_1$. The anterolophid is gently convex anteriorly and very obliquely directed posterolingually. Near its extremity it is connected to the hypolophid by a short bridge, a vestige of the metalophid, which isolates an elongate, sinuous anterofossettid. The mesoflexid, which is in consequence short, extends down nearly to the base of the crown. Protoconid, ectolophid and hypolophid are in a nearly straight line. The posterolophid is an isolated, somewhat slipper-shaped lamella that preserves no vestige of a former connection to

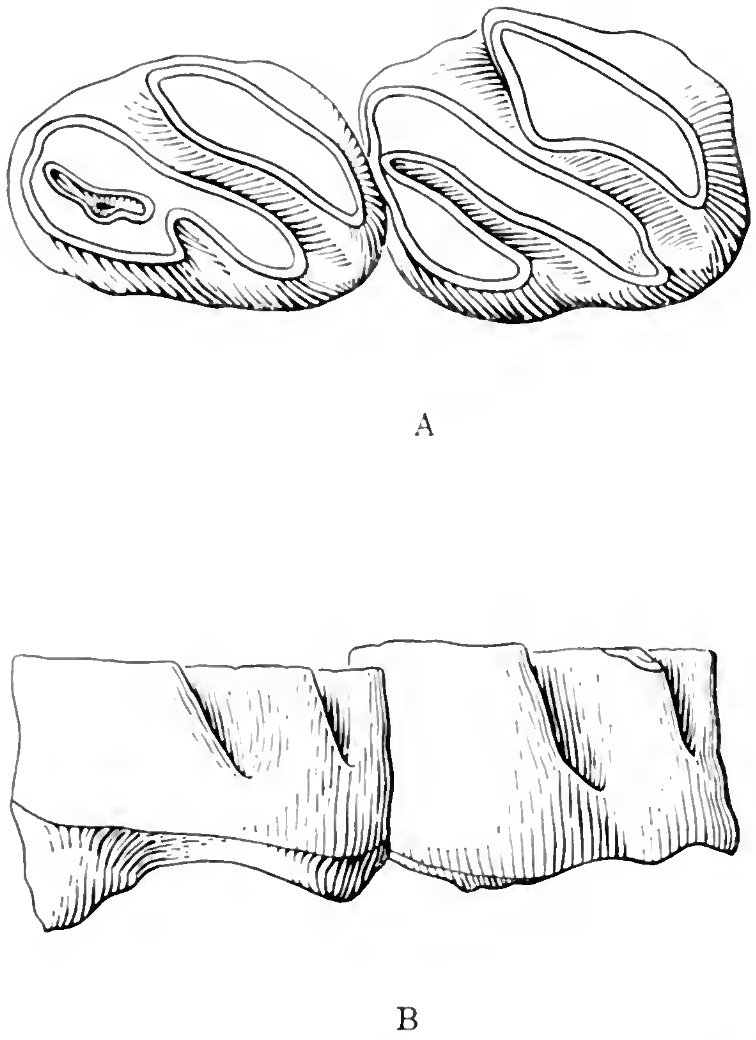

Fig. 3. *Paradelphomys fissus* gen. et sp. nov. × 10. Type. Museo municipal de Mar del Plata No. 125. *A*, Rdm$_1$ — M$_1$, crown view; *B*, Rdm$_1$ — M$_1$, lingual view.

the hypolophid-ectolophid. The combined hypoflexid-metaflexid is a narrow, deep, parallel-sided cleft extending diagonally across the tooth. Not as deep as the mesoflexid, it is somewhat deeper on the lingual than on the labial side; at an extreme stage of wear the bases of the protoconid and hypoconid would be joined.

M_1 is square in outline anteriorly and tapers posterolingually at the crown surface, although not at the base. The anterolophid is nearly transverse anteriorly and curves posteriorly in the region of the metaconid. The mesoflexid is a diagonal slit that extends almost to the anterior extremity of the tooth and reaches downward nearly to the base of the enamel. The hypolophid-ectolophid is slightly more sinuous than in dm_4. The posterolophid is also an isolated lamella, but, unlike that of dm_4, it is decidedly convex anteriorly, the convexity marking the site of an earlier junction with the hypolophid. Posteriorly, its wall slopes outward and downward in a postero-labial direction so that its area would increase considerably with wear. The hypoflexid-metaflexid is deeper at the center than at the extremities; at an extreme stage of wear an elongate, narrow fossettid would be isolated.

Enough of the ramus is preserved to reveal that the masseteric crest began beneath the anterior end of M_1.

TABLE 1

Tooth measurements (in mm) of type specimens of *Xylechimys obliquus* and *Paradelphomys fissus*

		X. obliquus	*P. fissus*
dm_4,	antero-posterior	—	4.0
	width, anterior	—	2.1
	width, posterior	—	2.7
M_1,	anteiio-posterior	3.1	3.7
	width, anterior	2.5	2.9
	width, posterior	2.5	2.7
M_2,	antero-posterior	3.2	—
	width, anterior	2.8	—
	width, posterior	2.8	—
M_3,	antero-posterior	2.9	—
	width, anterior	2.8	—
	width, posterior	2.3	—

DISCUSSION

Xylechimys invites comparison with its contemporary, *Deseadomys.* The former is more primitive as regards retention of the metalophid and anterofossettid on all molars and in the lingual extension of this lophid beyond the connection with the metaconid. It is more advanced in the greater obliquity of the hypolophid and posterolophid and in the nearly median position of the lingual end of the posterolophid. Wood and Patterson (1959:306, 309, 312) called attention to various characters of *Deseadomys arambourgi* and of *D. loomisi* that suggested close relationship, if not actual ancestry, to the Santa-Cruzean *Stichomys* and *Adelphomys,* respectively. This view still seems reasonable. *Xylechimys* does not resemble these later forms to the same extent.

Paradelphomys is decidedly specialized in the loss of the metalophid in M_1, the very marked obliquity of the lophids and the complete separation of the posterolophid. It is, in fact, in these features the most specialized member of the Adelphomyinae so far known. There are, however, resemblances between it and *Xylechimys,* such as a nearly comparable degree of obliquity of the hypolophid and posterolophid, the lingual end of the posterolophid not extending much beyond the mid-line of the tooth until after heavy wear and the tendency toward separation of the posterolophid present in *Xylechimys.* Elimination of the metalophid, straightening of the protoconid-ectolophid-hypolophid crest, and further separation of the posterolophid would convert molars of *Xylechimys* structure into those of *Paradelphomys.* It is, of course, quite uncertain if the two stood in ancestor-descendant relationship — the more exact resemblance between the species of *Deseadomys* and *Stichomys* and *Adelphomys* would argue against this possibility — but on present evidence it seems likely that they were more closely related to each other than to any of the genera previously known.

Its name notwithstanding, *Protadelphomys* Ameghino of the Colhuehuapian is neither ancestral to *Adelphomys* nor a member of the Adelphomyinae. Ameghino (1902:112) based his concept of relationship on the lower incisors, which are relatively large, flat anteriorly, and have the transverse (mesio-distal) and anteroposterior diameters nearly equal in both. This is the only close similarity between the two forms and it is more than offset by the structure of the molars, which in *Protadelphomys* are short and quadrate rather than elongate, retain reduced metalophids on M_{1-2}, have the hypolophid directed lingually and the posterolophid deeply separated from the hypolophid. The last character is a point of resemblance to *Paradelphomys* but it is the only one and, in view of the tendency toward lamellar structure that crops up in several of the echimyid subfamilies, we do not consider it to be indicative of any close affinity. *Protadelphomys* is known only from one incomplete ramus with broken or deeply worn teeth. What can be seen of the structure suggests that the genus represents an early and specialized offshoot of the Heteropsomyinae, and more than this cannot at present be said.

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B R E V I O R A

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GEOMYERSIA GLABRA, A NEW GENUS AND SPECIES OF SCINCID LIZARD FROM BOUGAINVILLE, SOLOMON ISLANDS, WITH COMMENTS ON THE RELATIONSHIPS OF SOME LYGOSOMINE GENERA

Allen E. Greer and Fred Parker[1]

Abstract. A new genus and species of skink, *Geomyersia glabra,* is described from Bougainville, Solomon Islands. Notes on the reproduction and ecology of the species are presented along with a generic diagnosis and description.

The large group of skinks centering on *Leiolopisma* (as used in its broadest context) is divided into two major subgroups on the basis of the relationships of the bones in the secondary palate; the alphas are wide ranging throughout the Old and New World whereas the betas, which appear to be derived from the alphas, are confined to subsaharan Africa and the Australian Region. *Geomyersia glabra* is a beta skink. The relationships between the African and Australian Region betas are obscure as yet, but the relationships of the taxa within these two groups are somewhat clearer. *G. glabra* appears to be a part of the radiation of the betas in the Australian Region.

INTRODUCTION

Recently one of us (Parker) obtained in the highlands of Bougainville a new species of cryptic skink that possesses the following combination of characters unique in lygosomine skinks: translucent spectacle in the movable lower eyelid; prefrontals absent; single frontoparietal; a single median scale situated between the single pair of nuchal scales; minute external ear opening; and pentadactyl limbs.

As the proper generic allocation of the new species was not clear from these external characters, a skull was prepared for comparison with the skulls of more than 350 species of skinks. The skull morphology immediately allowed us to recognize the nearest relatives of the new skink and determine that skull characters in combination with the external characters warrant separate generic status for the species.

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[1] Kundiawa, Chimbu District, Territory of New Guinea.

SYSTEMATIC DESCRIPTION

The new genus and species may be known as:

GEOMYERSIA GLABRA[1] new genus and species

Holotype: Museum of Comparative Zoology 93714, collected by natives for Fred Parker at Mutahi, Bougainville (elevation 2200-3200 feet) on 18 May 1966.

Paratypes (7 specimens): MCZ 87611, 93710, 93712, Naturhistoriska Riksmuseet (Stockholm) 67-0001, same data as holotype, but collected in the period 10-19 May 1966. MCZ 93713, Melilup, Bougainville (elev. 3000 ± 500 feet) on 14 May 1966. MCZ 93711, Ramazon River, Bougainville (elev. 1600-2400 feet) on 19 May 1966. MCZ 93708, Turiboiru, Bougainville (elev. 500 feet) on 21 March 1966.

Generic diagnosis: The genus is similar to an assemblage of lygosomine skinks inhabiting the Australian Region and subsaharan Africa. This assemblage may be characterized by the following suite of skull characters: palatal rami of pterygoids somewhat expanded and deeply emarginated posteriorly and separated medially by medioposterior processes from the palatines, which project into the interpterygoid vacuity (beta palatal pattern, see p. 10 and Figure 4); 11-15 teeth on the premaxillae; no postorbital bone; supratemporal fenestra absent or minute; and Meckel's groove obliterated by the overlapping and fusion of the dentary.

The genus *Geomyersia* may be distinguished from all other taxa in this assemblage (see p. 11) by its depressed body form, the complete absence of prefrontal scales, and the presence of a single median scale between the single pair of nuchal scales. All other taxa in the assemblage possess well-defined prefrontals and lack an "internuchal" scale. No other skink, in fact, is known to have such an internuchal scale as a normal feature (Figure 1).

Species diagnosis: The species diagnosis is the same as that for the genus.

Description (Figure 1): In general appearance *Geomyersia glabra* is a small (32-36 mm in snout-vent length), very dark, brownish black skink with a markedly depressed body form. The

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[1] The genus is named for Professor George Sprague Myers of the Division of Systematic Biology, Stanford University, who stimulated the early interest of the senior author in systematic and evolutionary biology. The specific name (*glabra*) refers to the extremely smooth appearance of the species.

limbs are pentadactyl and fail to meet when adpressed to the body.

Head noticeably depressed; rostral about twice as wide as deep, forming an almost straight suture with the very large frontonasal; external naris centered in a rectangular nasal; a single loreal between the nasal and two superposed preoculars; prefrontals entirely lacking; frontal short, as long as the medial longitudinal length of the fused interparietals, and forming a shallow, but broad, concave suture with the frontonasal; frontal in contact with the two anteriormost of the four supraoculars; lower eyelid movable with a large translucent spectacle; small scales of eyelid separated from supralabial scales by complete row of suboculars; 6-6 supralabials, 4th supralabial below center of eye; frontoparietals fused into a single scale; interparietal distinct, shorter than medial longitudinal length of the single frontoparietal; parietals large, forming a suture approximately two-thirds the length of interparietal; each parietal bordered posteriorly by a single large nuchal and temporal; a small, median scale separates the pair of nuchals.

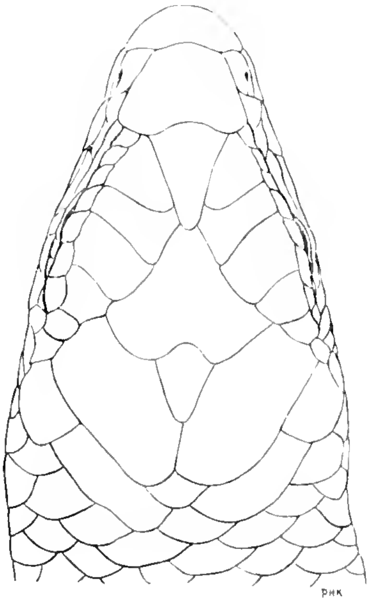

Figure 1. Dorsal view of the head of the holotype of *Geomyersia glabra* (MCZ 93714). Notice the absence of prefrontal scales and the presence of the single frontoparietal and internuchal.

Tympanum sunk below level of epidermis; external ear opening present but minute and without auricular lobes; body scales smooth, slightly iridescent, and disposed in 22-24 longitudinal rows around midbody; a median pair of enlarged preanal scales bordered laterally by two subequal scales; median row of subcaudal scales transversely enlarged.

Dorsal surface of digits covered by a single row of scales (Group 1 of Brongersma, 1942); 11-15 subdigital lamellae beneath 4th (longest) toe; lamellae folded into a median and two lateral ridges.

Color: The dorsum and sides are dark grayish brown to brownish black; a median series of anteriorly-directed dark brownish black chevrons begin on the base of the tail and extend forward to the nape; three or four horizontal streaks composed of long dark dashes extend along the centers of the lateral scale rows between the fore and hind legs. Color does not appear to alter with preservation.

The head is as dark as the dorsum, except for light cream stripes along the sutures between the supralabials. The venter is light with thickly clustered dark spots which become more confluent and dense posteriorly. The underside of the tail is so heavily spotted as to be almost uniformly dark.

Distribution (Figure 2): The species is known only from middle elevations (500-3500 feet above sea level) in the highlands of northern and southern Bougainville.

Reproduction: Geomyersia glabra is oviparous and apparently lays only a single egg at a time. Three of the seven individuals known were gravid. MCZ 87611 and MCZ 93712 (snout-vent lengths 35.5 and 34 mm respectively) each contained 1 oblong, leathery shelled egg. MCZ 93714, with a snout-vent length of 33 mm, contained a single, large yolky egg in the oviduct.

Ecological observations: Geomyersia glabra has been collected between 500-3500 feet. Only one specimen (MCZ 93708) has any precise ecological information associated with it. This individual was found in decayed vegetable matter in secondary forest. All the specimens of *G. glabra* were brought in by native collectors along with large numbers of *Sphenomorphus* (especially *solomonis* and *tanneri*). Apparently the natives do not distinguish *Geomyersia glabra* from the small sympatric *Sphenomorphus* (see Morphological Comparisons with Other Small Solomon Islands Skinks).

The few (six) specimens of *Geomyersia glabra* obtained in the Mutahi-Melilup area, in proportion to the thousands of individuals of other species collected in the same area, indicate that the species is either extremely rare or is more or less restricted to a peculiar habitat that was not widely sampled during the overall collecting.

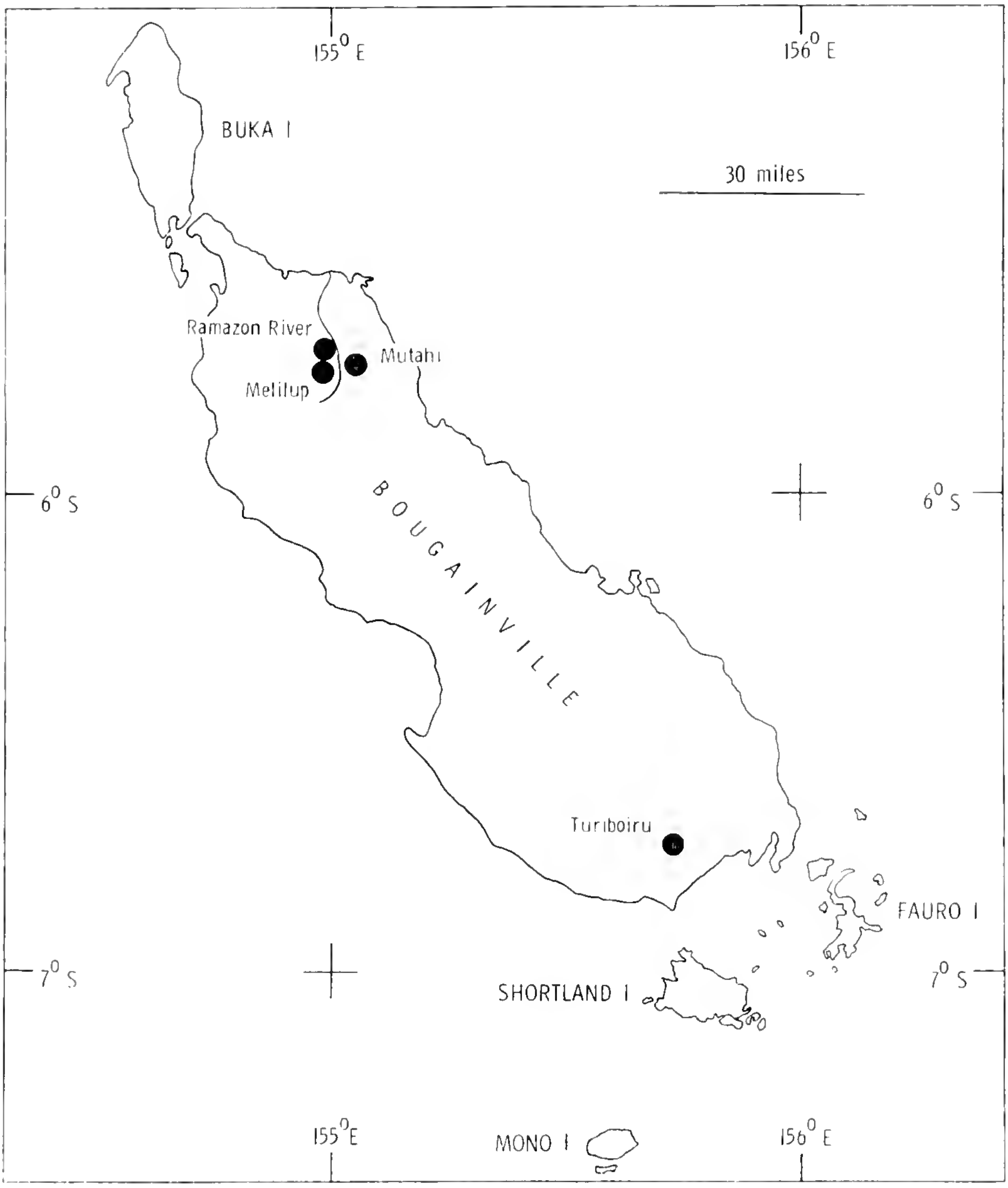

Figure 2. Bougainville and neighboring islands showing the known localities from which *Geomyersia glabra* has been collected.

The apparent rarity is not solely the result of size, as many juveniles of the small skinks are collected and the natives were offered incentives to collect the species. (Interestingly enough the largest skink in the Mutahi-Melilup area, *Sphenomorphus taylori,* is as infrequently collected as is *Geomyersia glabra.*)

Morphological Comparisons with Other Small Solomon Islands Skinks: No close relatives of the monotypic *Geomyersia* are known to occur naturally in the Solomon Islands,[1] although there are three small to medium sized skinks with a more or less uniform dark dorsal coloration in the Solomons with which the new species might be confused. Two of these three, *Sphenomorphus solomonis* and *S. tanneri*, occur together with *G. glabra* on Bougainville, while the third, *S. bignelli*, is known at present only from the southern Solomon Islands. The distinguishing features of the four species are outlined in Table 1.

Discussion: Among lygosomine skinks there is a large group centering on the genus *Leiolopisma*, as used in its broadest sense, that may be distinguished on the basis of (1) a single pair of nuchal scales behind the parietals, each of which is in contact with a single large temporal scale laterally, (2) the upper sides of the digits covered by a single row of scales (Group I of Brongersma, 1942), (3) the lower eyelid usually, but not invariably, with a clear spectacle, and (4) preanal scales often subequal or at least not greatly enlarged.

Correlated with these external characters are the following skull characters: (1) palatal rami of pterygoids separated on the midline — often by medioposterior projections from the palatines into the interpterygoid vacuity, (2) 11 or more premaxillary teeth, (3) a small or minute supratemporal fenestra, (4) no postorbital bone, and (5) Meckel's groove obliterated by the overlapping and fusion of the dentary.

Within this large group, two subgroups may be recognized on the basis of the presence or absence of a medial, posteriorly projecting process from the palatal ramus of the pterygoid and a concomitant emargination in the palatal ramus (Figures 3 and 4).

One group, the alpha group for the purposes of this discussion, has the palatal rami of the pterygoids gradually and smoothly diverging posteriorly from the midline (Figure 3). In the other

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[1] *Carlia fusca*, a close relative of *Geomyersia glabra* (see below), is known to occur in the Solomon Islands only on tiny Sohano Island in the strait between Buka and Bougainville, on Faisi Island and at Buin, Bougainville. The species is as yet unknown from any other localities in the Solomons, and it has almost certainly been introduced in the known localities. *C. fusca* is very common around the town of Rabaul, New Britain, the port from which Bougainville receives most of its supplies. The ecology of the species in Rabaul, the Solomons, and New Guinea is similar. It is a grass-dweller, preferring the thick tussock grass of open areas.

TABLE 1

Distinguishing characteristics of *Geomyersia glabra* and three similar, but apparently only distantly related, Solomon Islands skinks.

	Geomyersia glabra	*Sphenomorphus solomonis*	*Sphenomorphus tanneri*	*Sphenomorphus bignelli*
Snout-vent length (mm)	32-36	27-72	23-52	30-35
Scales around midbody	22-24	24-30	28-32	22
Subdigital lamellae (4th toe)	11-15	13-17	13-20	18-20
Prefrontals	Absent	Separated	Meet	Separated
Frontoparietals	Fused	Distinct	Distinct	Distinct
Lower eyelid	Translucent window	Scaly	Scaly	Scaly
Distribution	Bougainville	Faro (type locality), Bougainville, Shortland, Choiseul, Isabel, Ramos, Florida, Moe, Guadalcanal	Bougainville (type locality), Shortland	Kulambargra (type locality), Malaita, Guadalcanal

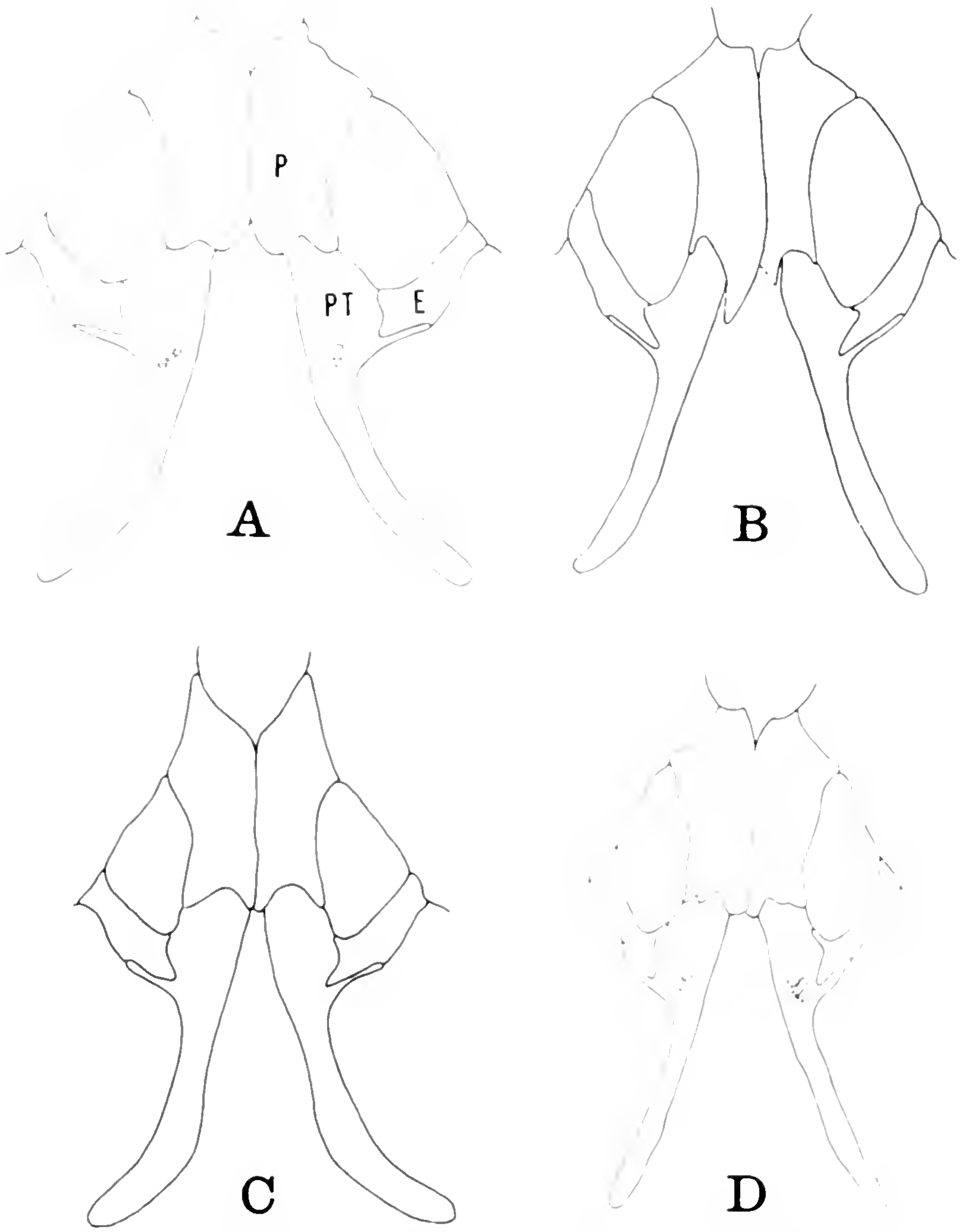

Figure 3. The alpha palatal pattern (ventral view): (A) *Mabuya polytropis* (MCZ 8103), Kribi, Cameroon; (B) *Leiolopisma metallica* (MCZ 67129), Mt. Toolbewong, Healesville, Victoria; (C) *Emoia samoense* (MCZ 16931), Fiji Islands; (D) *Eumecia anchietae* (MCZ 41562), Kaimosi, Kenya. Not drawn to scale. Abbreviations: E, ectopterygoid; P, palatine; PT, pterygoid.

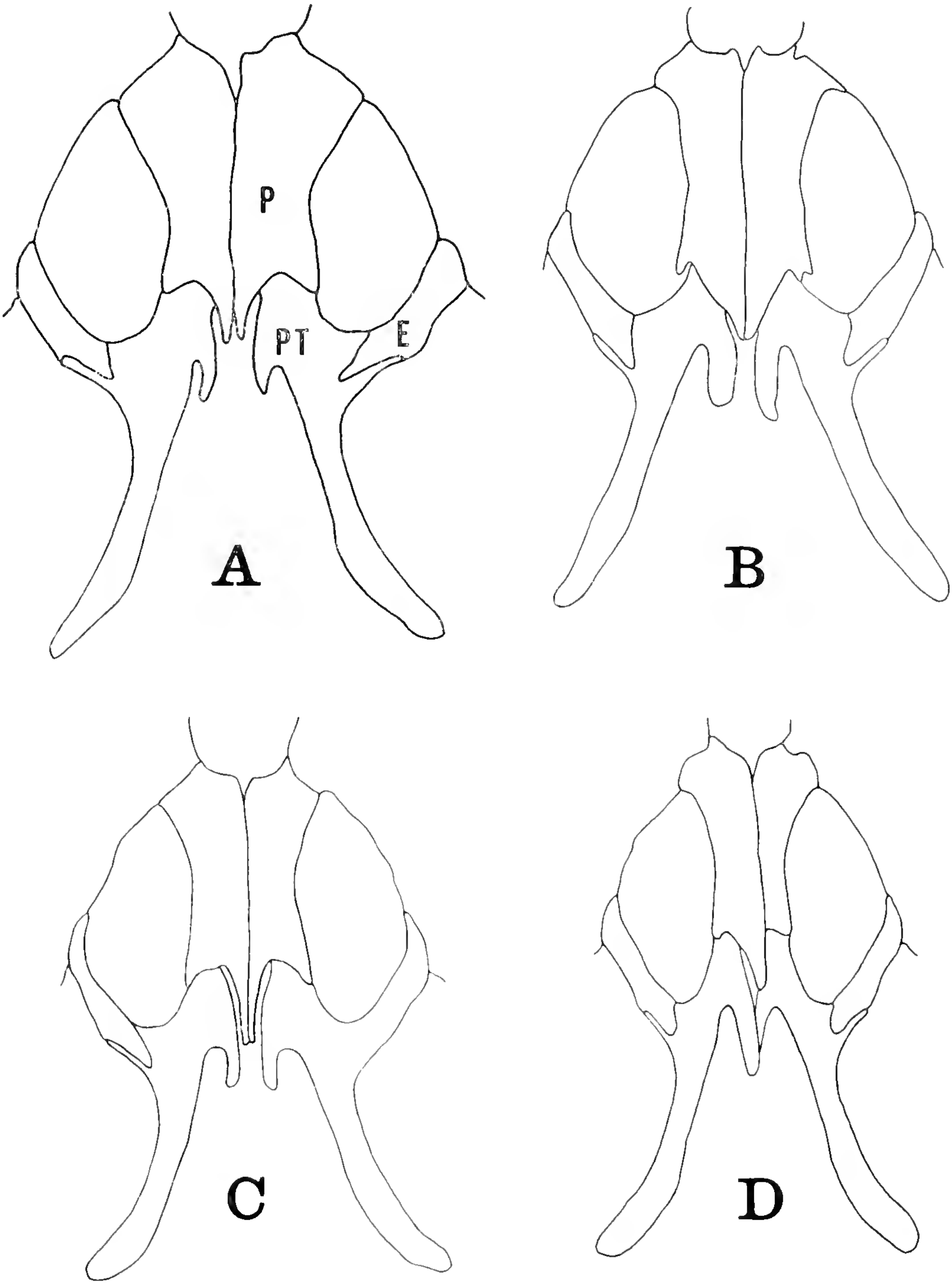

Figure 4. The beta palatal pattern (ventral view): (A) *Carlia bicarinata* (MCZ 64315), Port Moresby, New Guinea; (B) *Leptosiaphos blochmanni* (MCZ untagged), Upper Mulinga, Idjwi Island, Democratic Republic of the Congo; (C) *"Ablepharus" smithi* (MCZ 42880, paratype), Nyonga, Democratic Republic of the Congo; (D) *Geomyersia glabra* (MCZ 87611, paratype), Mutahi, Bougainville. Not drawn to scale. Abbreviations as in Figure 3.

group, here called the beta group,[1] the palatal rami of the pterygoids have medial, posteriorly projecting processes set off by emarginations lateral to them. In addition, whereas medial, posteriorly projecting processes from the palatines are present only in some alphas, they are a constant feature of the beta palatal pattern (Figure 4).

The functional significance of the deeply emarginated palatal ramus of the pterygoid in the beta group (Figure 4) is not perfectly clear. The emargination may serve as a "catch" for the basipterygoid process as the quadratal ramus of the pterygoid slides backward along the outer edge of the process. Such a movement on the part of the quadratal ramus is evident in freshly prepared skulls when the forward part of the skull is depressed (hinging at the transverse frontal-parietal suture), and the whole palatal complex is displaced backward. In freshly prepared skulls, the basipterygoid process can catch in the emargination, stopping the posterior displacement of the palatal complex, thus limiting the amount of strain put on the skull. The skull is probably capable of such movement during active feeding, but the differences in feeding behavior or habits that would make this "catch" mechanism an advantage to the skinks of the beta group are unknown.

The taxonomy of the alpha and beta groups is extremely complex and will be dealt with in future papers. It is of interest for the present discussion, however, to list, using current generic concepts, those skinks, with their distributions, which belong to the alpha and beta groups. The number of species in each genus in each area is given in parenthesis.

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[1] The beta skinks may be of mono- or diphyletic origin. Present evidence, largely geographic, suggests to us that the betas of subsaharan Africa and of the Australian Region have probably independently originated from an alpha ancestry, i.e., they are diphyletic. If so, use of the word "assemblage," which carries no connotations of close relationship for zoologists, would perhaps be more appropriate than the word "group," which does connote close relationships, when discussing the beta skinks as a unit. In the diagnosis of *Geomyersia* the word "assemblage" was used for the beta skinks, but in the following discussion, largely as a matter of stylistic balance with the term "alpha group" (on present evidence the alphas are monophyletic in origin), the term "beta group" will be used. It should be borne in mind, however, that the mono- or diphyletic origin of the beta skinks is still a problem needing further research.

alpha	beta
Ablepharus Australia (part, 11); Asia (8)	*Ablepharus* Africa (6); Australia (*greyi* and *burnetti*)
Anotis New Caledonia (3)	
Didosaurus mauritianus, subfossil on Mauritius	
Emoia Indo-Australian archipelago, N. Australia, and Pacific islands (40)	*Carlia* Australian Region (21)
Eugongylus New Guinea, N. Australia, and Solomon Islands (5)	*Geomyersia* Solomon Islands (1)
Eumecia subsaharan Africa (1 or 2)	
Leiolopisma Asia (17); North America (6); Indo-Australian archipelago (20); Australia (part, 8); Lord Howe Is. (1); New Caledonia (6); New Zealand (16); Mauritius (1)	*Leiolopisma* Africa (7); Australia (*weeksae, challengeri, mustelina, guichenoti, delicata*)
Mabuya Central and South America; to Indo-Australian archipelago (66)	*Leptosiaphos* Africa (7
Sphenomorphus New Guinea (*minutus*); Solomon Islands (*bignelli*); New Zealand (*pseudornatus*)	*Panaspis* Africa (7)

Within the beta group, the group to which *Geomyersia* belongs, relationships are complex and still incompletely worked out. For the moment, therefore, our purpose will only be to discuss some of the clearest groupings within the beta group and with this information assess the relationships of *Geomyersia*.

(1) It is implicit in the list of alpha and beta skinks given above that the genus *Ablepharus*, characterized by "no movable eyelids, [and] a transparent disk covering the eye" (Boulenger, 1887), is not monophyletic; indeed, the genus is an assemblage of species, derived from diverse stocks, with a clear spectacle in the movable lower eyelid (Smith, 1935 and 1937; Greer, 1967a; Fuhn, in an unpublished discussion of the polyphyletic origin of *Ablepharus*).

The Australian *A. greyi* and *A. burnetti* (beta group) are the only "*Ablepharus*" with a reduced digital formula (4 fingers and 5 toes),[1] and significantly, they occur in the same zoogeographic region as the only other group of beta skinks with a similarly reduced digital formula, i.e., *Carlia*. The fused frontoparietal and spiny auricular lobules of *A. burnetti* are shared with *Carlia* and suggest that *A. burnetti* is simply a *Carlia* in which the movable lower eyelid with its clear spectacle has fused almost completely[2] to the upper edge of the orbit.

The 4-5 digital formula and fused frontoparietals of *A. greyi* also argue for the close relationship of this species with *Carlia*, but the unique supraocular arrangement found in *A. greyi* would suggest separate generic rank. The generic name *Menetia* Gray, 1845, originally proposed for this species, is available.

(2) The other beta skinks in the Australian region, in addition to *Carlia* and its two ablepharine derivatives discussed above, are *Geomyersia glabra* and five species referred to *Leiolopisma: weeksae, challengeri, mustelina, guichenoti,* and *delicata*. In possessing 5 fingers these five species of *Leiolopisma*, as well as *Geomyersia*, display the primitive morphological condition from which the 4-fingered condition of *Carlia* and its two ablepharine relatives must have been derived.

Three of the 5 beta Australian *Leiolopisma* display yet another primitive character from which a more advanced character state displayed by all other beta Australian skinks must have evolved: *Leiolopisma weeksae, challengeri* and *mustelina* have paired frontoparietals while all other Australian betas have fused frontoparietals.[3]

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[1] The only other skinks with a reduced number of fingers and toes previously considered to be in the genus *Ablepharus* are six Australian species: *elegans, distinguenda, orientalis, muelleri, timida, lineata*. These species are now considered to be congeneric (genus *Lerista*) with the Australian skinks formerly referred to *Rhodona* (Greer, 1967a), and are only distantly related to any of the alpha or beta skinks discussed in this paper.

[2] In the single specimen of *Ablepharus burnetti* available to us (MCZ 6486) there is a small palpebral slit remaining along the dorsal edge of the lower eyelid. The eye is effectively "ablepharine," however, as this free dorsal edge is surely too short to allow much movement of the eyelid.

[3] *Geomyersia grabra* may be distinguished from the 2 beta Australian *Leiolopisma* with fused frontoparietals and 5 fingers (*guichenoti* and *delicata*) by the complete absence of prefrontal scales and the depressed body form.

These 3 primitive beta Australian *Leiolopisma* cannot, at this stage of the study, be distinguished morphologically as a group from the African beta *Leiolopisma,* all of which have 5 fingers and separated frontoparietals. This similarity could be the result of either convergence or close relationship. For the present the widely disjunct distribution of the two groups implies to us that the groups have arisen independently in each area, but, admittedly, this is an unsolved problem and will be dealt with elsewhere.

(3) Taken as a group the African betas are themselves taxonomically difficult at an infragroup level. Several characters might be used to distinguish taxa within the African betas: the presence of supranasals, presumably a primitive condition, serves to diagnose *Panaspis;* a scaly lower eyelid, minute ear opening and a group tendency toward an elongate body and reduced number of digits distinguishes *Leptosiaphos;* the ablepharine eye and reduced number of supraocular scales (3 instead of 4) defines the African *"Ablepharus,"* while an African group of *Leiolopisma* could be "diagnosed" negatively on the basis of showing none of these characters. Certain species, however, bridge these apparent taxonomic gaps. For example, *Panaspis cabindae* may have 3 instead of 4 supraoculars (Parker, 1936), and in *P. breviceps* the supranasal may be fused to the nasal (Smith, 1937); in addition, *Leptosiaphos kilimense* and *L. rhodurus* are atypical of other *Leptosiaphos* in displaying a transparent window in the movable lower eyelid. Such difficulties suggest that on the basis of these characters, it might be better to resort to, at most, a subgeneric scheme of ranking taxa.

(4) On the basis of geography, *Geomyersia glabra* would seem more closely related to Australian betas than to African betas. In addition the fused frontoparietals of *G. glabra* may be a morphological indication of relationship with the Australian betas which possess this advanced character in 26 of the 29 species. The African betas have divided frontoparietals, presumably the more primitive condition, in all but one of the 27 species. Only in the African beta *Ablepharus wahlbergi* are the frontoparietals normally fused,[1] a condition probably derived independently from that of the Australian betas with fused frontoparietals.

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[1] The fusion of the frontoparietals and their fusion with the interparietal is a variable condition in *A. wahlbergi* (personal observation and de Witte, 1953).

Geomyersia glabra does, however, have 5 fingers — a character which is predominant in the African betas and which might, therefore, be thought to indicate greater likelihood of relationship with African rather than Australian beta skinks. However, 5 fingers is the primitive condition for both the African and Australian betas, and although in the Australian betas the 4 fingered species are a conspicuous element in that group's radiation, the 5 fingered *G. glabra* can be readily interpreted as a relic of an early stage in the evolutionary history of Australian betas. It would presumably represent a stage later than that of *Leiolopisma weeksae*, *L. challengeri* and *L. mustelina* and approximating that of *L. guichenoti* and *L. delicata*, but with specializations of its own.

Certainly the island of Bougainville on the periphery of the Australian region would be a logical refuge in which to find a relic of an early stage of a radiation taking place in this region.

A dendrogram of the Australian beta skinks, assuming on the basis of present evidence — mainly geographic — that they are monophyletic, is presented in Figure 5.

The radiations of the Australian and African beta skinks will be discussed further in forthcoming papers.

Comparisons with Morphologically Similar Species: It is desirable to mention briefly those species in the Australian Region that are confusingly similar to *Geomyersia glabra* on the basis of external morphology. Only those skinks displaying the external characters of the alpha and beta skinks are discussed.

Leiolopisma mccooyi (Lucas and Frost, 1894) from Victoria lacks prefrontals and has a minute external ear opening as does *G. glabra*, but the frontoparietals of *mccooyi* are divided, the body is not depressed, and the palate is of definitely alpha type.

Lygosoma graciloides Lönnberg and Anderson, 1913 (=*Lygosoma scharffi* Boulenger, 1915) has been collected twice and is known from 4 specimens. Although described twice under the genus *Lygosoma*, the species has the clear spectacle and other external characteristics of the alpha and beta skinks outlined above. Like *Geomyersia glabra* the prefrontals are absent and the ear opening is minute, but *L. graciloides* differs from *Geomyersia glabra* in having paired frontoparietals and only 4 fingers. More important, however, are the palatal differences, for *L. graciloides* is an alpha skink.

The three endemic *Anotis* (or *Siaphos*) on New Caledonia — *mariae*, *gracile*, and *slevini* — are undoubtedly closely related to

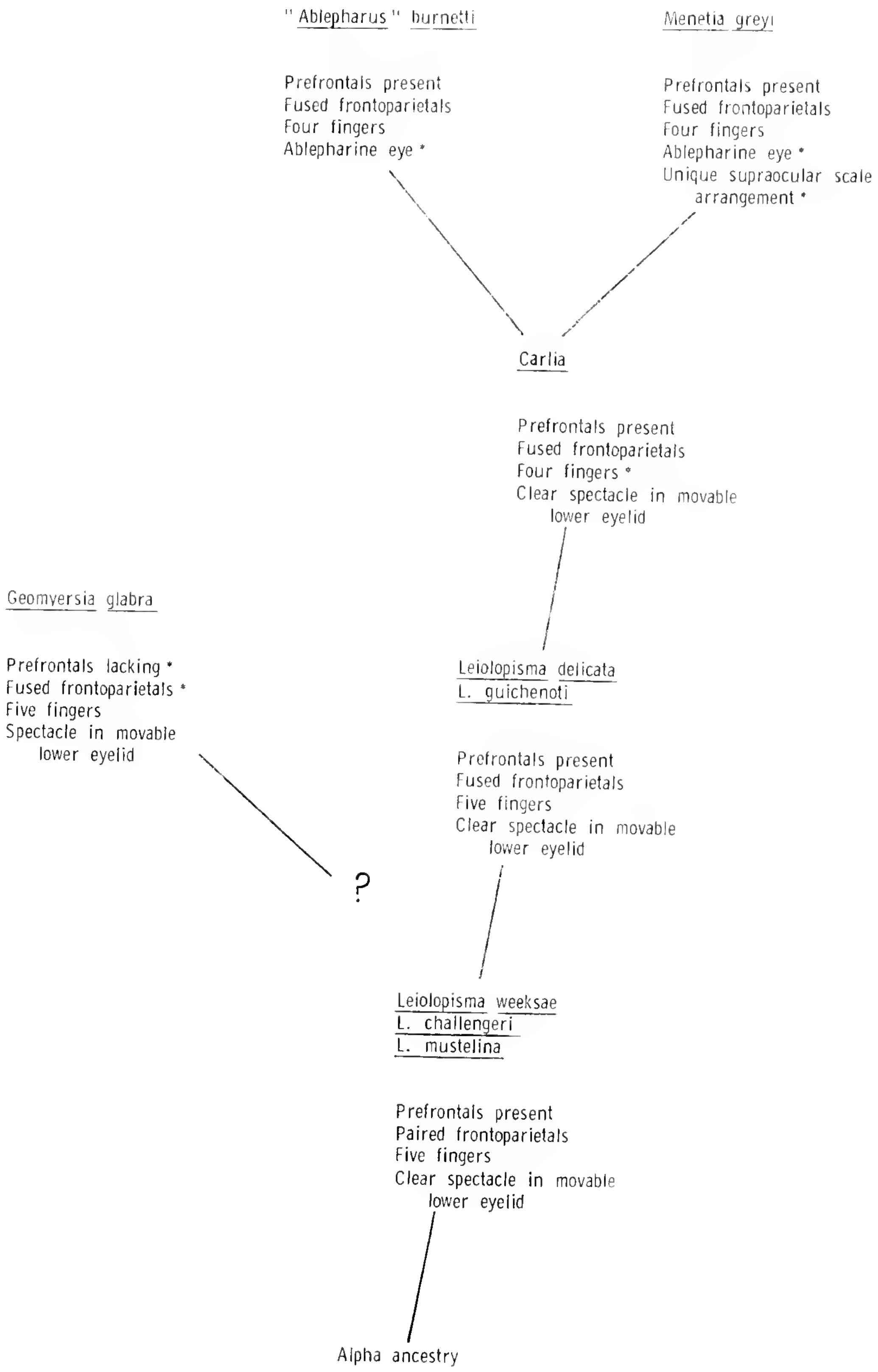

Figure 5. A dendrogram of the Australian Region beta skinks. Changes in character states of a taxon over its immediate hypothetical ancestral condition are marked with an asterisk (*).

each other and rather similar to *Geomyersia glabra* in gross appearance. These three species differ from *G. glabra*, however, in possessing minute prefrontals and, judging from a single skull of *mariae* (MCZ 92393), the group has the alpha palatal pattern.

Although the literature to date on these three species states or implies that there is a clear spectacle in the lower eyelid, the two specimens of *mariae* (MCZ 19605, 46177) and the one specimen of *slevini* (MCZ 9295, holotype) in the Museum of Comparative Zoology clearly show sutures across the eyelid. In the single specimen of *gracile* (MCZ 46172) available, the situation in regard to the eyelid is equivocal. In *G. glabra*, on the other hand, there is a distinct single translucent window in the lower eyelid.

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REVIEW OF THE GENERA OF THE TRIBE LOBERINI (Coleoptera: Languriidae)

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Abstract. The subfamily Loberinae (Bruce 1951) and the tribe Loberini are fully characterized for the first time; the genera of Loberini are redefined; three new subgenera of *Hapalips* are introduced, and a key to the adults of the subgenera of *Hapalips* is given; a new species *Hapalips acaciae* and the larva of *Hapalips prolixus* are described; a key to the genera of the adults of the tribe Loberini is given.

INTRODUCTION

Bruce (1951) was the first author to point out that species of *Telmatophilus* Heer have male genitalia like those of *Cryptophagus* Herbst and unlike those of *Hapalips* Reitter, *Loberus* LeConte, and *Toramus* Grouvelle. He also noted that in the confusedly punctured elytra, *Telmatophilus* agrees with *Cryptophagus* and differs from the last three genera mentioned above, in which the punctures form regular rows. He proposed the name Loberinae for the old Telmatophilinae, excluding *Telmatophilus* but including *Leucohimatium* Rosenhauer, which, despite the simple tarsi, have male genitalia and elytral punctation similar to those in *Loberus*. Sen Gupta and Crowson (1967) considered *Pharaxonotha* Reitter and related genera, including *Leucohimatium* and *Xenoscelis* Wollaston, as comprising the tribe Pharaxonothini of the Loberinae. Recently, Martinez and Berrera (1966) established a new genus *Loberopsyllus*, in the family Cryptophagidae and related to *Loberus*, which is here considered to be in the Pharaxonothini because of the simple tarsi, rather short trochanters, absence of femoral lines on the first ventrite, and narrowly open front coxal

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cavities. The genus *Toramus* and its allies are considered by me (1967) as a subfamily Toraminae of the Languriidae. The characters of the larvae of *Hapalips*, *Pharaxonotha*, and *Bolerus* Grouvelle, given by Rymer Roberts (1939) and Rymer Roberts and Van Emden (1958), and of the larva of *Eicolyctus* Sahlberg, described by Sen Gupta and Crowson (1967), support the classification here proposed.

The chief characters in which the Loberinae differ from the Cryptophagidae are as follows:

Elytral epipleura well defined up to the apex, and elytral punctation usually in regular rows. Wing always with subcubital fleck and radial cell, never with five anal veins. Tarsal formula never 5-5-4 in male. First ventrite not markedly longer than second. Aedeagus turned on one side in resting condition, with long, threadlike, double median struts. Sternal fitting between the mesocoxae with a single knob (found only among the Atomariinae in the Cryptophagidae). Larvae never with annular spiracles, single jointed labial palpi, bifid apex, or serrated caudal margin of prostheca. Larvae with five to six ocelli on each side of head, and granulated upper body surface.

The subfamily Loberinae may be defined by the following characters:

With general characters of Clavicornia, Languriidae (according to Crowson, 1955).

1) Head often with stridulatory files; fronto-clypeal suture absent; transverse line on occipital region sometimes present; anterior part of gular region with (Fig. 20) or without a transverse groove, sometimes with a large transverse cavity (Fig. 23).

2) Antennal insertions hidden by the sides of frons; antennal club three-jointed, sometimes very weakly developed. Mandible with well-developed mola (Fig. 13); maxillary lacinia with three apical spines, galea narrow and elongated (Fig. 8); labium with apical segment of palpi somewhat transverse, mentum sometimes with single or paired cavities on ventral side; ligula usually poorly developed.

3) Front coxal cavities internally open behind (Figs. 2, 6, 24), externally moderately wide open (Fig. 6) to nearly (Fig. 24) or completely closed behind (*Xenoscelis*).

4) Elytra glabrous or pubescent, usually regularly punctured, scutellary striole often present. Wings (Figs. 18, 19) always with four anal veins, radial cell, r-m cross vein; anal cell sometimes present.

5) Mesocoxae usually closely situated, and sternal fitting between them with a single knoblike projection (Fig. 9). Mesosternal pockets (Fig. 9) rarely present, mesepisternal pockets usually well developed (Fig. 9).

6) Metendosternite with anterior tendons separated by slightly less than width of basal stalk, and lateral plates narrow (Figs. 21, 25).

7) Tarsi lobed or simple; trochanters broadly elongate (Fig. 26) or broad and short.

8) Ventrite 1 with (Fig. 1) or without femoral lines. Ovipositor as in Figure 12, with styli attached at the apex of coxites, except in *Leucohimatium,* where the styli are attached slightly above the apex of coxites. Aedeagus of Erotylidae-Languriidae type (Figs. 10, 11).

9) Larvae as far as known with mandibular prostheca large, translucent, and triangular; ocelli usually five to six on each side of the head, sometimes absent; dorsal surface granulated; two tarsungular setae; larvae not endophytic as in Languriinae.

TRIBE LOBERINI

(Loberinae Bruce, 1951: 4, partim.)

This group includes those members of the Loberinae that have lobed tarsi, front coxal cavities that are usually clearly open behind, and cryptophagid-like facies, but that have regular rows of punctures on the elytra. Previously these genera have been included in the family Cryptophagidae. According to present knowledge, the tribe includes seven genera: *Loberus* LeConte, *Telmatoscius* Sharp, *Hapalips* Reitter, *Truquiella* Champion, *Pseudohenoticus* Sharp, *Pseudhapalips* Champion, and *Bolerus Grouvelle.* Of these, only the two largest, *Loberus* and *Hapalips,* occur in both the New and Old Worlds. The genera *Telmatoscius, Truquiella, Pseudohenoticus,* and *Pseudhapalips* are restricted to the New World, and the genus *Bolerus* to the Old World. The species occur mainly in tropical and subtropical climatic zones, a few species of *Loberus* and *Hapalips* extending into warm temperate climates. None have been recorded from Europe. The only previously known larvae are those of *Bolerus* (=*Platycladoxena*) *angulosus* Arrow and a Mexican *Hapalips,* both described by Rymer Roberts (1939). The larva of *Hapalips prolixus* (Sharp) from New Zealand is described below.

The tribe Loberini may be defined by the following characters: With general characters of Languriidae, Loberinae.

1) Head never with a transverse line on vertex.

2) Transverse groove on anterior part of gular region (Fig. 20) almost always present.

3) A pair of stridulatory files on vertex often present (Fig. 22).

4) Antennal club well developed and three-jointed.

5) Front coxal cavities usually moderately wide open, sometimes very narrowly so (*Hapalips*, Fig. 24), but never completely closed behind.

6) Elytra rarely glabrous, usually with punctures in regular rows, and sometimes with scutellary striole.

7) Wing with (Fig. 18) or without (Fig. 16) anal cell.

8) Mesocoxae closely situated except in *Pseudhenoticus;* mesepisternal pockets well developed (Fig. 9).

9) Tarsi pseudotetramerous and trochanters broadly elongated (Fig. 26).

10) Femoral lines on first ventrite always present, and ovipositor of Loberinae-type (Fig. 12); styli attached at the apex of coxites.

11) Larvae as far as known with granules of tergites arranged in regular transverse and longitudinal rows (Fig. 34), frontale without endocarina (Fig. 27), and mandible without hairy appendages at the base of mola (Fig. 29).

Genus Loberus LeConte

Loberus LeConte, 1861: 98. Type species, by subsequent monotypy, *Loberus impressus* LeConte, 1863: 70.
Glisonotha Motschulsky, 1863: 430.

LeConte (1861) established this genus in the family Cryptophagidae but did not name a species of it until 1863. This is the largest genus of the tribe; Schenkling (1923) included 59 species, and Bruce has subsequently added another nine from Africa, Java, and Mexico. Grouvelle (1919) gave a key to the Old World species known at the time, and another for American species that he had seen.

Description. With general characters of Loberinae, Loberini. Facies somewhat cryptophagid-like. Head usually with a pair of stridulatory files; eyes large and moderately coarsely faceted; clypeus with straight apical margin. Antenna with scape longer than pedicel, which is shorter than segment 3; segments 4-8 equal in length, segments 9 and 10 semicircular and transverse, segment 9 slightly narrower than 10, terminal segment slightly longer than broad, its apical margin rather asymmetrically rounded. Prothorax (Fig. 4) transverse, side margins weakly curved, more or less smooth, front and hind margins almost equal in breadth, front angles obtuse, hind angles more acute; prebasal impressions on pronotum present; prosternal process narrow and its apex almost straight. Elytra usually pubescent, rarely almost glabrous, pubescence often double with recumbent setae and sparsely distributed long erect ones as in *Toramus;* punctation on elytra usually in more or less regular rows, rarely quite irregular; scutellary striole absent; epipleura narrow, rather indistinct toward the apex as in *Toramus.* Wing without anal cell (cf. Fig. 15). Mesocoxae closely situated, mesepisternal pockets well developed; metasternum wider than its length, median impressed line extending half of its length. Tarsi with segment 1 very slightly longer than segment 2, segment 3 lobed below, segment 5 almost equal to first three segments together, excluding the lobes; tibiae narrow, not widened at apex. Ventrite 1 with intercoxal process broad at base, narrowed to a pointed apex. Aedeagus as figured (Fig. 11); ovipositor of Loberinae-type (cf. Fig. 12).

Species examined. The species *L. impressus* LeConte and *L. humeralis* Reitter have been studied in detail for the characterization of the genus.

Habitat. Nothing recorded, and larva undescribed.

Geographical distribution. Very extensive, occurring in both the New and Old Worlds, species recorded from North and South America, Ethiopian and Madagascar regions, Indo-Malayan region, and Australia, but absent from Palaearctic region except for the Far East, and not known from New Zealand. It is unfortunate that no authors have made critical comparisons between the New and Old World species of *Loberus.*

Genus TELMATOSCIUS Sharp

Telmatoscius Sharp, 1900: 581. Type species, by monotypy, *Telmatoscius claviger* Sharp.

Sharp (1900) established this genus for a single described species, placing it in the Cryptophagidae, close to *Loberus.* Grouvelle (Grouvelle and Raffray, 1912) added another species, but none has been described since.

Description. With general characters of Loberinae, Loberini. General appearance as in *Loberus* and not very easily distinguishable from it. Differs from *Loberus* in having comparatively long, dense recumbent setae on elytra; prothorax more narrowed in front, and segment 9 of antenna narrower in comparison to segment 10 than in *Loberus.* Head as figured (Fig. 22), with a pair of well-separated stridulatory files; eyes large, fairly coarsely faceted; clypeus with straight apical margin. Antennae with scape slightly larger than pedicel, which is as long as segment 3, segment 4 slightly shorter than 3 and 5, segments 6-8 equal in length, segment 10 distinctly larger than segment 9, terminal segment wider than long, its apex slightly depressed. Prothorax (Fig. 7) weakly narrowed in front, side margins curved and smooth, front angles more or less rounded, hind angles acute; prebasal impressions on pronotum present; prosternal process as in *Loberus*. Elytra without scutellary striole. Meso- and metasterna as figured (Fig. 9), metasternum longer than in *Loberus*, median impressed line extending half of its length. Metendosternite as figured (cf. Fig. 25). Legs and abdomen as in *Loberus*. Aedeagus and ovipositor as figured (cf. Figs. 11, 12).

Species examined. A male and female of *T. claviger* have been studied in detail for generic characters.

Habitat. Nothing recorded, and larva undescribed.

Geographical distribution. Central America.

Genus HAPALIPS Reitter

Hapalips Reitter, 1877: 122. Type species, by present designation, *Hapalips mexicanus* Reitter.

Reitter (1877) established this genus in the family Rhizophagidae, Gorham (1898) transferred it to Languriidae, Fowler (1908) retained it in Languriinae, Champion (1913) and Grouvelle (1919) placed it in Cryptophagidae, and Arrow (1929a) proposed that *Hapalips*, together with all Cryptophagidae having lobed tarsi, be placed in Languriidae. Rymer Roberts (1939) placed *Hapalips* with *Bolerus* (=*Platycladoxena*) *angulosus* in Languriidae, Cladoxeninae, after studying larvae of the two genera. Bruce (1951) noted that the aedeagus of *Hapalips* is similar to those of *Leucohimatium*, *Loberus*, and *Toramus*. Crowson (1955) retained *Hapalips* in the Languriidae and considered it as a transitional form between that family and Erotylidae. This is the second largest genus of the tribe Loberini. Reitter (1877) described eight species, Schenkling (1923) listed 47, to which Arrow (1927) added another one, and more recently, Bruce (1952, 1963) added five more species and excluded one of his older species, *H. spegazzini*, because of its different type of aedeagus. Thus the genus at present consists of 54 valid species. There appears to have been no previous designation of a type for this genus, so I here designate as type *H. mexicanus*, one of the original species described by Reitter (1877) and quite common in Mexico.

Description. With general characters of Loberinae, Loberini. General appearance more or less as in *Xenoscelis* Wollaston; form narrow, elongate, rather flattened, and more or less parallel sided. Head (Fig. 23) with broad clypeus, its front margin evenly rounded; antennal insertions completely hidden by the sides of frons. Stridulatory files rarely present and, if so, paired and well separated; sometimes files represented by a pair of longitudinal ridges without any striations (e.g. *H. fuscus* and *H. acaciae*). Transverse groove on anterior part of gular region sometimes replaced by transverse cavity (Fig. 23). Antenna of moderate length, scape small but longer than pedicel, which is often shorter than segment 3, segments 4-8 usually equal in length, segments 9 and 10 transverse and equal in size, terminal segment equal in breadth to segment 10 and more or less rounded at apex. Prothorax (Fig. 24) usually elongate with side margins smooth, more or less parallel sided, front and hind margins equal in width, all the angles rather obtuse; prebasal impressions on pronotum often indistinct. Front coxal cavities usually with narrow, sometimes slitlike (Fig. 24) opening behind; prosternal process with its apical margin straight. Sometimes shape of pronotum differs between male and female. Elytra with regular rows of strial punctures, usually with a scutellary striole, and pubescence absent or fine and recumbent. Wing with (Fig. 18) or without (Fig. 16) anal cell, radial cell rarely without spur of radial sector (Fig. 17). Mesocoxae closely situated; mesepisternal pockets often obscured; metasternum elongate or as broad as long; median impressed line of metasternum usually extending ⅔ of its length. Tarsi short and compact, first three segments rather broad and equal in length, segment 3 lobed below, segment 4 minute, received in the lobe of segment 3, segment 5 about equal in length to first three together; tibiae rather short, broad at apex, which is obliquely truncate with two normal spurs. Ventrite 1 with intercoxal process pointed at apex. Ovipositor and aedeagus as figured (Figs. 12, 10).

Species examined. The species *H. mexicanus* Reitter, *H. eichelbaumi* Grouvelle, *H. cribricollis* Gorham, *H. grouvellei* Gorham, *H. nigriceps* Reitter, *H. nitidulus* Champion, *H. filum* Reitter, *H. scotti* Grouvelle, *H. prolixus* Sharp, *H. fuscus* Reitter, *H. acaciae* sp. n., and also *H. taprobanae* Grouvelle (external characters only), have been studied in detail for generic characters.

Habitat. Little is known about the habitat of members of this genus. *H. filum* has been recorded from Cuba in corn (maize) stalks, and *H. annulosus* Grouvelle from Guadeloupe in flowers of the cactus *Cereus triangularis*. *H. prolixus* has been recorded from

New Zealand in tree ferns, and more recently R. A. Crowson collected both larvae and adults of this species under the sheathing bases of dead palm leaves. *H. championi* Grouvelle and *H. scotti* Grouvelle are recorded from the Seychelles, both from the bases of palm leaves.

Geographical distribution. This genus is widely distributed in both the New and Old Worlds, mainly in tropical and subtropical regions; a few species extend into warm temperate areas. No species are yet recorded from Australia, and only one species, *H. prolixus*, is known from New Zealand.

Subgenus HAPALIPS *sensu stricto*

Description. With the general characters of *Hapalips.* Form more convex, less parallel-sided; elytra with scutellary striole; wing (Fig. 18) with anal cell and radial cell with spur of Rs. Head sometimes with a pair of stridulatory files; a transverse groove present on gular region (Fig. 20); eyes large, facets moderately coarse. Pronotum more convex, length and breadth more or less equal. Metasternum not elongate, more or less equal in length and breadth.

This subgenus includes the majority of the species.

CAVOPHORUS *subgenus novum*

Type species, *Hapalips fuscus* Reitter

Description. With the general characters of *Hapalips.* General appearance as in *Hapalips sensu stricto.* Head with vestiges of stridulatory files, represented by two longitudinal ridges without striation (Fig. 23). On the gular region, in place of the usual transverse line, there is a large trilobed cavity (Fig. 23), opening ventrally and protected by hairs. Eyes large, as in *Hapalips sensu stricto.* Elytra, wing venation, shape of pronotum and metasternum as in *Hapalips sensu stricto.*

According to present knowledge, this subgenus includes only two Central American species, *H. fuscus* Reitter and *H. acaciae* sp. n.

XENOSCELOIDES *subgenus novum*

Type species, *Hapalips prolixus* Sharp

Description. With the general characters of *Hapalips.* Form more flattened and parallel-sided. Wing without anal cell (Fig. 16), radial cell sometimes without spur of Rs (Fig. 17). Elytra often without stridulatory files; gular region with a transverse groove as in *Hapalips sensu stricto.*

This subgenus includes *Hapalips prolixus* Sharp, *H. filum* Reitter, *H. scotti* Grouvelle, and possibly *H. taprobanae* Grouvelle. I have not been able to check in detail the characters of *H. taprobanae,* which is less flattened than the other species; if it truly belongs in this subgenus, then Grouvelle's name *Loberina* will have priority over *Xenosceloides.*

KEY TO THE SUBGENERA OF HAPALIPS

1. Anterior part of gular region with a large cavity (Fig. 23) . . *Cavophorus*
   Anterior part of gular region without cavity but with a transverse groove (Fig. 20) 2
2. Wing with anal cell (Fig. 18); body shape more convex and less parallel sided; elytra with scutellary striole. Prothorax and metasternum more or less equal in length and breadth. Stridulatory files on head sometimes present; eyes large with moderately coarse facets . . . . *Hapalips*
   Wing without anal cell (Fig. 16); body shape more flattened and parallel sided; elytra often without scutellary striole. Prosternum (Fig. 24) and metasternum longer than broad. Stridulatory files on head absent; eyes smaller with finer facets . . . . *Xenosceloides*

HAPALIPS ACACIAE *species novum*

Holotype, ♀, and paratype ♂, Cotaxtla Exp. Sta., Veracruz, MEXICO, VIII-15-1962, D. H. Janzen coll., seed pods of *Acacia cornigera,* deposited in the Museum of Comparative Zoology, Cambridge, Mass. (holotype MCZ No. 31604). Paratype (on slide), same data, deposited in the Department of Zoology, The University, Glasgow, Scotland.

Measurements of holotype. Total length: 5.58 mm; width of head across eyes: 1.18 mm; length of antenna: 1.26 mm; length of prothorax along midline: 1.23 mm, width across middle: 1.40 mm; length of elytra: 3.60 mm, width across middle: 1.45 mm.

Description. With the general characters of Loberini, *Hapalips (Cavophorus).* Larger and more elongate than *H. fuscus* Reitter; upper surface uniformly reddish brown. Head (Fig. 23) transverse; eyes large and rather coarsely faceted. Vestiges of stridulatory files represented by a pair of widely separated longitudinal ridges without transverse striations. Occipital region glabrous, anterior half of dorsal side of head sparsely clothed with recumbent setae. A large transverse trilobed cavity (Fig. 23) present on anterior part of gular region, opening ventrally and protected by fine hairs. Antenna with scape about double the length of pedicel, which is shorter than segment 3, segments 4-8 equal in length, segments 9 and 10 roughly semicircular, segment 9 slightly less wide than segment 10, terminal segment asymmetrically rounded in apical part and longer than preceding two segments. Prothorax slightly wider than its length, side margins more or less parallel sided, bordered by fine hairs, posterior angles pointed and anterior angles obtuse. Punctation on pronotum coarser and closer than on head, setae minute and directed toward center. Elytra uniformly reddish brown, strial punctures in rows, interstices with sparse fine punctures, scutellary striole rather irregular and indistinct, pubescence short and recumbent. Scutellum minute, narrowed in front and weakly angulate on posterior margin, pubescent. Wing with anal cell. Mesocoxal lines present but very short; mesepisternal pockets obscured. Tarsi densely hairy on underside, first three tarsal segments more or less equal in length, segment 5 about as long as first three segments together. Femoral lines on ventrite 1 very short; intercoxal process narrow and pointed.

KEY TO THE SPECIES OF CAVOPHORUS

1. Species larger and more elongate, about 5.80 mm in length; prothorax more or less equal in length and breadth. Femoral lines on ventrite 1 very short .... *H.* (*c.*) *acaciae* sp. n.
   Species smaller and less elongate, about 3.80 mm in length; prothorax distinctly transverse. Femoral lines on ventrite 1 fairly long .... *H.* (*c.*) *fuscus* Reitter

DESCRIPTION OF A LARVA OF HAPALIPS PROLIXUS SHARP

One larva recorded from New Zealand under the base of dead palm leaves (*Rhopalostylis sapida*) along with the adults, by R. A. Crowson, deposited in the Glasgow University Zoology Department.

Total length 3.48 mm; length of head including labrum 0.64 mm, width across the middle 0.56 mm; width of prothorax across the middle 0.64 mm; width of 9th abdominal segment across the front margin 0.48 mm.

General appearance narrow, elongated, somewhat flattened, tapered in front and behind. Dorsal surfaces bearing many granules symmetrically arranged in a definite pattern of lines, except on pronotum and head, wartlike setiferous tubercles on either side of each tergite, setae near middle line minute and blunt, becoming longer towards sides. Setae on ventral surface rather short, fine and pointed.

Head rather elongate, shape of head and arrangement of setae on dorsal surface as figured (Fig. 27), dorsal surface granulated. Frontal suture rather indistinct, as figured (Fig. 27); endocarina absent. At the base on either side of occipital foramen there are three microscopic peglike setae. Ocelli not distinct. Antennae short, narrow, length of the segments 1:2:2, sensory appendage lying ventrally, ⅔ of the length of segment 3. Mandible (Fig. 29) with two equal teeth, mola well developed bearing transverse ridges and asperites. Between the apical teeth and mola the prostheca translucent and pointed at apex. Ventral crushing tubercle well developed; single sensory pit present in the middle of dorsal side of mandible, another one on ventral side anterior to dorsal one. Maxillary mala (Fig. 31) acute at apex, with three apical spines as in *Hapalips* sp. larva described by Rymer Roberts (1939), a row of seven setae present on dorsal side of inner margin of mala; at the base of these setae on dorsal side a group of small denticles, similar denticles present at the base of palpiger (Fig. 31). Cardo rather long, narrow, at right angle to stipes; maxillary articulating area well developed and oval. Labium (Fig. 32) with two jointed palpi, palpiger not distinguishable; ligula rather indistinct; hypopharynx with well developed hypopharyngeal bracon.

Pronotum slightly wider than head; granulation on dorsal surface irregular. Meso- and metathorax slightly shorter and progressively wider than prothorax; granulation on dorsal side in a regular symmetrical pattern as in abdominal tergites (Fig. 33). Abdominal segments 1-6 equal in length and breadth and equal to metasternum, segments 7-9 progressively narrower. Arrangement of setae and granulation are similar on meso- and metanotum and first 8 abdominal tergites, on tergite 9 granules and setae are arranged as in Figure 33. Each segment with two transverse rows of four minute blunt setae; two pairs of tubercles on either side of each segment, anterior pair carrying two blunt and comparatively short setae, posterior pair with single long and pointed seta (Fig. 33). Urogomphi well developed, as figured (Fig. 33), not hooked or upturned, projecting posteriorly. A pair of setiferous tubercles (pregomphal process) present anterior to urogomphi. Pygopod small, rounded, and not projecting.

All spiracles are bicameral (Fig. 34), lying on body surface, lateral air tubes directed posterolaterally. Legs fairly long, coxae closely situated, claws simple with two tarsungular setae.

This larva may be distinguished from that of *Hapalips* sp. described by Rymer Roberts (1939) by the following key:

Urogomphi long, not hooked (Fig. 33). Mandibular prostheca not narrow or hooked at apex (Fig. 29). Ocelli obscured. Tubercles on each segment with pointed and blunt setae (Fig. 33) ....*H. prolixus* Sharp

Urogomphi short, hooked. Mandibular prostheca rather narrow and hooked at apex. Ocelli 5 posterior to antenna. Tubercles on each segment with single long pointed seta ....*Hapalips* sp.

Discussion. Although all the species of *Hapalips* are restricted to the warmer climatic zones, the two larger subgenera are represented in both the New and Old Worlds; even within these subgenera there are no obvious general differences between the New and Old World forms. The subgenus *Cavophorus*, with only two known species, both restricted to the New World, appears to represent a specialized development from *Hapalips sensu stricto*, at least in respect to the vestigial stridulatory files and the big cavity in the anterior part of the gular region, apparently developed from the transverse groove which is present in other *Hapalips* in the same position. The subgenus *Xenosceloides* is another group which may represent a specialized off-shoot of *Hapalips sensu stricto;* the main differences between *Xenosceloides* and *Hapalips sensu stricto* parallel those between the genus *Hemipeplus* Berth and its relatives in the Mycteridae (Heteromera). Typical *Hemipeplus* spp. as far as known occur under leaf bases of palms, as do *Xenosceloides* adults. Thus the distinguishing features of *Xenosceloides* may be adaptive to this mode of life and may have originated independently in the Old and New Worlds, in which case *Xenosceloides* would not be a natural subgenus. Further research will be needed to establish whether this is in fact the case. The only specifically identified larva of this genus is that of *H. prolixus* from New Zealand, which shows considerable differences, as well as similarities, when compared with the larva of *Hapalips* sp. described by Rymer Roberts (1939) from Mexico; the differences are such that the two larvae would be expected to represent at least different subgenera. If the Mexican larva is really of a *Hapalips sensu stricto*, then larval characters support the separation of *Hapalips sensu stricto* and *Xenosceloides* as subgenera; if, on the other hand, the Mexican larva proves to be of a *Xenosceloides*, this will strongly support the theory that the New and Old World forms of the subgenus are not really related.

Genus TRUQUIELLA Champion

Truquiella Champion, 1913: 87. Type species, by monotypy, *Truquiella gibbifera* Champion.

This monotypic genus was established by Champion (1913) under Cryptophagidae; I have found no subsequent references to it. Champion described it as having tetramerous tarsi, but I found its tarsi to be pseudotetramerous, as in other Loberini. The genus seems to be very closely related to *Hapalips*.

Description. With general characters of Loberinae, Loberini. General facies more or less as in *Hapalips*. Head with fairly large and coarsely faceted eyes. Stridulatory files apparently absent. A pair of protuberances present on anterodorsal side of eyes (Fig. 3) in both sexes, more prominent in male; clypeus broad with rounded apical margin as in *Hapalips;* antennal insertions completely hidden by frons. Antenna moderately long, with scape small but larger than pedicel, which is shorter than segment 3; segments 4-8 equal in length and shorter than segment 3; segments 9 and 10 weakly transverse, terminal one elongate with rounded apex. Prothorax weakly transverse, side margins smooth, front and hind margins more or less equal in breadth, front angles slightly projecting forward and weakly acute, hind angles obtuse. Prebasal impressions on pronotum obscured; front coxal cavities rather narrowly open behind; prosternal process narrow and truncated at apex. Elytra with regular rows of punctures, scutellary striole present. Wing with closed anal cell, venation as in *Hapalips eichelbaumi* Grouvelle (Fig. 18). Mesocoxae closely situated; mesepisternal pockets weakly developed; metasternum weakly transverse; median impressed line extending ⅔ of its length. Tarsi with first three segments equal in length, segment 3 lobed below, segment 4 minute and segment 5 about as long as first four together; tibiae weakly broadened at apex with two normal spurs. Intercoxal process of ventrite 1 narrow and pointed at apex.

Habitat. Unknown, larva undescribed.

Geographical distribution. Mexico.

Genus PSEUDHAPALIPS Champion

Pseudhapalips Champion, 1913: 112. Type species, by monotypy, ***Pseudhapalips lamellifer*** Champion.

Champion (1913) established this genus under Cryptophagidae, and described it as closely related to *Hapalips,* although he noted several dissimilarities from *Hapalips,* e.g. the extraordinary form of head, very prominent eyes and thorax, as in *Platoberus*, etc. He described the front coxal cavities as closed behind, but careful study of a slide preparation reveals that these cavities are distinctly open behind (Fig. 6). Arrow (1929a) described *Pseudhapalips* as having stridulatory files on the head, but neither I nor Mr. R. D. Pope of the British Museum could find stridulatory files on the head of *P. lamellifer*. It seems that the genus may be related to *Hapalips*, as suggested by Champion and Arrow, but not very closely. Since Champion's description only one species has been added to this genus, and that was by Grouvelle (1919) from French Guiana.

Description. With general characters of Loberinae, Loberini. Head transverse, in male with a strong ridge between the eyes; in female this ridge is less distinct and flattened in front; clypeus broad with rounded apical margin. Eyes large, markedly projecting and moderately coarsely faceted. Antenna moderately long with scape slightly longer than pedicel, which is slightly shorter than segment 3, segments 3-8 equal in length, club loose, segment 9 very slightly wider than segment 10, terminal segment rather transverse and rounded at apex.

Prothorax (Fig. 6) strongly transverse, slightly narrowed behind, side margins weakly undulate or dentate, front angles slightly projecting and obtuse, hind angles acute. Prebasal impressions on pronotum strongly marked; prosternal process weakly broadened posteriorly with straight apical margin (Fig. 6). Elytra glabrous, strial punctures in regular rows and with a scutellary striole. Wing as figured (Fig. 15), without anal cell. Mesepisternal pockets weakly developed; metasternum elongate and median impressed line extending to ⅔ of its length. Tarsi are unlike *Hapalips*, first three segments lobed below, segment 5 equal to length of first two segments together; tibiae broadened at apex. Ventrite 1 with intercoxal process narrow and pointed at apex.

Habitat. Unknown, larva undescribed.

Geographical distribution. Amazon, Surinam, and French Guiana.

Genus PSEUDHENOTICUS Sharp

Pseudhenoticus Sharp, 1900: 596. Type species, by monotypy, *Pseudhenoticus parallelus* Sharp.

Sharp (1900) established this genus under Cryptophagidae and placed it just before *Henoticus*. Grouvelle (1919) added 10 species to it, and more recently, Bruce (1943) described another species from Madagascar. From Bruce's figure and description it seems very doubtful whether this specimen is a true *Pseudhenoticus* or even a member of Loberini; if it is a *Pseudhenoticus,* then the genus will manifest a distribution pattern unusual in Clavicornia, though it is known in some other organisms.

Description. With general characters of Loberiinae, Loberini. Head transverse, clypeus less broad than in *Hapalips,* broad at base, narrowed in front, its apical margin rounded. Unlike *Hapalips,* frons scarcely projecting over antennal insertions. Stridulatory files apparently absent; eyes of moderate size and very finely faceted. Antenna rather short and stout, scape, pedicel and segment 3 more or less equal in length, segments 4-8 slightly shorter than segment 3 and equal in size, segments 9 and 10 somewhat semicircular, and terminal segment elongated, about double the length of segment 10. Prothorax (Fig. 5) transverse, weakly narrowed in front, side margins undulate or more or less dentate, prebasal impressions on pronotum present. Front coxal cavities rather narrowly open behind; prosternal process broad at apex as in *Bolerus* (cf. Fig. 2). Elytra with regular rows of punctures and without scutellary striole, pubescent. Meso- and metacoxae moderately widely separated, sternal fitting between the mesocoxae in a straight line. Metasternum transverse, narrowed in front, median impressed line extending ⅔ of its length. First three tarsal segments more or less equal in length, segment 2 weakly and segment 3 strongly lobed below and narrow, segment 5 almost equal in length to first three segments together; tibiae slightly broadened at apex. Ventrite 1 with intercoxal process moderately broad and its apical margin rounded.

Habitat. Unknown, larva undescribed.

Geographical distribution. Panama, Bolivia,? Madagascar.

Genus BOLERUS Grouvelle

Bolerus Grouvelle, 1919: 93. Type species, by present designation, *Crotchia minuta* Fleutiaux, 1887: 68.

Thallisellodes Arrow, 1925: 257. Type species, by original designation, *Thallis transversus* Gorham, 1895: 325.

Platycladoxena Kraatz (partim), — Arrow, 1929a: 316.

Crotchia Fowler (partim), — Fleutiaux, 1887: 68.

The nomenclature of this genus is very complicated. The genus *Platycladoxena* (type *P. castanea* Kraatz) was established by Kraatz (1899), in the Languriidae. Arrow (1925) synonymized it with *Microlanguria* Lewis and erected a new genus *Thallisellodes* with four species. He later (1929a) stated that *P. castanea* and

P. javanica of Kraatz are congeneric with *Thallisellodes* and sank the latter name. In the same paper, he listed 13 valid species in this genus. Grouvelle (1919) described the genus *Bolerus*, which he considered to be related to *Hapalips* and *Loberus*, and transferred *Crotchia minuta* Fleutiaux to the genus *Bolerus*. Arrow (1929a) pointed out that the species of *Bolerus* are congeneric with *Thallisellodes*. Villiers (1961), having seen the type material of *Platycladoxena castanea* Kraatz, stated that the two specimens represented two distinct species, both of the genus *Microlanguria;* the lectotype should be named *Microlanguria castanea* (Kraatz), while the other specimen was described as *M. angulosa* Villiers. The above facts indicate that the genus *Bolerus* Grouvelle (1919) must have priority over *Thallisellodes* Arrow (1925). Unfortunately, Grouvelle did not specify a type of his genus *Bolerus;* therefore I here designate *Crotchia minuta* Fleutiaux as type species. This is one of the species originally included by Grouvelle (1919).

The species *Bolerus minutus*, which I have studied in detail, seems to be very similar to *Thallisellodes angulosus* Arrow and *T. transversus* (Gorham). I have found its characters more similar to those of the Loberini than to those of Cladoxenini (e.g. front coxal cavities internally open behind and ovipositor like other Loberini with styli attached at the apex of coxites). Rymer Roberts (1939) described the larva of *Bolerus* (=*Platycladoxena*) *angulosus* Arrow and stated that it is very similar to the larva of *Hapalips*. The present study supports the view of Grouvelle and Rymer Roberts and shows that the genus is actually related to *Hapalips* and probably *Pseudhenoticus*.

Description. With the general characters of Loberinae, Loberini. General appearance less linear than in *Microlanguria* and prothorax strongly transverse. Head transverse, with a pair of closely situated stridulatory files; eyes fairly large and moderately coarsely faceted. Clypeus broad at base and narrowed in front, with straight or weakly rounded apical margin; antennal insertions less hidden under frons than in *Hapalips*. Transverse groove on anterior gular region weak but distinguishable. Antenna with scape and segment 3 longer than pedicel, club rather compact and segments 9, 10, and 11 transverse and equal in length, apical segment rounded at apex and slightly less transverse than segment 10, sometimes club loose and apical segment elongate and pointed at apex. Prothorax (Fig. 2) parallel sided, side margins more or less smooth or finely dentate, front angles rather rounded, hind angles somewhat acute, prebasal impressions on pronotum strongly marked. Front coxal cavities rather narrowly open behind, prosternal process as figured (Fig. 2), sometimes sinuate at apical margin. Elytra glabrous, strial punctures in regular rows and with scutellary striole. Wing as figured (Fig. 19), with an anal cell. Mesocoxae moderately widely separated; mesepisternal pockets well developed; metasternum weakly transverse; mesocoxal lines short; median impressed line extending about ⅔ of its length. Metendosternite broad and short, as figured (Fig. 21). Tarsi as in *Hapalips;* tibiae broad at apex and obliquely truncated. Ventrite 1 with intercoxal process slightly broad, shape as figured (Fig. 1); sometimes a second pair of lines present on outer sides of the normal femoral lines (Fig. 1).

Habitat. Adults and larvae of *B. angulosus* have been found on a lichen-covered rock in a cave in Malaya.

Geographical distribution. Indo-Malayan region.

KEY TO THE GENERA OF THE TRIBE LOBERINI

1. Trochanters short and broad; tarsi simple, except in *Xenoscelis,* where segment 3 is very slightly lobed below. Femoral lines on first ventrite absent; anterior part of gular region without transverse groove. Front coxal cavities usually narrowly open, rarely completely closed behind (*Xenoscelis*) ....Tribe Pharaxonothini

— Trochanters broadly elongate (Fig. 26); tarsi distinctly lobed below, with minute segment 4. Femoral lines on first ventrite present; anterior part of gular region with a transverse groove (Fig. 20) or a cavity (Fig. 23). Front coxal cavities usually fairly widely, more rarely narrowly open behind ....Tribe Loberini....2

2. Mesocoxae more widely separated and sternal fitting between them in a straight line. Prothorax (Fig. 5) with anterior part of side margins undulated. Intercoxal process of first ventrite broad with more or less rounded apical margin ....*Pseudhenoticus*

— Mesocoxae more closely situated and sternal fitting between them with single knob (Fig. 9). Prothorax not as above. Intercoxal process of first ventrite narrow and pointed at apex (except in *Bolerus*) 3

3. Prothorax as figured (Fig. 2), with prosternal process broad at apex. Elytra glabrous; mesocoxal line on metasternum present. Intercoxal process of first ventrite broad, as figured (Fig. 1) ....*Bolerus*

— Prothorax with prosternal process not as above. Elytra usually hairy; mesocoxal lines on metasternum absent. Intercoxal process of first ventrite narrow and pointed 4

4\. Species larger, narrow and elongated, less Cryptophagidae-like in form. Elytra with scutellary striole (except in *Hapalips scotti* Grouvelle); wing often with anal cell (Fig. 18). Tibiae broad and truncate at apex; tarsal lobes broad. Metasternum less transverse 5

— Species smaller, more elliptical and Cryptophagidae-like in form. Elytra without scutellary striole; wing without anal cell. Tibiae slender, not broadened at apex; tarsal lobes narrow. Metasternum more transverse 7

5\. Prothorax as figured (Fig. 6), side margins dentate or undulate, front angles projecting forward. Tarsal segments 2 and 3 lobed below. Anterior part of dorsal side of the head with transverse ridge . . . . *Pseudhapalips*

— Prothorax not as above, side margin not dentate or undulate, front angles not projecting forward. Only tarsal segment 3 lobed below. Head not as above 6

6\. Head with a pair of humps on anterodorsal sides of eyes (Fig. 3). Prebasal impressions on pronotum indistinct. Elytra pubescent. *Truquiella*

— Head without humps as above. Prebasal impressions on pronotum usually distinct. Elytra glabrous or pubescent . . . .*Hapalips*

7\. Prothorax narrowed in front, shape as figured (Fig. 7). Antenna with segment 9 considerably smaller than segment 10, which is markedly broad . . . .*Telmatoscius*

— Prothorax not narrowed in front, shape as figured (Fig. 7). Antennal segment 9 very little smaller than segment 10, which is less transverse . . . .*Loberus*

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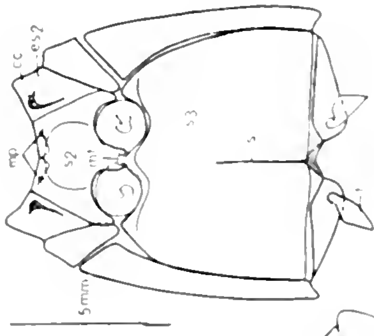
EXPLANATION OF LETTERING ON FIGURES

ac — anal cell
as — apical spine
at — anterior tendon
cc — mesepisternal pocket
cp — corpotentorium
ct — coxite
es2 — mesepisternum
ga — galea
hr — hypopharyngeal bracon
hu — hump
la — lacinia
lp — lateral plate
ls — longitudinal line on metasternum
lt — laminatentorium
m — mola
ml — median lobe
mp — mesosternal pocket
ms — median strut
mt — metasternal knob or projection
my — pocket or mycangium(?)
p — paramere
pa — peglike setae
Pp — paraproct
pr — prostheca
s2 — mesosternum
s3 — metasternum
si — styli
sl — stridulatory file
su — supratentorium
tc — trochanter
tg — transverse groove on anterior part of gular region
ur — urogomphi
vf — valvifer
vp — sensory appendage
vt — ventral crushing tubercle



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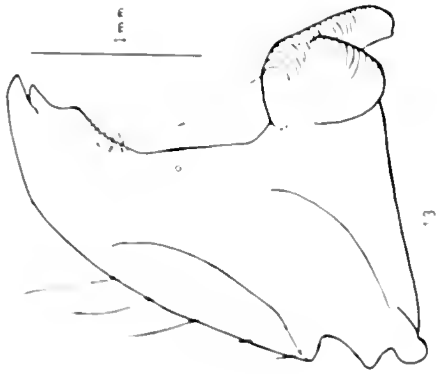

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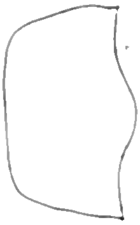

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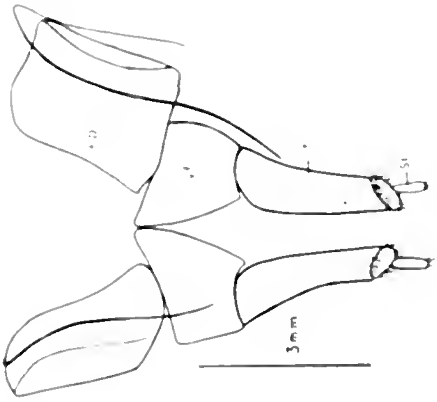

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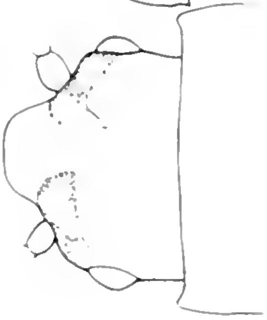

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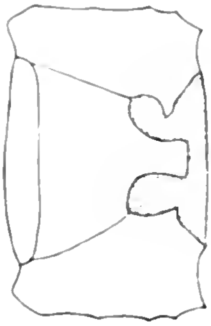

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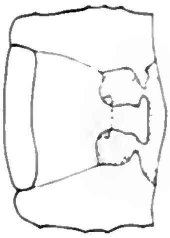

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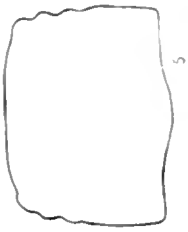

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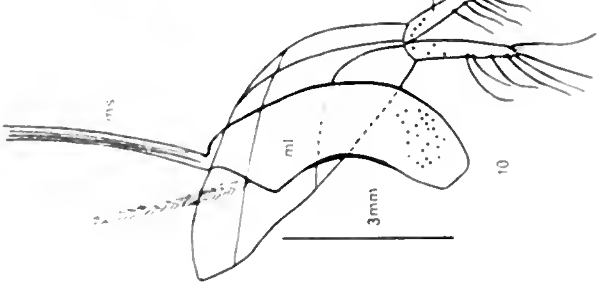

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FIGS. 1-14. 1. First ventrite of *Bolerus minutus;* 2. Prothorax, ventral view of *Bolerus minutus;* 3. Head, dorsal view of *Truquiella gibbifera;* 4. Pronotum of *Loberus impressus;* 5. Pronotum of *Pseudhenoticus parallelus;* 6. Prothorax, ventral view of *Pseudhapalips lamellifer;* 7. Pronotum of *Telmatoscius claviger;* 8. Right maxilla, dorsal view of *Hapalips nitidulus;* 9. Meso- and metathorax, ventral view of *Telmatoscius claviger;* 10. Aedeagus of *Hapalips nitidulus;* 11. Aedeagus of *Loberus impressus;* 12. Ovipositor of *Hapalips acaciae;* 13. Right mandible, ventral view of *Telmatoscius claviger;* 14. Aedeagus of *Hapalips prolixus.*


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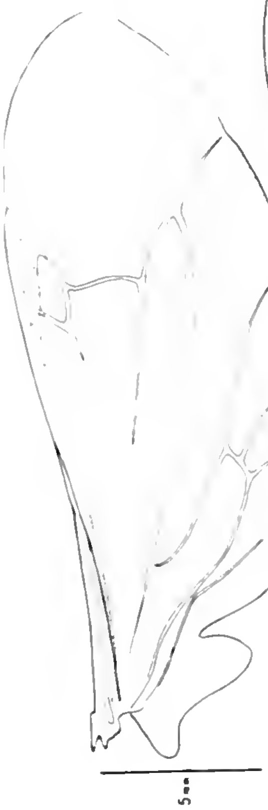

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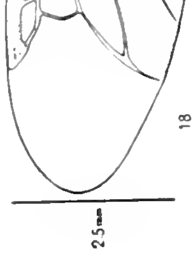

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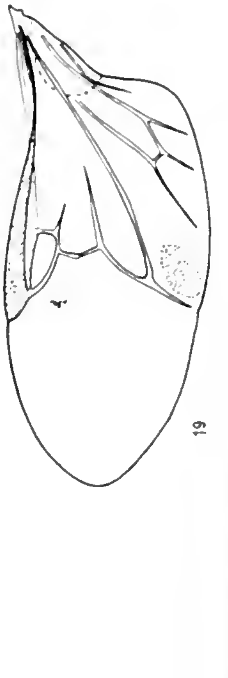
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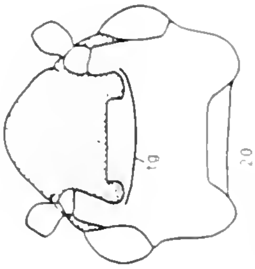

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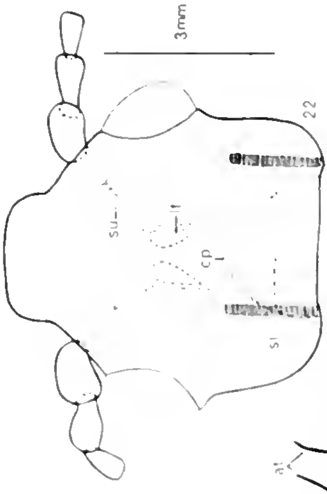

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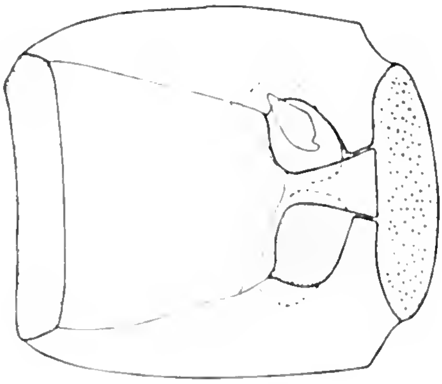
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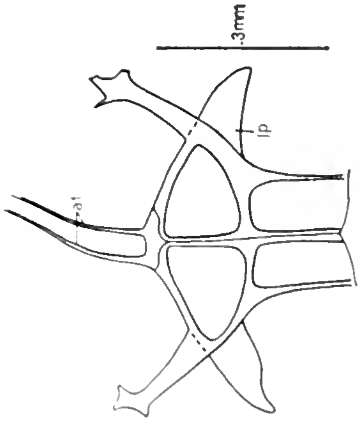

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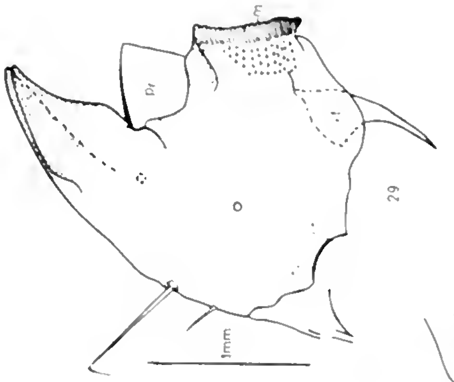
FIGS. 15-26. 15. Wing of *Pseudhapalips lamellifer;* 16. Wing of *Hapalips filum;* 17. Radial cell (wing) of *Hapalips scotti;* 18. Wing of *Hapalips eichelbaumi;* 19. Wing of *Bolerus minutus;* 20. Head, ventral view of *Hapalips cribricollis;* 21. Metendosternite of *Bolerus minutus;* 22. Head, dorsal view of *Telmatoscius claviger;* 23. Head, ventral view of *Hapalips acaciae;* 24. Prothorax, ventral view of *Hapalips filum;* 25. Metendosternite of *Hapalips acaciae;* 26. Hind trochanter of *Hapalips cribricollis.*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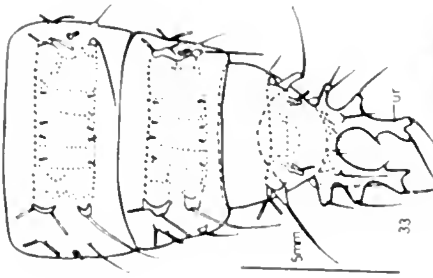
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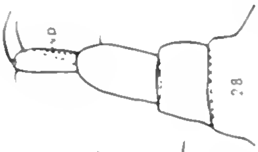
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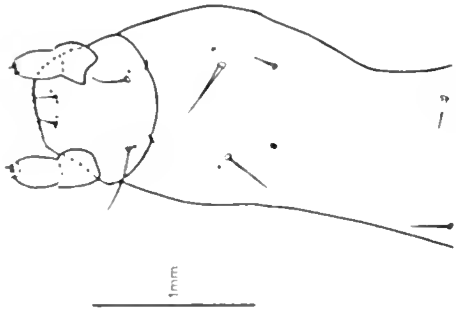
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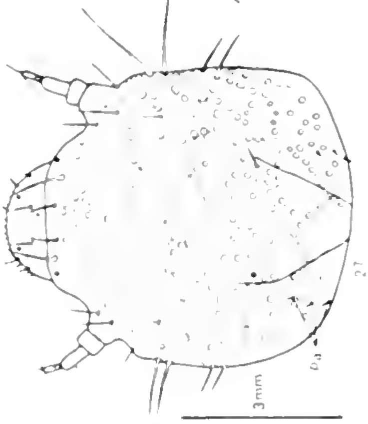
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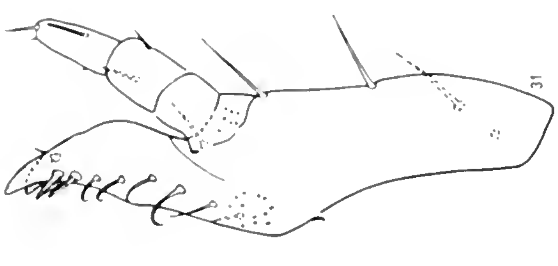
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FIGS. 27-34. Larva of *Hapalips prolixus*. 27. Head, dorsal view; 28. Antenna, dorsal view; 29. Left mandible, dorsal view; 30. Hypopharynx; 31. Left maxilla, dorsal view; 32. Labium, ventral view; 33. Posterior segments, dorsal view; 34. 5th abdominal spiracle.

BREVIORA

Museum of Comparative Zoology

Cambridge, Mass. 31 December, 1968 Number 304

REDESCRIPTIONS OF *ANACHIS AVARA* (SAY) AND *ANACHIS TRANSLIRATA* (RAVENEL) WITH NOTES ON SOME RELATED SPECIES (PROSOBRANCHIA, COLUMBELLIDAE)[1]

Amelie H. Scheltema[2]

ABSTRACT

Both *Anachis avara* (Say) and *A. translirata* (Ravenel) are found from Massachusetts to southern Florida. The shell of *avara* varies geographically from short and broad with many fine ribs in the north to tall and slender with a few heavy ribs in the south. *A. translirata* does not vary in shell morphology over its range. In New England the two species are very commonly found together at mean low water and have usually been confused with each other because of a superficial similarity in ribbing on the shell. Egg capsules and veliger larvae of northern and southern populations of *avara* are morphologically similar. Egg capsules, larvae, and radulae of *translirata* are different from those of *avara*.

In southwestern Florida, *avara* is replaced by *A. semiplicata* Stearns, which appears to be a species endemic to that area. The relationships of an *Anachis* species in the western Gulf of Mexico are not clear. Egg capsules of *A. floridana* Rehder show it to be a species distinct from *avara*. *A. similis* (Ravenel) is considered to be a *nomen dubium*.

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[1] Contribution No. 1888 from the Woods Hole Oceanographic Institution, Woods Hole, Massachusetts.

[2] C/o Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543.

INTRODUCTION

Two very common gastropod species living along the shores of southern New England are the columbellids *Anachis avara* (Say, 1822) and *A. translirata* (Ravenel, 1861). The shells and living animals of both are quite similar, and the two species have a long history of being confused with each other. South of New England misidentifications have been fewer for two reasons: first, *translirata* is much less common near the tideline from New Jersey south (see Table 1); second, *avara* is highly variable in shell form, and those from southern localities are less similar to *translirata* than those from New England.

Gould (1841), in his early work on New England invertebrates, recognized only one species, *avara*. Verrill (1873) noted correctly that another species of *Anachis* occurs in New England, which he called *A. similis* (Ravenel, 1861). However, I regard *similis* a *nomen dubium* (see p. 12) and *translirata* the correct designation. Verrill figured *similis* with a shell of *avara* reproduced from Gould (1870). From Verrill's work until the present time, "*avara*" has been the name more usually applied to both species; when *translirata* has been recognized as a distinct form, the names "*similis*" and "*translirata*" have been used indiscriminately, often as varieties or subspecies of *avara* (e.g., Dall, 1889; Johnson, 1934). Abbott (1954) gave correct names and descriptions of the two species, but unfortunately the plate figures are reversed and the geographic ranges are not correct.

Recently, Scheltema and Scheltema (1963) described the egg capsules and veliger larvae of *translirata* as those of *avara*, because the adults from which egg capsules were obtained were compared with misidentified museum specimens. The error became evident when new keys to invertebrates in the Woods Hole region were being compiled (Smith, ed., 1964). Subsequently, *avara* were collected alive in Beaufort, North Carolina, and held in aquaria; these snails deposited egg capsules that were distinctly different from those of *translirata*. This fortunate circumstance made possible the identification of similar capsules often found attached to eel grass in the Woods Hole area, and consequently larvae have been reared from both Beaufort and Woods Hole populations of *avara*. These larvae were morphologically the same, and distinctly different from those of *translirata* in their soft external anatomy (Scheltema, MS in preparation). Therefore, on the basis of capsules and larvae, it has been verified that the two New England forms of *Anachis* are distinct species, and also that the southern and northern forms of *avara* constitute a single species.

The necessity for redescribing the two species and for determining their geographic ranges became obvious if common errors in identification were to be corrected.

ACKNOWLEDGMENTS

Material has been made available to me through the generosity of many individuals and museums. I would like particularly to thank Emma B. Richardson of the Charleston Museum, Joseph Rosewater and George Radwin of the U.S. National Museum (USNM), R. Tucker Abbott and Robert Robertson of the Academy of Natural Sciences of Philadelphia (ANSP), and William J. Clench of the Museum of Comparative Zoology (MCZ). Robert H. Parker, Jack B. Pearce, and Edmund H. Smith, formerly of the Systematics-Ecology Program, Marine Biological Laboratory, Woods Hole, kindly allowed me to make use of their *Anachis* collections. I am extremely grateful to Louise Ridge for her many efforts and hours of collecting to provide me with live specimens of *Anachis floridana,* which she mailed from Florida. John R. Hall and Robert Robertson made the photographs of the shells on Plate I, for which I am very appreciative. Thanks are due also to Ruth D. Turner and Kenneth J. Boss, who gave this paper a critical reading and made several helpful comments.

Finally, I take pleasure in acknowledging the financial support of The Radcliffe Institute, a grant from which has made this work possible.

ANACHIS TRANSLIRATA (Ravenel)

Plate 1, figs. 1, 2, 6; Text-figs. 1b, 2b; Table 1

Columbella translirata Ravenel 1861, Proc. Acad. Nat. Sci. Philadelphia 1861: 42 (no fig.) ("off Charleston bar" [South Carolina]). [Type specimen probably destroyed.][3]

Columbella avara Say. Gould 1841, Invertebrata of Massachusetts, pp. 313-314 (in part), fig. 197; Tryon 1883, Manual of Conchology, **5**: 159 (in part).

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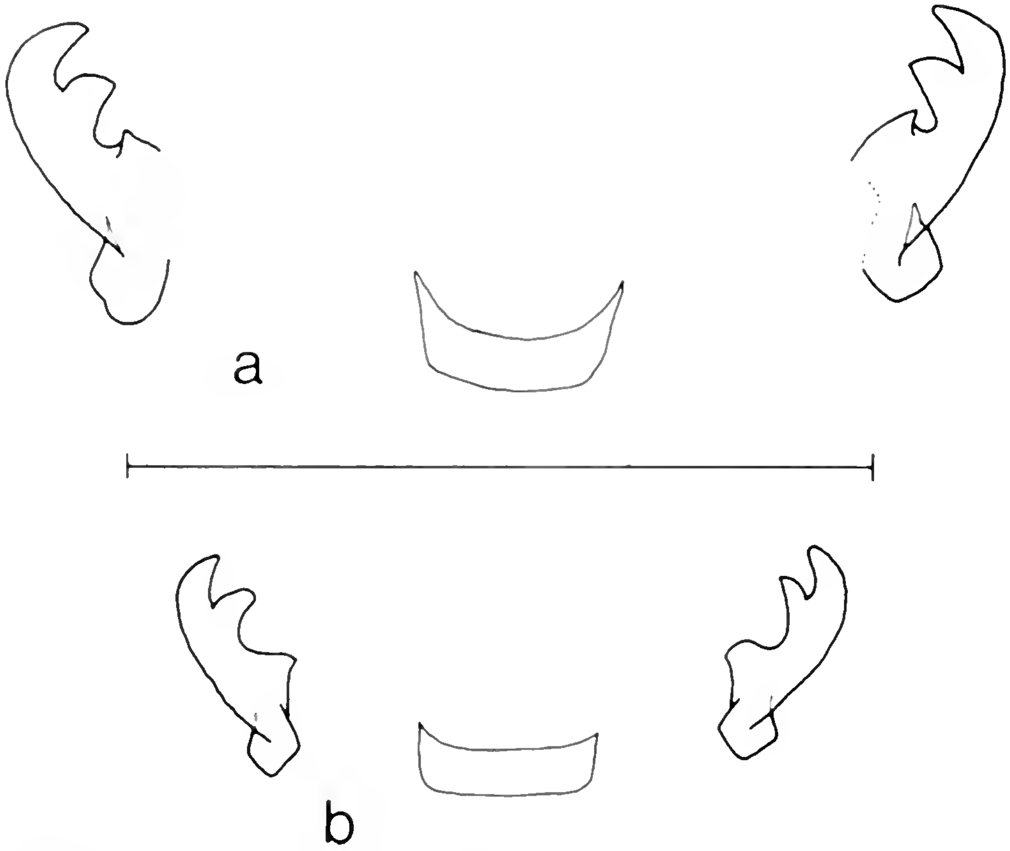
[3] Much of Dr. Ravenel's collection, which lay in the line of General Sherman's march through South Carolina in 1865, was destroyed; no labeled specimens of either *A. translirata* or *A. similis* remain in his collection at the Charleston Museum. Ravenel's description of *translirata,* although not figured, is sufficiently precise to enable one to ascertain the species to which he was referring.

Anachis avara (Say). Perkins 1869, Proc. Boston Soc. Nat. Hist. **13**: 113 (in part); Sumner, Osburn, and Cole 1913, Bull. U.S. Bur. Fish. **31**(2): 710-711, 712 (in part); M. Smith 1945, East Coast Marine Shells, p. 119, pl. 46, fig. 24; Abbott 1954, American Seashells, pl. 25, fig. ee (fig. only); Scheltema and Scheltema 1963, Hydrobiologia **22** (1-2): 85-91, 13 text-figs. (egg capsules and larvae).

Anachis similis (Ravenel). Verrill 1873, Rept. U.S. Comm. Fish. and Fisheries 1871-1872: 644-645 (description only, not fig. 109).

Anachis avara translirata (Ravenel). Dall 1889, Bull. U.S. Nat. Mus. **37**: 116.

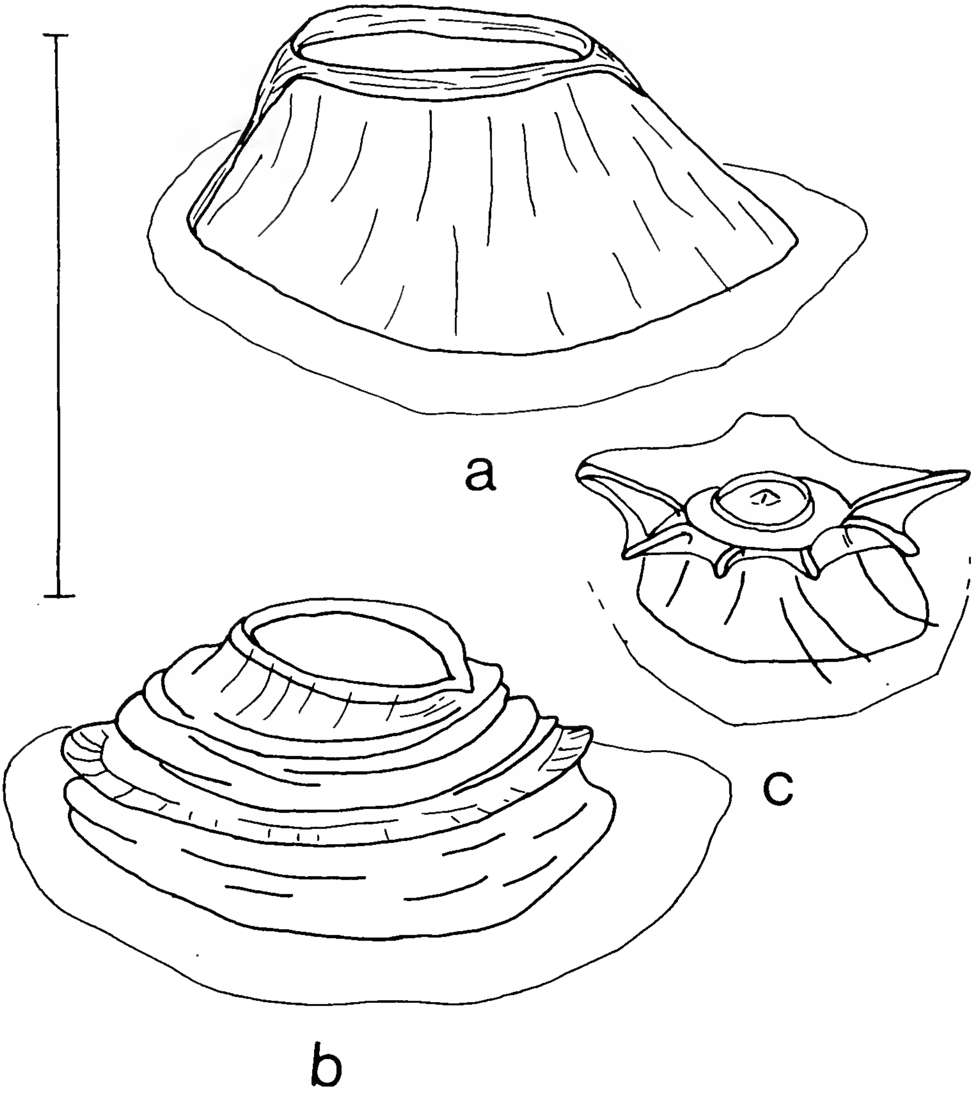
Anachis avara similis (Ravenel). Dall 1889, Bull. U.S. Nat. Mus. **37**: 116; M. Smith 1945, East Coast Marine Shells, p. 119, pl. 46, fig. 19 (juvenile).



Text-Fig. 1. Radular teeth of (a) *Anachis avara* and (b) *Anachis translirata*. Scale line equals 0.2 mm.

Description. Shell elevated, conical, whorls flattened and regularly ribbed. Height to 17.5 mm, width to 6.5 mm, median range in height 12.5 to 14.0 mm. Average width to length ratio 0.40. Aperture a little less than one-half total height of shell. Larval whorls (protoconch) three, smooth, rounded, and translucent.

Post-larval whorls seven or eight, nearly flat, with distinct, regularly spaced, straight axial ribs and less distinct spiral striae. Suture indented. Ribs usually parallel to shell axis, and most elevated at the suture. Those on the spire extend from suture to suture and are about the same width as the interspaces. Ribs on the body whorl average 15 (range 11 to 20), are not as closely spaced as those on upper whorls, and extend from the suture to just below the periphery, except that those near the aperture extend only to the periphery. Periphery somewhat angulated. Faint axial ridges sometimes apparent below periphery, extending between ends of ribs of body whorl. Outer lip often thickened so as to obliterate one or more ribs. Spiral striae usually distinct between ribs.



Text-Fig. 2. Egg capsules of (a) *Anachis avara,* (b) *Anachis translirata,* and (c) *Anachis floridana.* Scale line equals 1.5 mm.

The first spiral stria following the suture is the widest, uually the most deeply impressed, and crosses the ribs, producing the subsutural nodules that are the distinctive shell character of the species. Other striae may or may not cross ribs, giving a more or less cancellate appearance; the first two post-larval whorls in particular are often beaded. Spiral striae least impressed at periphery. Below periphery, spiral striae are deeply impressed and form the dominant shell sculpture; they produce weak beading as they cross the axial ribs and ridges. Aperture elliptical. Outer lip thin or thick, recurved anteriorly to form a short siphonal canal. When the lip is thickened it is recurved posteriorly into an anal notch. Teeth may be present on outer lip when it is thickened, and range from three to nine (average 6) in number, often indistinct, the largest posterior. Parietal callus, when present, is narrow, sharp-edged, and bears a number of teeth, which are the ends of the spiral striae. Columella is smooth. Shell is dull, color varying from straw-yellow to chestnut-brown, often with spiral streaks of white, especially at subsutural knobs and angulation of periphery, emphasizing these characters. Juveniles are without thickened lip or callus, and with the periphery sharply angulated.

Operculum elliptical, concentric, with eccentric nucleus.

The radula is rachiglossan; the median tooth is a flat plate; the lateral tooth has three cusps, with the proximal one rounded (Text-fig. 1b).

Pigmentation of head and foot similar to that of *A. avara* (*q.v.*), except that the white posterodorsal tip of the foot is small and grades into the mottling of the rest of the foot.

Egg capsule volcano-shaped, ringed by sculpture of concentric ridges, with one ridge more pronounced than the rest (Text-fig. 2b).

Remarks. The shell of *A. translirata* is differentiated from that of *A. avara* by its usually more flattened whorls and greater height, and by the spiral subsutural stria that crosses the axial ribs and is the widest stria. (This stria may not be evident on all whorls, especially on an eroded or fouled specimen.) In *avara,* the spiral striae are usually not as pronounced and do not cross the ribs. The ribs of the first two post-larval whorls of *avara* are therefore smooth, whereas those of *translirata* are beaded. Juveniles of the two species are easily distinguished by the difference in width-length ratio, which is less variable in juveniles and therefore more obvious, and by the shape of the body whorl, which is sharply angulated in *translirata* but rounded in *avara* (Pl. 1, figs. 5, 6). The posterodorsal tip of the foot and the egg case of each species also serve to differentiate them. The lateral teeth of the radulae have one small consistent difference between the two species: in *avara* the proximal cusp bears a denticle; in *translirata* it is rounded (Text-figs. 1a, b).

The Pliocene fossil figured as *Anachis (Costoanachis) avara translirata* (Ravenel) by Gardner (1948, pl. 30, figs. 36, 37) is probably not this species.

Habitat and distribution. This species lives on shelly bottoms, rocks, pilings, or other firm substratum, from below mean low water to 48 fathoms, from Cape Cod Bay and Georges Bank south to Florida (see Table 1). It is very common subtidally in New England, where it can also be found in beds of eel grass with *A. avara.*

Specimens examined. The entire collections of *translirata* of the MCZ and the USNM were examined. Shell measurements and descriptions are based on specimens from the following localities:

Nobska Point, Woods Hole, Mass. (Scheltema collection)	19 (living)
Quicks Hole, Mass. (Scheltema collection)	54 (29 living)
Sullivans Island, S.C. (MCZ 260887)	34
Hadley Harbor, Mass. (R. Parker collection)	30
Wellfleet, Mass. (MCZ 19372)	32
Beaufort, N.C. (MCZ 256848)	1 (living)

Radulae were examined from four of the specimens taken from Quicks Hole. Descriptions of the pigmentation of the head-foot are based on the 19 specimens from Nobska Point.

ANACHIS AVARA (Say)

Plate 1, figs. 3-5, 7-10; Text-figs. 1a, 2a, 3 and 4; Table 1

Colombella [sic] avara Say 1822, Jour. Acad. Nat. Sci. Philadelphia **2**: 230 (no fig.) ("coast of the southern states"). [Lectotype, here selected, Academy of Natural Sciences of Philadelphia No. 16887, *ex* Mrs. Say's collection, "Florida."] *Non C. avara* Duclos 1840, Histoire Naturelle Coquilles Univalves Marines, pl. 1, figs. 1, 2.

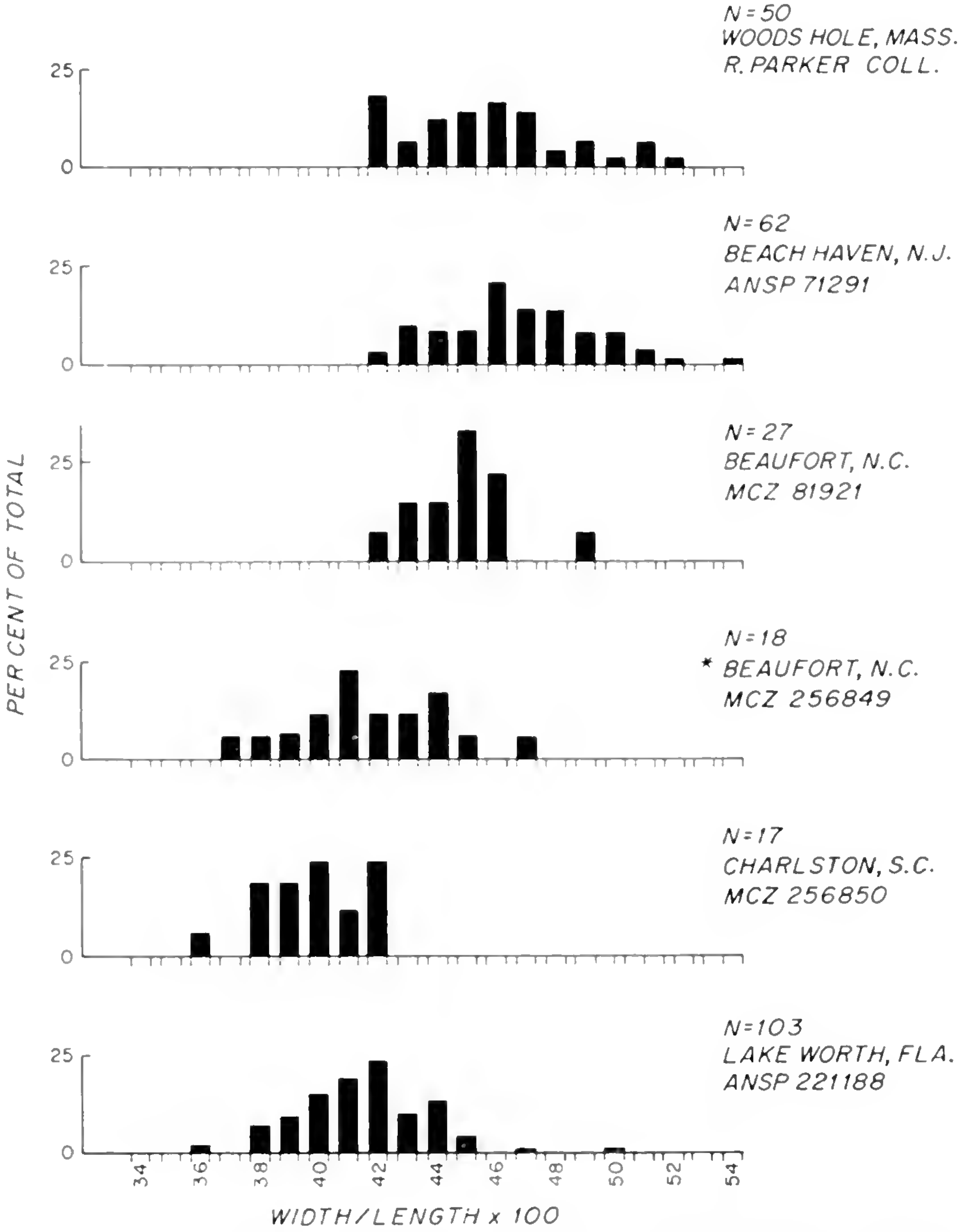
Columbella avara Say. Gould 1841, Invertebrata of Massachusetts, pp. 313-314 (in part, not fig. 197); DeKay 1843, Natural History of New York **5**, Mollusca: 139-140, pl. 8, fig. 179.

Amycla (Astyris) avara (Say). H. and A. Adams 1858, Genera of Recent Molluscs **1**: 187.

Anachis avara (Say). Perkins 1869, Proc. Boston Soc. Nat. Hist. 1869-1871, **13**: 113 (in part).

Anachis avara 'Perkins.' Verrill 1873, Rept. U.S. Comm. Fish and Fisheries 1871-1872: 643-644 (no fig.).

Anachis similis (Ravenel). Verrill 1873, Rept. U.S. Comm. Fish and Fisheries 1871-1872: pl. 21, fig. 109 (fig. only, not description pp. 644-645).



Text-Fig. 3. Frequency distribution of width to length ratios of *Anachis avara* from selected localities between Massachusetts and Florida (expressed in percentage). N is sample size. Larvae were reared from the Beaufort, North Carolina, population indicated by an asterisk.

Anachis avara translirata (Ravenel). M. Smith 1945, East Coast Marine Shells, p. 119, pl. 46, fig. 23.

Anachis translirata (Ravenel). Abbott 1954, American Seashells, pl. 25, fig. ff (fig. only).

Description. Shell variable, elevated, conical, whorls slightly ventricose and ribbed. Height to 14.5 mm, width to 6.3 mm, median range in height 10.5 to 12.0 mm. Width-length ratio ranges from 0.37 to 0.56; the more slender shells (ratio less than 0.42) occur in populations south of Cape Hatteras (Pl. 1, figs. 7, 8, 9). Aperture about one-half total height of shell, slightly less in slender shells, slightly more in broad shells. Larval whorls (protoconch) three, smooth, rounded, and translucent. Post-larval whorls six to eight, with variable sculpture. Suture indented. Axial ribs on first two or three post-larval whorls; very rarely absent. Succeeding whorls ribbed (Pl. 1, fig. 3) or smooth (Pl. 1, figs. 4, 7, 8, 9). Ribs present on body whorls straight or curved, highest at the periphery; however, those near the lip disappear above the periphery. Outer lip often thickened so as to obliterate one or more ribs. Ribs on body whorl range in number from 7 to 21; populations north of Cape Hatteras range from 10 to 21 (Pl. 1, figs. 4, 10), those south of Cape Hatteras from 7 to 14 (Pl. 1, figs. 7, 8, 9). Ribs heaviest on shells from southern populations. Spiral striae faint to strong, but not crossing ribs, and strongly impressed below periphery. Aperture elliptical, wider in northern populations than in southern. Outer lip thin or thick, recurved anteriorly to form a short, slightly recurved siphonal canal; when lip is thickened, it is recurved posteriorly into an anal notch. Teeth often present on outer lip if it is thickened, and range from 4 to 12 (average 8 or 9) in number. Largest tooth usually penultimate one before anal notch. Parietal callus, when present, is narrow and sharp-edged, and bears a number of teeth, which are the ends of spiral striae. The columella is smooth. Juveniles (Pl. 1, fig. 5) without thickened lip or parietal callus, body whorl with or without ribs. Shell color varying from straw-yellow to chestnut-brown, and usually with conspicuous white round or elliptical mottlings, although these may be lacking (Pl. 1, fig. 4) in some populations; ribs of body whorl often tipped with white at suture. Shell may be dull or lustrous.

Operculum elliptical, concentric, with eccentric nucleus.

The radula is rachiglossan; the median tooth is a flat plate; the lateral tooth has three cusps, the proximal one ending in a sharp denticle (Text-fig. 1a).

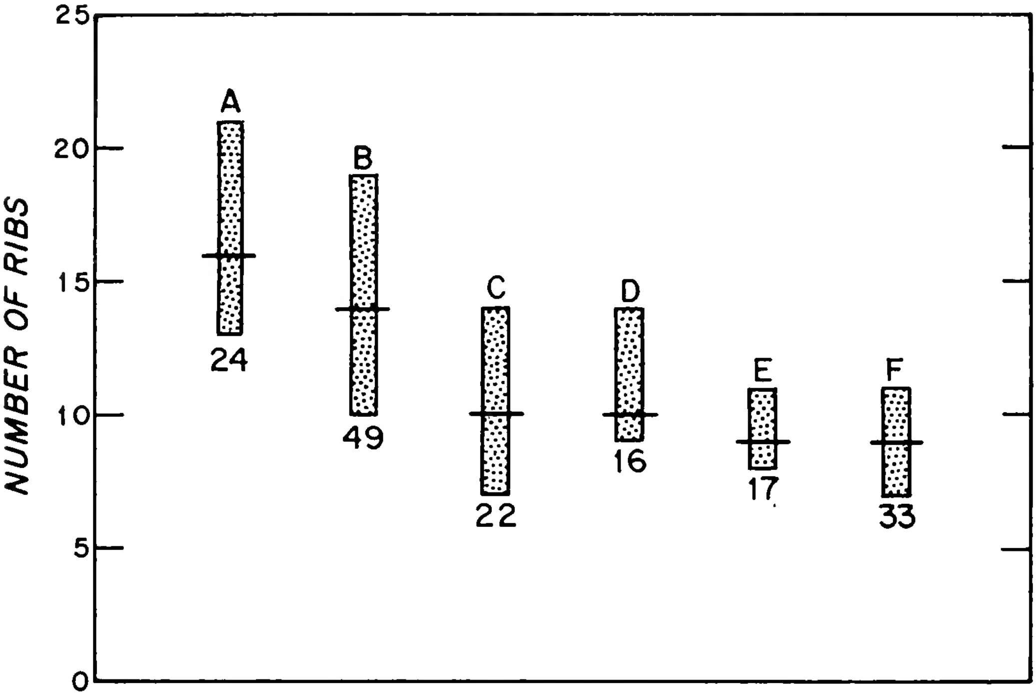
Head and foot are mottled black and white. Tentacle and siphon tips are white, and usually have a black stripe around them. The anterodorsal part of the foot has two large white spots; the posterodorsal tip of the foot is white, and is sharply demarcated from the mottling of the rest of the foot.

Egg capsule volcano-shaped, sculptured by fine striae running from base to apex (Text-fig. 2a).

Remarks. (See also remarks under *A. translirata.*) Northern and southern populations of *A. avara* are sufficiently different (Pl. 1, figs. 4, 7) in shell character to warrant investigating the possibility of the existence of subspecies. A number of populations from throughout the range of *avara* (listed below under *Specimens examined*) were examined in detail to determine whether there is any basis for differentiating subspecies by shell characters alone. Lengths and widths of about 440 shells were measured, and ribs on the body whorl and teeth on the outer lip were counted. Shell color, thickness, luster, and number of post-larval whorls were noted. Width to length ratios and rib numbers show an essentially clinal change north to south, from short, broad shells with many ribs to tall, slender ones with few ribs (Text-figs. 3, 4). The more slender shells may have an extra whorl. The numbers of teeth seem to bear no relationship to other shell characters; for example, the range is 4 to 12 in the population from Hadley Harbor, Massachusetts, and 7 to 11 in one from Beaufort, North Carolina. Shells with high luster are in collections from Delaware Bay, Chincoteague Bay, and Lake Worth. The thinnest, darkest colored shells occur from New Jersey northward. As in many shelled mollusks of the eastern United States, the largest shells are from Chincoteague Bay.

These data on shell characters do not provide sufficient evidence for differentiating subspecies. Also, the length of larval life (up to 5 weeks in the laboratory) is long enough for the larvae to be dispersed over considerable distances, making genetic interchange likely between local populations. That the slenderest, heaviest shells and fewest specimens are from South Carolina, Georgia, and Florida (see Table 1) may be a reflection of greater isolation of populations, for suitable habitats (see below) may be separated by vast stretches of sand banks and large backwater areas with black, sulfurous muds bordered by marsh grass.

Two shells from southern localities (the paralectotype from "Florida" [Pl. 1, fig. 3] and a single shell from Sullivan's Island, South Carolina) have the shape and rib count of northern shells. They may have been collected from the ocean side of the outer



Text-Fig. 4. Range in rib number on body whorl of *Anachis avara* from selected localities between Massachusetts and Florida. Means are indicated by horizontal lines; sample sizes by numbers under the vertical bars. Those individuals with body whorl incompletely ribbed are not included. Letters above bars refer to locality: A, Woods Hole, Mass. (MCZ 203663); B-F as in Text-Fig. 3: B, Beach Haven; C and D, Beaufort; E, Charleston; F, Lake Worth.

sand banks, rather than from the embayments from which most of the *avara* collections south of Cape Hatteras have been made.

Habitat and distribution. A. avara is found chiefly in eel grass; it is also common below mean low water on a variety of firm substrata, often with *translirata.* It is distributed along the entire coast from Massachusetts Bay and Nantucket Island to Lower Matecumbe Key, Florida (Table 1). It is chiefly subtidal, but has been taken from the following depths: Massachusetts Bay, 5 fathoms; Chesapeake Bay, 25 fathoms; off Cape Charles, 10 fathoms; off Beaufort, N.C., 9 fathoms; off Cape Kennedy (Canaveral), 10 fathoms.

Specimens examined. The entire collections of *avara* in the MCZ, USNM, and ANSP were examined. The descriptions are based on specimens from the following localities:

Gunning Point, Woods Hole, Mass. (Scheltema collection)	12 (living)

Nobska Point, Woods Hole, Mass. (Scheltema collection)	2 (living)
Beaufort, N.C. (MCZ 256849)	20 (living)
Hadley Harbor, Woods Hole, Mass. (R. Parker collection)	50
Woods Hole, Mass. (MCZ 203663)	24
Beach Haven, N.J. (ANSP 71291)	85
Barnegat Bay, N.J. (ANSP 106708)	23
Delaware Bay, Cape May, N.J. (ANSP 182645)	8
Delaware Bay, Little Creek, Del. (MCZ 198032)	13
Chincoteague Bay, Va. (MCZ 197795)	6
Beaufort, N.C. (MCZ 81921)	27
Beaufort, N.C. (ANSP 145680)	21
Charleston, S.C. (MCZ 256850)	17
St. Augustine, Fla. (USNM 416015)	17
St. Augustine, Fla. (ANSP 140800)	8
Lake Worth, Fla. (ANSP 221188)	107

Radulae of three specimens from Gunning Point, two from Beaufort, N.C., and one from Lake Worth, Fla. (ANSP 221188), were examined.

NOTES ON RELATED SPECIES

The following remarks on some other western Atlantic species of *Anachis* are offered as notes. Anatomical studies, such as those of Marcus and Marcus (1962, 1964) on Brazilian Columbellidae, are greatly needed for species along the entire coast and Gulf of Mexico.

ANACHIS SIMILIS (Ravenel)

Columbella similis Ravenel 1861, Proc. Acad. Nat. Sci. Philadelphia 1861: 41-42 (no fig.) ("common on the coasts of North and South Carolina").

No type material has been found (see footnote 3 under *A. translirata*), and it is impossible from the description to know precisely to what species Ravenel was referring. The description fits juvenile *A. avara* as well as a number of small species of Columbellidae. Probably the small, ribbed columbellid common in shallow water in western Florida should not be referred to *A. similis* (e.g., Perry and Schwengel, 1955). Gardner (1948) has figured a fossil *A. avara similis* (Ravenel) that is too large to fit Ravenel's description.

Anachis similis (Ravenel) should be considered a *nomen dubium*.

ANACHIS SEMIPLICATA Stearns

Plate 1, figure 13

Anachis semiplicata Stearns 1873, Proc. Acad. Nat. Sci. Philadelphia 1873; 344-347, 4 text-figs. (west coast of Florida); Perry and Schwengel 1955, Marine Shells of the Western Coast of Florida, p. 159, pl. 51, fig. 345 (egg capsules); *non avara semiplicata* 'Stearns' of various authors (western and northern Gulf of Mexico).

This appears to be a valid species that is endemic to southwestern Florida. The shell is higher and narrower (average width to length ratio 0.36, 20 specimens from ANSP 221189) than that of *avara* and either lacks spiral striae or has only very faint ones; the egg capsules, as described by Perry and Schwengel (1955), seem to be different from those of *avara,* although unfortunately the figure is not clear. In addition, the juvenile shells are more elongate than those of juvenile *avara.* The radula has not been studied.

The northern and western Gulf of Mexico species of *Anachis* found on jetties, pilings, and oyster beds (Pl. 1, fig. 12) does not appear to be *A. semiplicata* (e.g., Puffer and Emerson, 1953; Pulley, 1952). It most closely resembles Beaufort, N.C., populations of *avara,* but is smaller (median range in length, 9.1-10.0 mm, 29 specimens from USNM 606003). The lateral radular tooth (1 specimen examined) is the same as that of *avara.* The status of this species is not at all clear; it may possibly be a relic population (see Deevey, 1950) of *avara* now differentiated at either a specific or subspecific level, or it may have affinities with populations of *Anachis* sp. to the south (see Weisbord, 1962: 313-315). Abbott (1954) has included both this species and *A. semiplicata* in his range for *avara.*

ANACHIS FLORIDANA REHDER

Plate 1, figure 11; Text-figure 2c

Anachis floridana Rehder 1939, Nautilus **53** (1): 20, pl. 6, fig. 6 (near Cape Canaveral, Brevard County, Florida, in 30 feet of water; USNM 473202).

This species differs from *A. avara* in having a smooth rather than an indented suture and flattened whorls lacking spiral striae. Egg capsules obtained from animals held in the laboratory most closely resemble those of *A. brasiliana* (Marcus and Marcus, 1962). The lateral radular tooth (1 specimen examined) is similar to that of *A. translirata* and lacks the pointed denticle on the proximal cusp of *avara.*

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TABLE 1

Distributions of *Anachis avara* (Say) and *Anachis translirata* (Ravenel) based upon collections of the U.S. National Museum (U), Museum of Comparative Zoology (M), Academy of Natural Sciences of Philadelphia (A), and the author's (S).*

		Anachis	*Anachis translirata*	
Locality or Region	*Collection*	*avara*	*Inshore*	*Offshore*
? Maine — Grand Manan Island	U	+	+	
off Georges Bank (1 juvenile, dredged)	M			45 fms
Massachusetts				
Boston	A	+		
Cape Cod Bay — Duxbury	M, U	+(U)	+(M)	
off Wellfleet (dredged)	M	5 fms	5 fms	
Cape Cod, all shores (numerous localities)	U, M, S	+	+	
Nantucket (several localities)	U, M	+	+	
Martha's Vineyard (several localities)	U, M	+	+	
off Gay Head (dredged)	U		+	
Vineyard Sound (dredged)	U	+	+	
Buzzards Bay (dredged)	U	7 fms	7 fms	
Shores of Buzzards Bay (numerous localities)	U, M, S	+	+	
Elizabeth Is. (dredged)	S	+	+	

* Specimens from inshore that were obviously dead when collected are not included. A few "dead" or "drilled" specimens from offshore, so noted, are listed. *Anachis avara* has been collected only from inshore localities.

Locality or Region	*Collection*	*Anachis avara*	*Anachis translirata* Inshore	*Anachis translirata* Offshore
Rhode Island				
Sakonnett Pt.	M	+	+	
Narragansett Bay (dredged several localities)	U		8-19 fms	
Bristol	M	+	+	
Westerly	U, M	+	+	
Connecticut and New York				
Stonington	U		+	
off Fisher's Is. (dredged)	M		+	
Long Island — Montauk Pt.	U	+	+	
Greenport	U	+	+	
Peconic Bay (? dredged)	U		+	
Long Island Sound (? dredged)	U		+	
New Haven	U	+	+	
New Jersey and Delaware				
Atlantic City	U	+		
Spray Beach	M	+		
Barnegat Bay	U, A	+		
Beach Haven	A	+		
Cape May	U		+	
off Cape May (dredged)	U		+	
Delaware Bay — Cape May	A	+		
Little Creek	M	+		
Maryland and Virginia				
Chincoteague	U, M, A	+		
Smith Is. (Va.)	U	+		
Isaacs	U	+		
off Cape Charles	U	10 fms		
off Cape Henry	U	4½ fms		
Chesapeake Bay (dredged, several localities)	U	4-25 fms	12 fms	
35 mi. east of Wallops Is. (shell drilled)	M			18 fms
North Carolina				
48 mi. East of Currituck Sd. ("dead" shell)	M			18 fms
23 mi. east of Currituck Sd. ("dead" shell)	M			18 fms
27 mi. east of Pamlico Sd.	M			24 fms
off Cape Hatteras	U			13, 16, 48 fms
Cape Hatteras Pt.	U		+	

		Anachis	*Anachis translirata*	
Locality or Region	*Collection*	*avara*	*Inshore*	*Offshore*
Cape Lookout	U	+		
Shackleford Is., Sound shore	M	+		
Beaufort region (several localities)	M, U, A, S	+	+	
off New River	U	+	+	
South Carolina				
Pawleys Is.	M	+		
Winyah Bay (mouth)	U	+		
Sullivans Is.	M	+	+	
Charleston	M	+	+	
Cooper R.	M	+		
Ashley R. (dredged)	M	+		
Beaufort	U	+		
off Beaufort	U	6-9 fms		
Georgia				
Tybee	U	+		
St. Simons	U	+		
Florida				
St. Augustine	A, U	+		
off Cape Canaveral (Kennedy)	U	10 fms		
Lake Worth	A	+		
off Lake Worth (drilled shells)	M			83-92 fms
Waveland, Dade Co.	U	+	+	
Lower Matecumbe Key	U	+		
15-35 mi. off Ft. Walton	M			13-19 fms

Plate 1

Figs. 1 and 2: *Anachis translirata* (Ravenel), Sullivans Island, South Carolina. MCZ 260887.

Fig. 3: *Anachis avara* (Say), paralectotype, "Florida." ANSP 306058. Note the similarity to the northern form shown in Fig. 4.

Fig. 4: *A. avara*, Wellfleet, Massachusetts. MCZ 19372.

Fig. 5: *A. avara*, juvenile, Woods Hole, Massachusetts.

Fig. 6: *A. translirata*, juvenile, Woods Hole, Massachusetts.

Fig. 7: *A. avara*, Lake Worth, Florida. ANSP 221188.

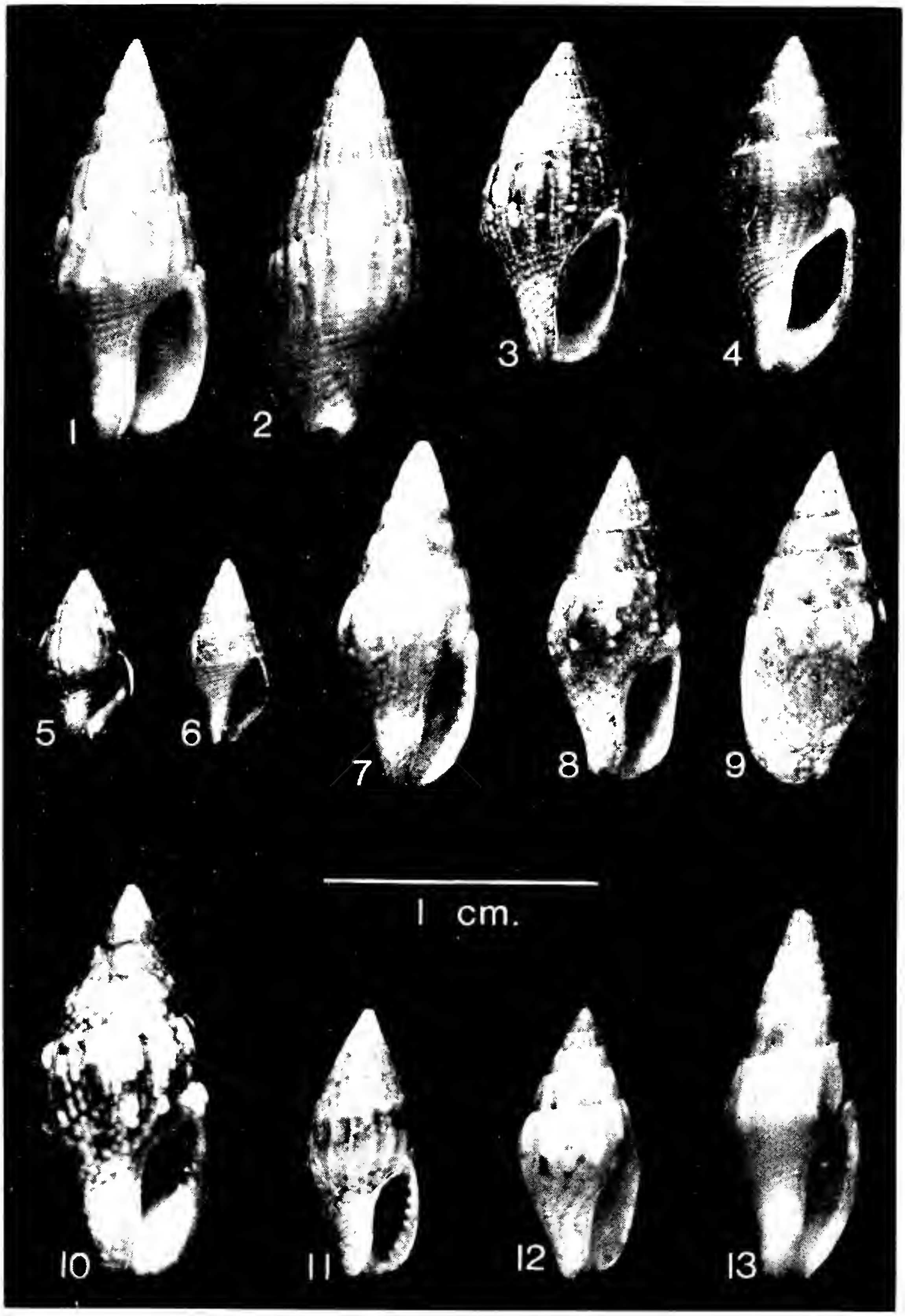
Figs. 8 and 9: *Anachis avara* (Say), lectotype, "Florida." ANSP 16887.

Fig. 10: *A. avara*, Chincoteague, Virginia. MCZ 197795.

Fig. 11: *Anachis floridana* Rehder, Matanzas Inlet, Florida.

Fig. 12: *Anachis* sp., Aransas Bay, Texas. USNM 606003.

Fig. 13: *Anachis semiplicata* Stearns, Venice Bay, Florida. ANSP 221189.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BREVIORA

Museum of Comparative Zoology

Cambridge, Mass. 31 December, 1968 Number 305

LYTECHINUS WILLIAMSI, A NEW SEA URCHIN FROM PANAMA

Richard H. Chesher[1]

ABSTRACT

A fourth species of *Lytechinus* from the Atlantic, *L. williamsi*, is described as a Panama endemic. It differs from the other shallow-water species, *L. variegatus*, in having fewer than 15 wedges per primary spine and fewer than 14 interambulacral plates per series in adults. Variation in several taxonomic features of *L. variegatus* is examined.

INTRODUCTION

During an underwater survey of the Atlantic coral reefs of Panama in September of 1967, a new species of sea urchin was discovered living in beds of leaf coral (*Agaricia agaricites* (Linnaeus)). The specimens, which were collected at Buena Ventura in depths of 5 to 10 meters, belong to *Lytechinus*, primarily an American genus, which now has four Atlantic and four Pacific species (see key, below). Two of the Pacific species are sympatric: *L. pictus* (Newport Bay, California, to Gulf of California) and *L. anamensus* (St. Barbara to Cedros Island, California). Mayr (1954) omitted *L. pictus* (Verrill 1867) in his zoogeographic discussion of the genus *Lytechinus* as a possible synonym of *L. anamensus* Clark 1912. Examination of specimens in the Museum of Comparative Zoology substantiates Mortensen's (1943) view that the two forms represent valid species. In the Atlantic, *L. callipeplus* (Carribean and Gulf of Guinea) is sympatric with *L. euerces* (Caribbean) in depths of 100 to 500 meters. *L. williamsi* (Panama) inhabits a very small portion of the geographic range of the shallow-water species *L. variegatus* (Brazil to

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Bermuda in the Western Atlantic and Cape Verde Islands in the Eastern Atlantic). Mortensen (1943) separted *L. variegatus* into several allopatric subspecies (see key, below), which were cited by Mayr (1954) as evidence for geographic speciation. The distribution of species indicates that tropical America has been the major center of speciation for this genus and that recent migrations, possibly through the Equatorial Undercurrent, are responsible for the presence of *L. callipeplus* and *L. variegatus* in the Eastern Atlantic (Chesher 1966).

To provide statistical data for comparison of the new species with *L. variegatus*, specimens of the latter were measured from localities ranging from Brazil to Bermuda (Table 3). The subspecific taxa were ignored, and it was found that the characters that were measured showed very little variation over the entire geographic range (Table 2, Fig. 5). Swan (1952, 1958) found considerable variation in the number of wedges seen in cross-sections of spines from *Strongylocentrotus* spp., but primary spines taken from the interambulacral areas above the ambitus of *L. variegatus* showed very little variability throughout the geographic range of the species. The number of wedges per spine may thus be considered a valid taxonomic character for this genus, providing that only primary interambulacral spines from above the ambitus are used and the wedges are counted in the proximal half of the spine. The spines afford a field character for separation of specimens of *L. variegatus* and *L. williamsi;* spines of the former appear smooth and glistening and of the latter distinctly ridged.

ABBREVIATIONS

The following abbreviations are used in this paper: HD, horizontal diameter of the test; IA, interambulacrum; Ln, the natural logarithm; S.D., standard deviation; C.V., coefficient of variation; r, coefficient of correlation; $S_{Y \cdot X}$ standard error of Y on the X axis (Croxton 1959). In the formulas, X = HD in mm and Y = the taxonomic features of the test. M.C.Z., Museum of Comparative Zoology; U.S.N.M., United States National Museum.

ACKNOWLEDGMENTS

The species is named after L. T. Williams, who provided his boat and hospitality for the investigation of the echinoid fauna of the Atlantic reefs of Panama and later found additional specimens for examination. I would like to thank him and his wife for their help. R. Waterhouse deserves special thanks for his assistance during diving operations. Dr. I. Rubinoff and the staff of the Smithsonian Tropical Research Institute were of great assistance during this project, which was supported by travel funds from the Smithsonian Institution. The Mollusk Department of the M.C.Z. provided travel funds for Mr. Waterhouse. The analyses and manuscript were completed during a National Science Foundation Postdoctoral Fellowship at Harvard University. Statistical data were calculated on the 940 computer at Harvard University with support from a Milton Fund grant to Dr. H. B. Fell. Dr. Kenneth H. Boss kindly read the manuscript, which has benefited from his suggestions.

LYTECHINUS WILLIAMSI new species

Figures 1, 2, 3a, c-i, 4, 5; Table 1

Types. The holotype (19mm HD, preserved in alcohol) is deposited in the U.S.N.M. (No. E10855), as are 14 paratypes (U.S.N.M. No. E10856). Eight paratypes are deposited in the M.C.Z. (Nos. 8194 and 8195).

Type locality. Buena Ventura, Panama, on top of a living coral reef 5 to 10 meters deep, 9°32′N, 79°42′W.

Material examined. Six specimens, 15.7 to 22 mm HD, seaward side of coral reef at Buena Ventura cove, Panama, 9°32′N, 79°42′W, 5 to 10 meters, Sept. 4, 1967, Chesher Coll. Seventeen specimens, 16 to 27.9 mm HD, same locality, Dec. 1967, Williams Coll.

Diagnosis. Number of wedges per primary IA spine from above the ambitus less than 15, milled ring of spines poorly developed; naked median areas near apical system in ambulacra and IA; globiferous pedicellariae purple; adults with less than 14 IA plates per series.

Description. Generic characters conform to those given by Mortensen (1943). All specimens have well-developed genital pores and are less than 30 mm HD.

Apical system. Each genital plate has one large primary tubercle and spine; secondary tuberculation poorly developed; all oculars exsert. The relative size of the apical system measured from the outer edge of ocular V to the outer edge of genital plate 2 is given in Table 1.

Ambulacra. Primary tubercles form a regular series just medial of the pore-pairs from the peristome to the oculars. Secondary tuberculation is poorly developed above the ambitus, resulting in a naked median zone from this point to the oculars. The number of ambulacral plates per plate-series is indicated in Table 1 and Figure 5. Tube-feet end with a well-developed, calcitic sucking disc, as is normal for species of *Lytechinus*. Spicules of the tube-feet are C-shaped (Fig. 3h).

Interambulacra. Primary tubercles form a regular series from the peristome to the apical system in each row of plates, and primary spines are well developed up to and including the genital plates. Secondary tubercles are poorly developed above the ambitus, resulting in a naked median area (Fig. 1). The number of IA plates is given in Table 1 and Figure 5.

Spines. The sharply pointed primary spines are about 40 to 50 per cent of the HD in length, with the exception of the small spines adjacent to the peristome. The milled ring is poorly developed and the base straight sided (Fig. 3i). The number of wedges seen in a cross-section of the proximal portion of primary IA spines is about 12 (Fig. 3a). Near the peristome, the number may decrease and the small oral spines may have as few as 9 wedges. The number of wedges was counted from 250 IA primary spines taken from between the ambitus and the apical system and broken in half about 2 mm from the milled ring. About 10 spines were taken from each specimen. The number of wedges varied from 11 to 15, with a mean of 12.34 wedges (S.D. 0.7683, C.V. 6.21).

Pedicellariae. Globiferous, tridentate, ophiocephalous, and triphyllous pedicellariae are present but not diagnostic (Fig. 3c-f). The pedicellariae are purple, and the color is retained after cleaning with bleach. Spicules of the globiferous pedicellariae are dumbbell-shaped (Fig. 3g). Large, white stalk glands are present on many globiferous pedicellariae.

Coloration. The spines are usually deep, rich green, although two of the specimens have white spines. The pedicellariae are purple, and the test is beige with a purple-brown stripe covering the median longitudinal suture of the ambulacra and interambulacra. After cleaning with bleach, the test is mottled green-grey.

Habitat. The specimens were found living in niches on the top of a living, shallow coral reef at Buena Ventura, Panama. Most of the specimens were associated with the leaf coral *Agaricia agaricites* (Fig. 4). The gut of one specimen was filled with small grey-green spheres, most of which were of unrecognizable origin. These urchins probably graze on algae and encrusting organisms of the reef. There was no evidence that they were feeding on coral. Unlike *L. variegatus* (and most other toxopneustid echinoids), *L. williamsi* does not cover itself with bottom debris.

The specimens collected in December began to spawn when placed in alcohol, which might indicate a winter spawning season. Moore *et al.* (1963), however, found that *L. variegatus* may spawn to some degree during the entire year.

Relationships. L. williamsi lives in the same depth range as *L. variegatus* and in a portion of its geographic distribution. Specimens of *L. variegatus* can be found in the grass areas at Buena Ventura. Although occasionally found on rocky areas or on soft sediments, *L. variegatus* normally occurs in grass areas (Moore *et al.* 1963; personal observations), while *L. williamsi* appears to be distributed only on living reef areas.

The new species differs from *L. variegatus* in several features, the most obvious of which is the number of wedges per primary interambulacral spine, which averages 12.34 in the former and 24.14 in the latter (Fig. 3b, Tables 1 and 2). The relative size of the apical system and peristome is greater in the new species than in *L. variegatus.* The number of plates per ambulacral or IA series is much greater in *L. variegatus* than in *L. williamsi* (Fig. 5). Jackson (1912, 1914), after examining 1,443 specimens of *L. variegatus*, found none with all oculars exsert, whereas all of the specimens of the new species have every ocular exsert.

L. williamsi can be separated from the two remaining, relatively deep-water, Atlantic species on the basis of the number of plates per series, the tuberculation, the coloring, and the spicules of the globiferous pedicellariae. *L. euerces* and *L. callipeplus* do not have naked areas in the median ambulacral and interambulacral area; the secondary tubercles are irregularly scattered on the test and are almost the same size as the poorly-developed primary tubercles. Whereas the spicules of the globiferous pedicellariae are dumbbell-shaped in *L. williamsi* and *L. callipeplus*, they are C-shaped in *L. euerces*. The naked test of *L. callipeplus* has red blotches on the dorsal side, which the new species lacks.

L. williamsi is most closely allied to *L. panamensis* of the Bay of Panama. It differs from that species, however, in having fewer IA and ambulacral plates (Fig. 5). In addition, the pedicellariae of *L. panamensis* are brown, whereas they are purple in *L. williamsi.* Ocular I is normally insert in *L. panamensis* and exsert in the new species, and the milled ring of the primary spines is well developed in *L. panamensis* and almost absent in the new species. The other Pacific species are separated from the new species in the following key.

KEY TO THE SPECIES OF THE GENUS *LYTECHINUS*

1. Secondary tuberculation poorly developed, leaving a naked median area in the aboral portion of the ambulacra and interambulacra; primary tubercles large 3

Secondary tuberculation scattered irregularly over the test, no naked areas, primary tubercles small 2

2. Large, red blotches dorsally on the cleaned test, spicules of globiferous pedicellariae dumbbell shaped (Caribbean, Gulf of Guinea, deep water) . . . . *L. callipeplus*

Test and spines white, spicules C-shaped (Caribbean, deep water) . . . . *L. euerces*

3. Spicules of globiferous pedicellariae C-shaped (California) . . . *L. pictus*

Spicules dumbbell-shaped 4

4. Primary IA spines from above ambitus with less than 16 wedges 5

Spines with more than 16 wedges 6

5. Adults with less than 14 IA plates per series, pedicellariae purple (Atlantic coast of Panama) . . . . *L. williamsi*

Adults with more than 14 IA plates per series, pedicellariae brown (Bay of Panama) . . . . *L. panamensis*

6. Ambital spines much longer than other primaries, producing a fringe: test low, mottled with purple (California) . . . . *L. anamensus*

Spines more or less uniform in size 7

7. Naked IA area granular, with a row of small tubercles along the horizontal sutures, pedicellariae purple, covering naked area (Galapagos, N.W. coast of South America) . . . . *L. semituberculatus*

Naked IA area not pronounced, smooth, pedicellariae white, confined to tuberculated areas 8

8. Test green, mottled with white, spines green or tinged with purple (Brazil, West Indies) . . . . *L. variegatus typicus*

Test not greenish or whitish 9

9. Buccal membrane not densely plated outside buccal plates (Cape Verde Islands, Africa) . . . . *L. variegatus pallidus*

Membrane heavily plated 10

10. Spines slender, dark purple (Bermuda) . . . . *L. variegatus atlanticus*

Spines reddish, stout (U.S. east coast) . . . . *L. variegatus carolinus*

TABLE 1

L. williamsi: equations for regression lines from plots of taxonomic features of the test.

Apical system (V-2 axis, in mm):
$\mathrm{LnY} = 0.8162\mathrm{LnX} - 0.7688$ $S_{Y.X} = 0.056$ $r = 0.89243$

Peristome (V-2 axis, in mm):
$\mathrm{LnY} = 0.7306\mathrm{LnX} + 0.0646$ $S_{Y.X} = 0.025$ $r = 0.97049$

Interambulacral plates per series:
$\mathrm{LnY} = 0.3832\mathrm{LnX} + 1.3117$ $S_{Y.X} = 0.039$ $r = 0.80026$

Ambulacral plates per series:
$\mathrm{LnY} = 0.7321\mathrm{LnX} + 0.5368$ $S_{Y.X} = 0.038$ $r = 0.93362$

Number of wedges per IA spine from above the ambitus ($N = 250$):
Mean = 12.34, S.D. = 0.7683, C.V. = 6.21

TABLE 2

L. variegatus: equations for regression lines from plots of taxonomic features of the test.

Apical system (V-2 axis, in mm):
$\mathrm{LnY} = 0.7245\mathrm{LnX} - 0.7219$ $S_{Y.X} = 0.081$ $r = 0.97798$

Peristome (V-2 axis, in mm):
$\mathrm{LnY} = 0.8247\mathrm{LnX} - 0.3291$ $S_{Y.X} = 0.043$ $r = 0.99107$

Interambulacral plates per series:
$\mathrm{LnY} = 0.3916\mathrm{LnX} + 1.6275$ $S_{Y.X} = 0.042$ $r = 0.97057$

Ambulacral plates per series:
$\mathrm{LnY} = 0.5397\mathrm{LnX} + 1.4525$ $S_{Y.X} = 0.037$ $r = 0.99248$

Number of wedges per IA spine from above the ambitus ($N = 500$):
Mean = 24.14, S.D. = 1.7924, C.V. = 7.4

TABLE 3

Material of *L. variegatus* examined.

M.C.Z. No.	*Locality*	*Size (HD in mm)*	*Number*
8179	Near Canal, Panama	21 to 39.6	3
——	Buena Ventura, Panama	22 to 27	2
1252	Bahia, Brazil	10 to 41.5	5
3346	Bahia, Brazil	41.5	1
7412	Pigeon Pt., Tobago	30	1
8042	Banes Bay, Cuba	15 to 33	2
5070	Jamaica	26.5	1
——	Santa Marta, Columbia	34.3	1
7939	Cedar Key, N.W. Florida	16 to 30.2	3
4444	Tortugas, Florida	5.5 to 63	5
1281	Beaufort, North Carolina	21.5	1
3340	Bermuda	26	1

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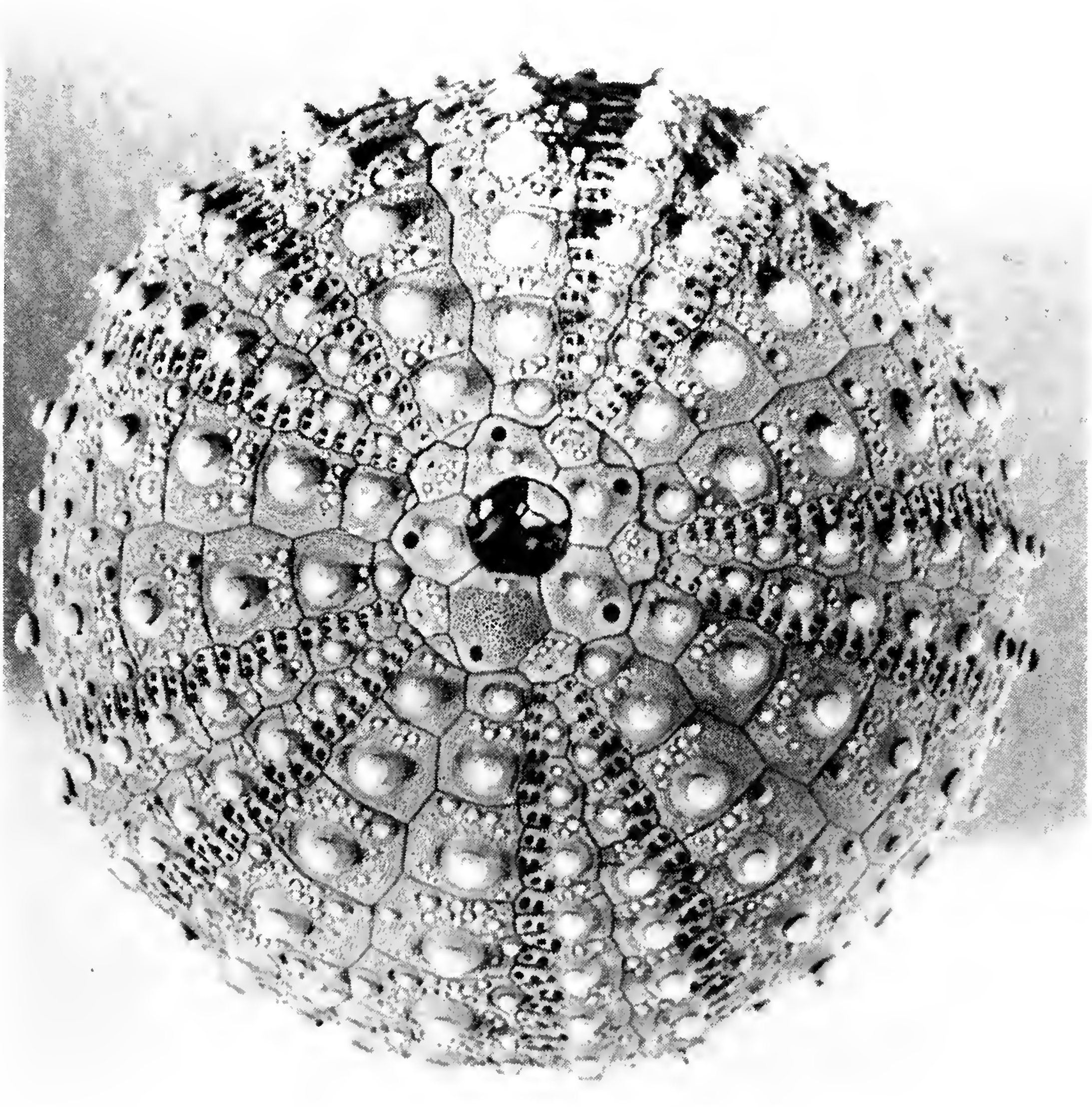

Figure 1. Dorsal view of *L. williamsi* (Paratype, 23 mm HD).

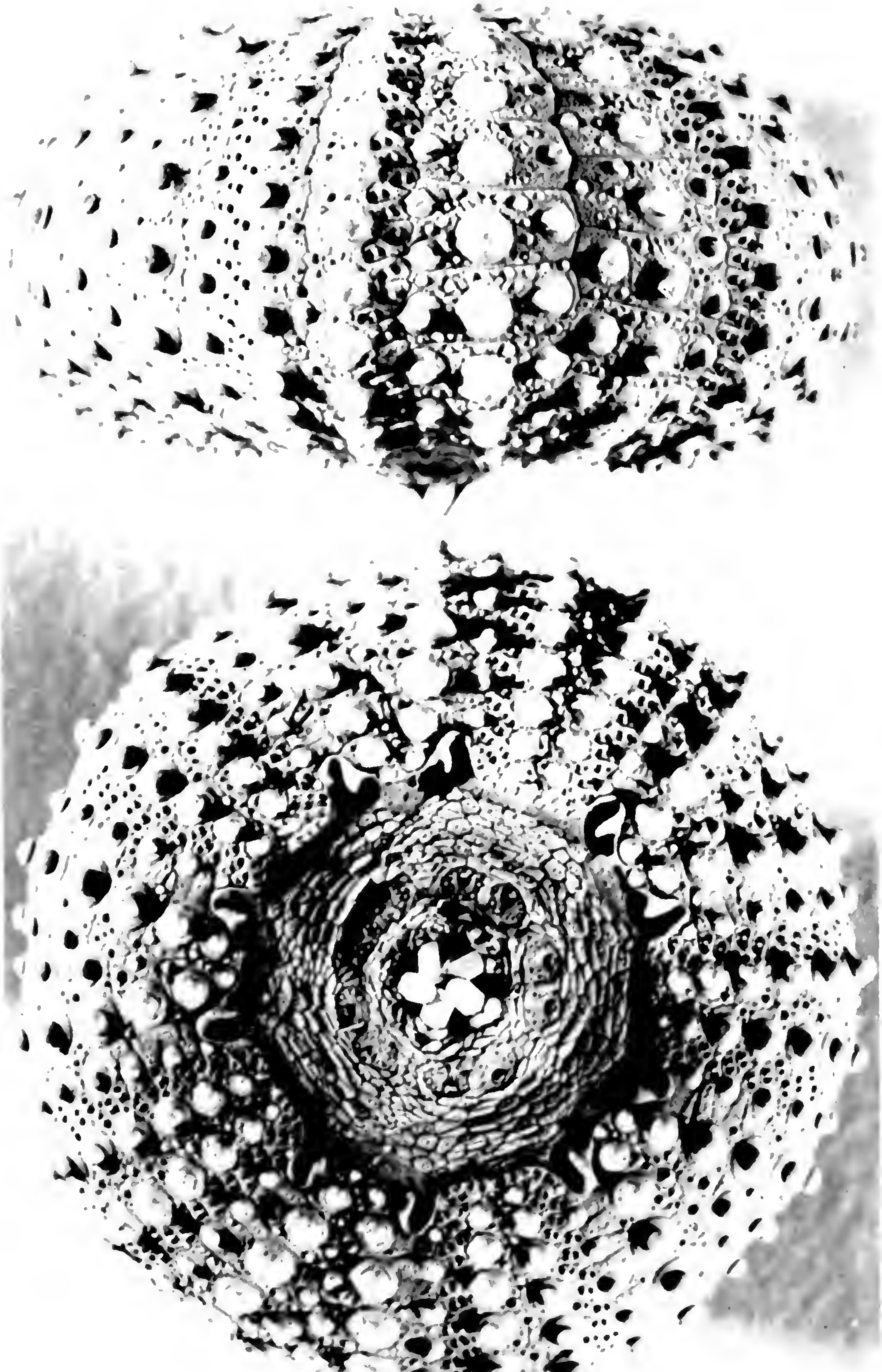

Figure 2. Lateral and ventral view of *L. williamsi* (Paratype, 23 mm HD).

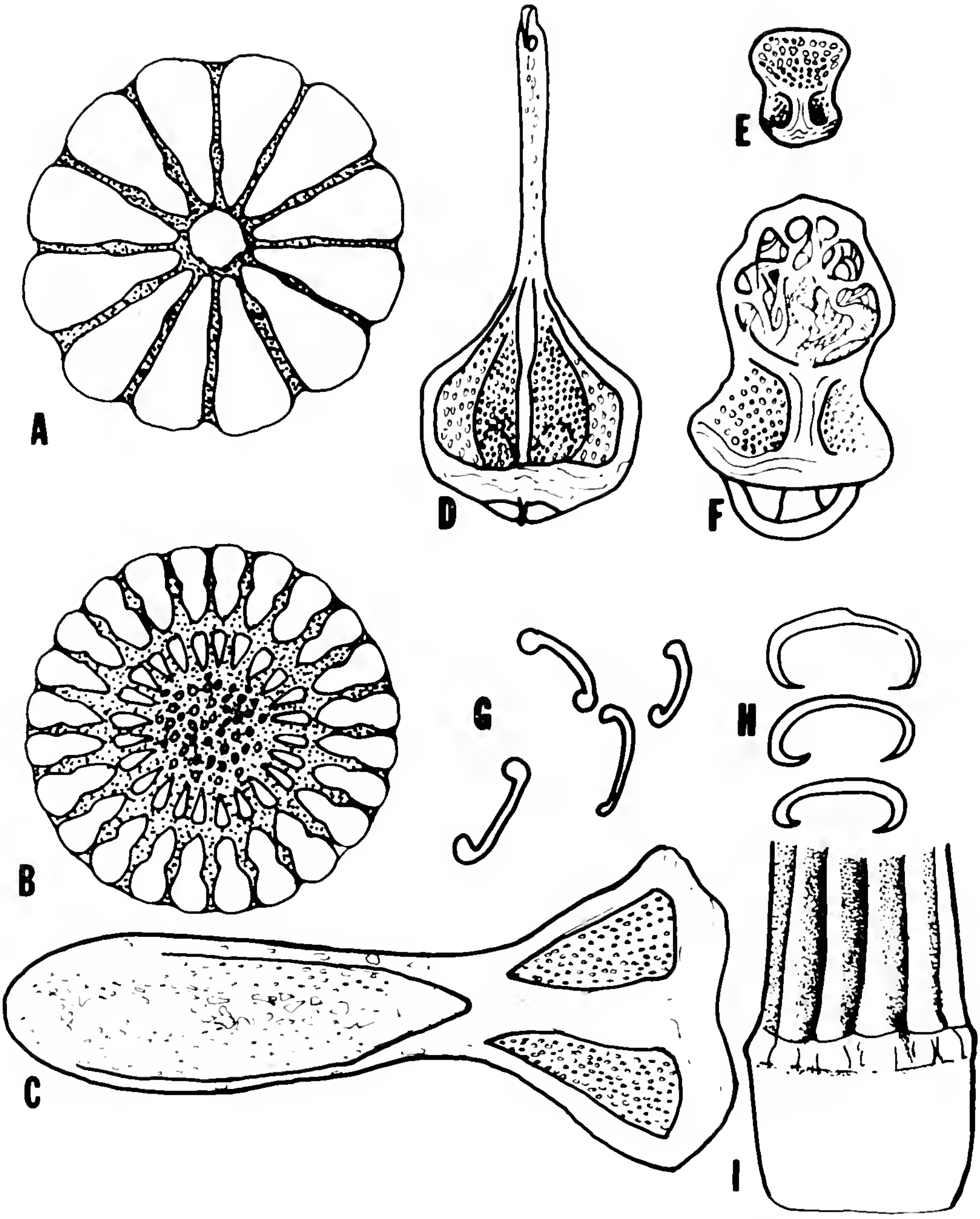

Figure 3. Spines, spicules, and pedicellariae of *L. williamsi*: A, cross-section of a primary interambulacral spine 0.7 mm in diameter; B, the same, from *L. variegatus* 0.65 mm in diameter; C, valve of a tridentate pedicellaria 1.09 mm long; D, valve of globiferous pedicellaria 0.8 mm long; E, valve of triphyllous pedicellaria 0.155 mm long; F, valve of ophicephalous pedicellaria 0.55 mm long; G, spicules of globiferous pedicellaria 0.04 mm long; H, spicules of the tube feet 0.04 to 0.047 mm long; I, base of a primary spine, 0.8 mm in diameter.

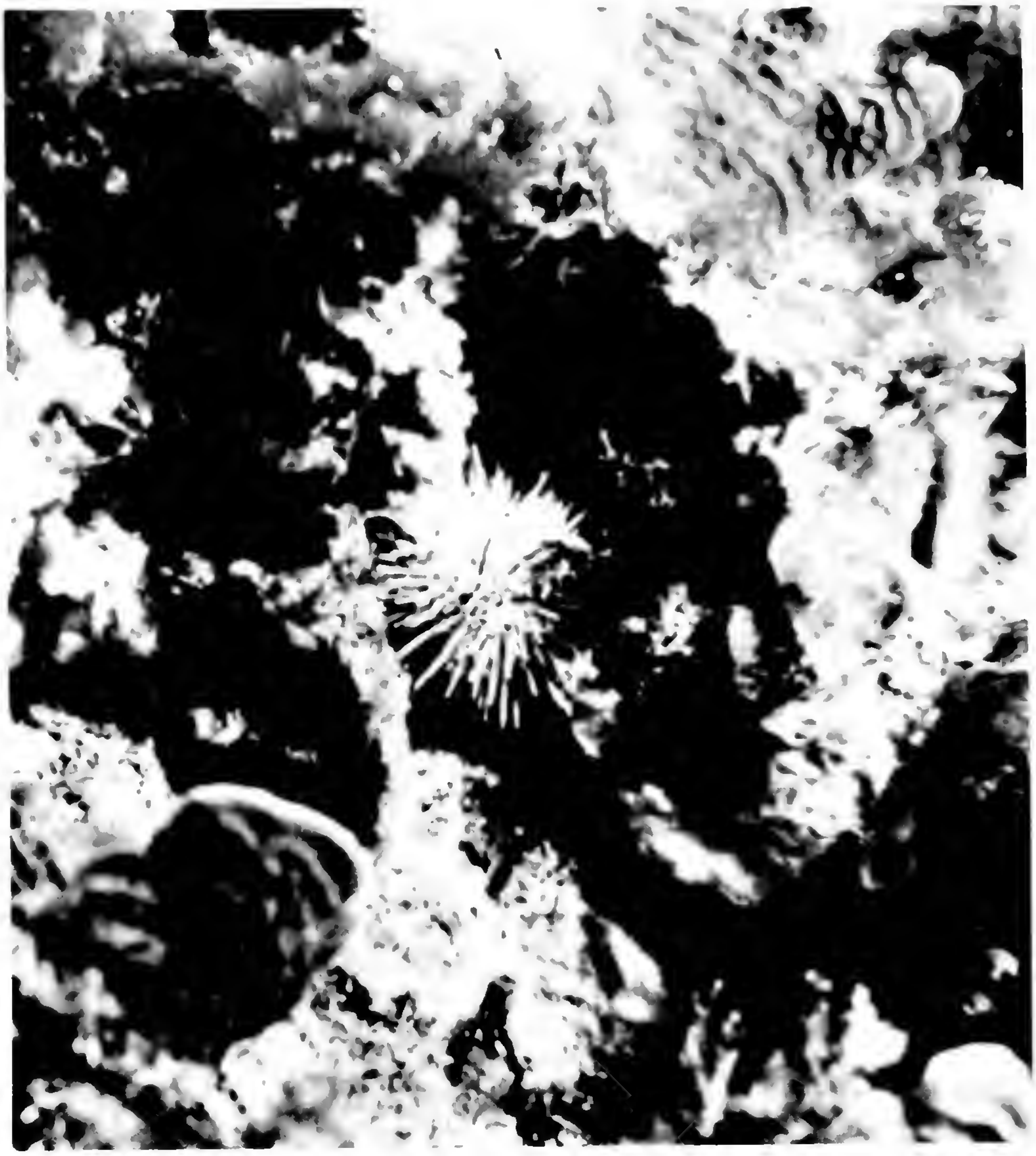

Figure 4. Underwater photograph of *L. williamsi* at the base of some leaf coral (*Agaricia agaricites*).

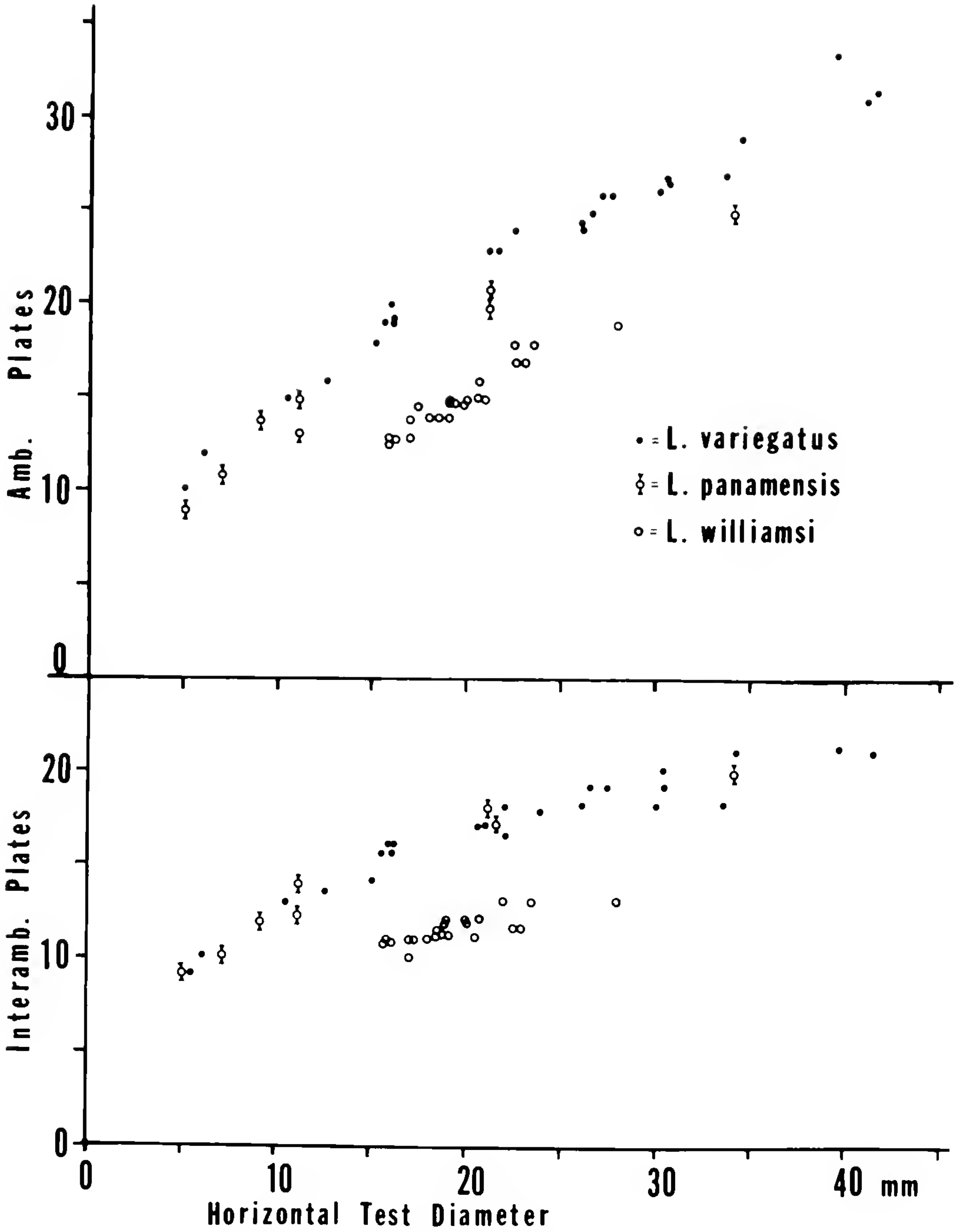

Figure 5. The number of plates in an ambulacral plate-series and an interambulacral plate-series for *L. williamsi*, *L. variegatus*, and *L. panamensis*.

B R E V I O R A

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A NEW SPECIES OF *ELEUTHERODACTYLUS* (AMPHIBIA, SALIENTIA) FROM THE GUAYANA REGION, EDO. BOLÍVAR, VENEZUELA

Juan A. Rivero

Abstract. A new species of *Eleutherodactylus*, *E. pulvinatus*, is described from the wet region of La Escalera, Estado Bolívar, Venezuela. The species is characterized by its small but distinct tympanum, poorly defined or absent vomerine teeth, large, transversely oval disks which are larger than the tympanum, a W-shaped marking on the occiput and non-spiny nuptial pads. The possible relationship between this frog and the genera *Eupsophus*, *Syrrhophus*, *Niceforonia*, *Trachyphrinus* and *Phrynopus* is discussed and evaluated.

Among the specimens recently collected by the author in the region of La Escalera, Estado Bolívar, Venezuela, there are seven specimens of a small and peculiar leptodactylid whose generic allocation has been somewhat difficult and problematical. In this species, the vomerine odontoids are very indistinct; in some individuals they appear to be absent altogether. As in *Eleutherodactylus*, the disks are well developed and the terminal phalanges are T-shaped, but there are two well-developed glandular pads on the inner side of the first digit, a character which does not seem to have been described in that genus.

It has been customary to allocate all *Eleutherodactylus*-like forms without vomerine teeth to the genus *Syrrhophus* (type locality, San Antonio, Texas) and all those with vomerine teeth but without disks to *Eupsophus* (type locality, Chile). In 1932, Parker violated convention by describing *Eupsophus wettsteini* (type locality, Pongo, Perú, 2000 m) as "the first species that has been described as belonging to the genus *Eupsophus* in which vomerine teeth are lacking" (p. 344).

Even a superficial examination reveals that Andean species of *Syrrhophus* are not closely related to the animals that are referred to that genus in Central America and the United States. Whether or not they have vomerine teeth, most of the Andean animals seem to be closely related and should perhaps be called *Eupsophus* until a more thorough study can be undertaken and their relationships established. It is evident that the three groups of *Eupsophus* (*Thoropa*, *wettsteini-peruanus*, and the Chilean forms) mentioned by Cei (1960, 1962) constitute different evolutionary lines, one of which (*wettsteini-peruanus*) appears to continue along the Andean Cordillera to Venezuela, where *Eupsophus ginesi* is known from glacial streams in the páramos of the Mérida Andes. It is now usually recognized that *Thoropa* is a separate genus, and perhaps the *wettsteini-peruanus-ginesi* group should be recognized as another, in which case, *Oreobates* Jiménez de la Espada, 1872, might appear to be the appropriate name. Yet, although *Oreobates* was described from Quijos (whence the name *quixensis*), and this name has been interpreted to mean Quito (Peters, 1955: 347; Gorham 1966: 117), Espada himself states: "It occurs in the Oriental province, formerly Quijos, in Ecuador, at the foot of the Cordillera" (Vertebrados del Viaje del Pacífico, 1875: 104). Specimens from the Napo-Pastaza region in the M.C.Z. correspond to the description of *quixensis*, which looks more like a *Thoropa* than a *Eupsophus*.

Two new genera, each based on a single individual from the high elevations of the Colombian Andes, were described by Goin and Cochran in 1963. The first, *Niceforonia*, has distinct vomerine teeth, no disks and no external tympanic disk; the other, *Trachyphrinus*, has no vomerine teeth but has small disks (and T-shaped phalanges) and a well-defined tympanum. In general physiognomy, both of these genera resemble the group of frogs here considered, and *Trachyphrinus* does not look at all like *Syrrhophus*, the genus in which it would be included if its classification were to be based on conventional morphological characters.

But all kinds of combinations of characters have been described in the high elevation species from Perú to Venezuela. Thus, in 1873, Peters described *Phrynopus peruanus* (now called *Eupsophus*, *fide* Gorham, 1966) with vomerine teeth and tympanum, but apparently without disks. The same combination is found in *Borborocoetes columbianus* Werner (now *Eupsophus*, *fide* Gorham, 1966), *Paludicola festae* Peracca (now *Syrrhophus*, *fide* Gorham, 1966), and *Eupsophus ginesi* Rivero. However, in *Paludicola simonsii* Blgr. (now *Syrrhophus*, *fide* Gorham, 1966), *Syrrhopus montium* Shreve and *Syrrhopus juninensis* Shreve (both now *Syrrhophus*, *fide* Gorham, 1966) there are no vomerine teeth, external tympanic disk, or disks. In *Eleutherodactylus whymperi* (Blgr.) and *E. surdus* (Blgr.), on the other hand, vomerine teeth and disks are present but the tympanum is not apparent externally, while in *Eupsophus wettsteini* there are no vomerine teeth or disks but there is a small tympanic disk. *Trachyphrinus myersi* and *Syrrhophus areolatus* Blgr. are alike in having disks and external tympana (small and ill defined in *S. areolatus*) but no vomerine teeth.

It is not the purpose of this paper to enter into the many problems pertaining to this interesting group (or groups?) of frogs. But these digressions have been necessary because of the difficulty of allocating the new species described in this paper. If this group of Andean frogs is found to constitute a natural assemblage, perhaps the name *Phrynopus* can be used for it. It is also possible that it may constitute two or more evolutionary lines, in which case the genera suggested by Goin and Cochran may be found useful. It appears to me, however, that this group, or most of it, constitutes a latitudinal extension of Chilean and Argentinian *Eupsophus* along belts of similar climatic conditions in the Andes. If, as has been reported, some of the species are limited to páramos in the Andean Cordillera, their present diversification is to be expected. In a group where the tympanum-vomerine odontoids-disks can occur in so many combinations, separation into various genera is hardly convenient and may actually be very confusing.

A number of "*Syrrhophus*" have been described from the lowlands or at most, from elevations below 800 m in Ecuador. Such is the case, for example, with *S. chalceus* (Peters), *S. calcaratus* Andersson, and *S. coeruleus* Andersson. *S. chalceus* has also been reported by Lutz and Kloss, 1952, from Iuarté, along the Río Uaupés. As the largest of the species described was 30 mm (*S. coeruleus*), all the others ranging from 18 to 29 mm, it is not improbable that the lack of vomerine teeth can be attributed to immaturity in some of them. It is possible, however, that they represent another line of *Eleutherodactylus* without vomerine teeth (since in this genus disappearance of the vomerine teeth does not seem to be a difficult process) or that they are in some way connected with the *Eupsophus* group from Chile and/or the more northern Andes.

Eleutherodactylus pulvinatus, the species described here, does not have the rotund physiognomy of the *Eupsophus* group, and its distribution does not suggest relationship. Nuptial pads have been described for some members of the Andean group (Parker, 1932:

363), but most of the species do not seem to have them. In the Chilean species (Cei, 1962), on the other hand, and in *Thoropa* (Cochran, 1955: 91), thumb and sometimes breast and axillar spines have been described for those species in which males are known. Similar modifications have been described for *Crossodactylodes* Cochran (type locality Macaé, Río de Janeiro), a monotypic genus with hidden tympanum and the vomerine teeth represented only by a roughened ridge. In view of the foregoing considerations, it has been found preferable to describe the new leptodactylid in the genus *Eleutherodactylus*, pending a more complete study of its anatomy and relationships.

Eleutherodactylus pulvinatus sp. n.

Type. M.C.Z. 64741, ♂, Paso del Danto, Región de la Escalera around 1400 m above San Isidro, road from El Dorado to Sta. Elena de Uairén, Estado Bolívar, Venezuela. Coll. J. A. Rivero and J. Pulido, 26 March 1968.

Diagnosis. A small *Eleutherodactylus* with small but distinct tympanum, vomerine teeth poorly defined or absent; two non-spiny nuptial pads on the inner side of the first digit of males; large transversely oval disks, larger than the tympanum; first finger shorter than second; adpressed heel extending to between eye and nostril; and a W-shaped marking behind the occiput.

Description. Head as long as broad; snout short, subtriangular; tongue free and slightly nicked behind; vomerine odontoids faintly indicated as two irregular elevations well behind and between the small choanae; eye diameter slightly greater than distance between eye and nostril but shorter than snout; interorbital space as broad as an upper eyelid; canthus rostralis rather indistinct, curved; loreal region only slightly sloping, concave; tympanum distinct, ⅓ the eye diameter; a flat, indistinct supratympanic fold; a line of small, whitish tubercles from elbow to wrist; two distinct, oval, metacarpal tubercles; a glandular pad at the base of the inner side of the first finger and another one distal and slightly dorsad to this; first finger shorter than second, its disk much broader than the phalanx; all fingers free; larger disks larger than the tympanum; a small, flat, whitish tubercle at the distal portion of the tibial segment; a distinct and prominent inner and an indistinct outer metatarsal tubercle; toes free, with prominent subarticular tubercles; heel of the adpressed hind limb extending to between eye and nostril. Skin above, shagreened, more coarsely tubercular in the tympanic area and anterior flanks. Below, finely granular on throat and anterior part of the belly; more distinctly granular on posterior part of the belly and thighs. A very large subgular vocal sac with a triangular anterior end; a space (about 2 mm) between tip of the jaw and anterior edge of sac. A "frenulum" in the anterior tip of the sac continues anteriorly almost to the tip of the jaw.

Color. Above, brownish gray, with a dark brown interorbital bar, a black supratympanic streak, a W-shaped marking on the anterior part of the back, and some large blotches and small spots on the posterior two-thirds of the back; on the flanks the blotches continue ventrally, forming oblique, wavy bars that are separated by light gray areas; anterior and posterior part of the thighs uniform brown, this color extending as bars across the gray color of the upper part of the thighs; limbs and fingers with cross-bars and blotches; upper lip with triangular blotches on a gray background; no canthal streak. Ventral surfaces dirty white, darker on the throat and distal portion of the limbs.

Measurements (in mm). Snout-vent 26.1; head breadth 9.8 (between tympana); head length 10; femur 13; tibia 14.1; foot 11.

Paratypes. There are six paratypes (U.P.R.-M.[1] 02214-02219), all coming from the type locality. All are males, and the size varies from 26.1 mm to 23 mm. In some of the smaller specimens the canthus seems to be less defined than in larger specimens, and a cross-section of the snout would be more or less rounded if it were not for the slight concavities of the loreal areas. The heel of the adpressed hind limb extends to the nostril in only one specimen, but the skin of the dorsal surfaces is more granular than in the type, at least in two examples. The belly and thighs are uniformly granular, the throat more finely so in most specimens. The vocal sac does not form the anteriorly triangular pouch that it forms in the type, but it is possible that it has been displaced, as a similar condition can be noticed in several specimens. The W-shaped marking is present in all specimens, but the oblique bands of the flanks are less distinct in some, although a trace of them can be noticed in all. Vomerine odontoids cannot always be seen, but they can be felt with a needle. They seem to be irregular in both size and position, and in some specimens seem to be almost totally absent.

Habits and relationships. All the specimens were collected at night, calling from low bushes (1 to 3 ft. from the ground) along the rocky bank of the road at an elevation of approximately 1400 m. At dusk, their calls seemed to come from under the rocks

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[1] University of Puerto Rico — Mayagüez.

lining the almost vertical road bank, but none could be collected at the time. Later at night, their calls were traced and recorded and the various specimens collected. In the dark the frogs are yellow or cream, but they turn dark gray in the daytime. Their voices were not heard much below the elevation where all the specimens were obtained. No other species of *Eleutherodactylus* was collected or heard in this area.

Only scattered low bushes, some soil bromeliads and, occasionally, thickets of lilaceous plants occur in the rather open areas where *E. pulvinatus* was collected. There were permanent and temporary streams everywhere, as the region is probably one of the rainiest in Venezuela.[1] The forest, 50 to 60 meters from the road, is a rather open montane forest, usually with many epiphytic bromeliads, orchids, and araceans. Most of the soil is a white quartziferous sand, which is covered in the forest by a layer of dead leaves and other organic matter.

Although many *Eleutherodactylus* have W-shaped markings on the back, the distinct markings of *E. pulvinatus* remind one of the condition of *E. w-nigrum* (Boettger), which, however, is a species from more than 3000 m in the Andes of Ecuador. Other species, from relatively adjacent regions, are: *E. inguinalis* Parker (New River, Guyana), *E. beebei* Cochran (Kartabo), *E. pliciferus* (Blgr.) and *E. ramagii* (Blgr.) (Iguarasú, Pernambuco, Brasil), *E. crepitans* Bockermann (San Vicente, Matto Grosso), *E. carvalhoi* B. Lutz (Itacoaí R., NW Brasil), *E. peruvianus* (Melin) (Roque, Perú), *E. vilarsi* (Melin) (Taracua, Río Uaupés), *E. rosmelinus* Gorham (Río Uaupés), *E. melini* Bokermann (Roque, Perú), *E. altamazonicus* Barbour and Dunn (upper Amazon) and *E. marmoratus* (Blgr.) (Mt. Roraima). In all these species there are well-defined vomerine teeth, and nuptial pads have not been described for any. *E. inguinalis* has on obtusely angular canthus, a broad interorbital space, much broader than the upper eyelid, and a black bordered, inguinal ocellus; *E. beebei* Cochran is a large species 85.5 mm in length; in *E. pliciferus* and *E. ramagii* the first finger is longer than the second; *E. crepitans*, from dry forest, is similar to *E. conspicillatus*, and its tympanum is ⅔ the eye diameter; *E. carvalhoi* does not have a tympanum; *E. peruvianus* and *E. vilarsi* are 50 and 39 to 41 mm, respectively, and may be synonyms of *E. conspicillatus; E. rosmelinus* has a depressed head, disks ⅓ the size of the tympanum and first finger

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[1] According to a report in a local newspaper, engineers working on the road from El Dorado to Sta. Elena could only work 60 to 80 days of the year, and even those were not always sunny days without any rainfall.

longer than second; *E. melini* has an indistinct tympanum and small disks; *E. altamazonicus* has a depressed and oval snout and a barely distinguishable tympanum; and *E. marmoratus* has a rounded snout as long as the orbital diameter, dark-edged marblings on the head, and a small size (only topotypical specimen: 19 mm).[1]

From the lowland "*Syrrhophus*" mentioned before, *E. pulvinatus* can apparently be distinguished by the nuptial pads it has in the inner side of the first finger. Other differences are as follows: In *S. chalceus* (Peters), from Pastaza River, the first finger is longer than the second; in *S. coeruleus* Andersson, from eastern Ecuador, the canthus is distinct and there are two pairs of dorsolateral folds; and in *S. calcaratus* Andersson,[2] from near Archidona, 800 m, there is a canthal streak, and the disk of the first finger is only slightly broader than the phalanx behind it.

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For the trip to La Escalera, the author relied on an invaluable assistant, Mr. Juan Pulido, always faithful and always willing to help during the difficult situations that often arise during such trips. Major Luis Alfonso Godoy, Commander, Engineering Corps at sector A of the road from El Dorado to Sta. Elena, was extremely helpful in providing facilities and assistance.

As always, the author is greatly indebted to Dr. Ernest Williams, not only for permitting the use of the facilities of the Museum of Comparative Zoology at Harvard, but also for reading the manuscript critically and for discussing various taxonomic and evolutionary problems. Mr. Benjamin Shreve has also read the manuscript and suggested changes. The author, however, assumes full responsibility for the shortcomings of this paper.

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[1] Frogs collected in Mt. Marahuaca by the author (Rivero, 1961: 80) and pronounced conspecific with *E. marmoratus* by Parker, do not represent *E. pulvinatus*. However, further comparisons should be made when more specimens of *E. marmoratus* become available.

[2] Among the group of frogs here discussed, the species name *calcaratus* was first used by Günther, 1881, for *Cacotus calcaratus*, now considered a synonym of *Eupsophus roseus*.

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Fig. 1 A, B. *Eleutherodactylus pulvinatus*, type, M.C.Z. 64741, from Paso del Danto, region of La Escalera, Estado Bolívar, Venezuela. A. Dorsal view; B. Lateral view of head region.

B R E V I O R A

Museum of Comparative Zoology

Cambridge, Mass. 31 December, 1968 Number 307

A NEW SPECIES OF *HYLA* (AMPHIBIA, SALIENTIA) FROM THE VENEZUELAN GUAYANA

Juan A. Rivero

Abstract. A small species of *Hyla*, *H. rodriguezi*, is described from the wet region of La Escalera, Estado Bolívar, Venezuela. The new form is characterized by having a large, well defined tympanum, about ⅞ the size of the eye; nearly webless fingers; ¾ webbed toes; speckled throat and orange-red areas in the thighs. It may be related to the *Hyla leprieurii* group but it is also similar to *Hyla grandisonae* Goin, from which it differs in coloration and in other details.

Among the new frogs collected by the author in the region of La Escalera, in southeastern Venezuela, there is a small species of a bromelicolous form that appears to be new to science. The new species is named *Hyla rodriguezi* in honor of Gilberto Rodríguez, of the Instituto Venezolano de Investigaciones Científicas, who made possible the expedition during which this and many other interesting species were collected. Dr. Rodríguez spared no effort in facilitating the author's investigations of the frogs of the Venezuelan Republic.

During this and other investigations pertaining to the Venezuelan frog fauna, the author has utilized the facilities and collections of the Museum of Comparative Zoology at Harvard. He is most thankful to the Curator of Herpetology, Dr. Ernest Williams, for his cooperation and unfailing willingness to be interrupted and consulted at any time.

HYLA RODRIGUEZI sp. n.

Type. M.C.Z. 64740, ♂, Paso del Danto, Región de La Escalera, ca. 1400 m above San Isidro, road from El Dorado to Sta. Elena de Uairén, Estado Bolívar, Venezuela. Coll. Juan A. Rivero and Juan Pulido, 26 March 1968.

Diagnosis. A small *Hyla* with bony head; strong, straight canthus rostralis; almost vertical, concave loreal region; anteriorly converging vomerine teeth; large tympanum, about ⅞ the size of the eye; tubercular dorsal surfaces (males?); red (alive) or white (preserved) areas on the thighs and speckled throat.

Description. Head slightly broader than long; snout short, rounded, concave above; nostrils forming a truncate tip; canthus rostralis strong and well defined; loreal region vertical, concave; interorbital space as broad as an upper eyelid; vomerine odontoids anteriorly converging, extending from level of palatines to about middle of inner margin of choanae; choanae moderate, oblique; tympanum large, distinct, about ⅞ the size of the eye; larger disks much smaller than tympanum; eye diameter as long as distance between eye and nostril; a line of whitish tubercles from elbow to wrist; metacarpal tubercles not well differentiated; subarticular tubercles well defined; fingers almost free, the first swollen at the base and with an elongated brown pad which covers ⅔ of its inner side; first finger not extending much beyond first subarticular tubercle of second; second finger shorter than last; a small tubercle at the heel; no tarsal fold; an elongated inner and a flattened, rounded, and less distinct outer metatarsal tubercle; subarticular tubercles of toes prominent; toes about ¾ webbed (taken in order from first to fifth, the following phalanges are free of web: 2; 1½; 1⅓; 2⅓; 1⅓); heel of the adpressed hind limb extending to the anterior corner of the eye. Skin above distinctly granular, most of the granules having a corneus tip; on the posterior half of the back, the anterior loreal region, the arms, and tibial segments, the granules become larger tubercles. Below, smooth on the chin and chest; finely granular on the throat; coarsely granular on the belly and postero-ventral aspect of thighs; one almost imperceptible furrow on each side of the throat.

Color. Above, dark brown, with two somewhat lighter and ill-defined bands from behind the eyes and over the level of the shoulders to near the sacral region; a dark, ill-defined streak along the flanks below the light brown band; other longitudinal, light brown spots can be noticed on the dorsum; a whitish, ill-defined spot or line under the eye, in front of the tympanum; disk of first finger white, of second finger half white and half brown; posterior portion of arm and axillar membrane white; flanks below dark brown streak white, this color extending dorsally to the illea on the posterior end; thighs pink, speckled and spotted with brown; rest of hind limbs and fore limb with transverse blotches or bars; web pink. Below, creamish white, uniform, except for the sides of the throat and lower lip, which are freckled with purplish brown.

The living animal appeared to be of a solid brown color with orange areas on the thighs, white forearms (posterior part) and axilla, creamish venter with purplish specks on the throat, rosy hind limbs (underneath), and with cream points along the forearm and at the sides of the anus.

Measurements (in mm). Snout-vent 34.5; head length 11.02; head breadth 11.2; femur 16; tibia 17.7; foot 12.4.

Paratypes. The paratypes are U.P.R.-M.[1] 02207-02012, all from the same locality and with the same data as the type. They vary from 21.6 to 35.2 mm in snout-vent length. In some specimens the heel of the adpressed hind limb may extend to between eye and nostril; in a few the web is less extensive than in the type, and the feet may perhaps be said to be not more than ⅔ webbed. The skin may be almost smooth in some of the smaller specimens.

There is some variation in coloration, although the pattern is rather similar in most specimens. In a few examples the longitudinal bands or spots are darker, not lighter than the background color, and in the smallest individual the background color is gray and there are many short longitudinal streaks on the dorsum. In all specimens, there is a light-colored spot or line in front of the tympanum, but in some it is very diffused, and in one it extends anteriorly along the upper lip. In preserved material, the ventral color is as described for the type, except for the fact that the freckles of the throat may not be limited to the margins and may also extend to the central area. In living animals the color is more variable, and the throat may be yellow with purplish freckles while the rest of the venter is cream or lighter yellow. Sometimes there is almost no orange on the thighs, while at others the orange becomes red and may extend, on the ventral side, to the tibial and metatarsal segments and the foot. The lower side of the forearm may also be orange or red

Habitat and relationships. The place where *H. rodriguezi* was collected is probably one of the rainiest in Venezuela, and when it is not raining it is usually foggy and misty. The vegetation can probably be classified as the wet montane type, and there is a great abundance of epiphytes, the Aracean *Philodendron nobile* being particularly evident.

Hyla rodriguezi was collected in ground bromeliads (apparently of the genus *Vriesea*) that grow along the road bank at an elevation

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[1] University of Puerto Rico — Mayagüez.

of about 1400 m. There was never more than one specimen in any one bromeliad, and only once was there another species of frog (*Hyla minuta*) in the same plant. All were collected at dusk. At night, no sound was heard in the area except that of a new species of *Eleutherodactylus* (Rivero, in press), and occasionally, the whistling call of *Leptodactylus rugosus*.

This species is well characterized, and if I were to relate it to any other known species, it would probably be to the *Hyla leprieurii* group. However, *Hyla rodriguezi* is a smaller species with a shorter snout, less webbing between the toes, and inconspicuous vocal sacs. It is also somewhat similar to *Hyla alboguttata*, but the head of *Hyla rodriguezi* is more bony, its canthus straighter and better defined, its feet less webbed, and its color different. The speckled coloration of the throat of *H. rodriguezi* seems to be very characteristic of this species.

Hyla grandisonae Goin (type locality, Mazaruni Forests, Guyana) agrees in many characters with *H. rodriguezi*, but on closer examination it is found that the two species may not even be too closely related. In *H. grandisonae*, the heel of the adpressed limb reaches almost to the nostril, the skin above is smooth, the ventral color is gray, and the species is said to be related to *Hyla parviceps* Boulenger, *H. rondoniae* Bokermann and *H. bokermanni* Goin, three species that do not seem to be close to *Hyla rodriguezi*.

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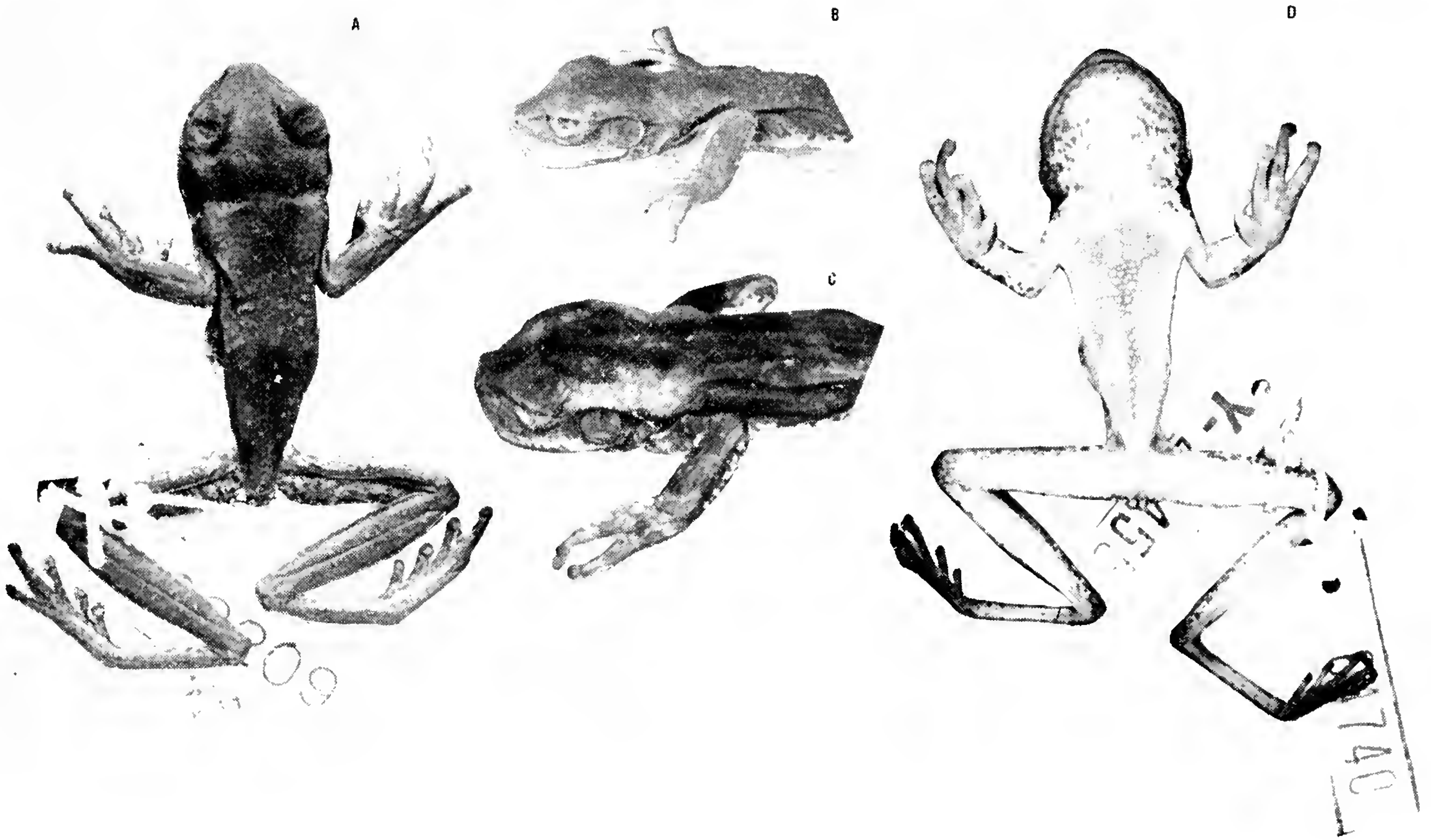

Fig. 1. A, B, *Hyla rodriguezi*, type, M.C.Z. 64740, from Paso del Danto, region of La Escalera, Estado Bolívar, Venezuela. A. Dorsal view. B. Lateral view of head region. C, D. *Hyla rodriguezi*, paratype, U.P.R.-M. 02209, from the same locality. C. Enlarged lateral view of head region to show common dorsolateral pattern. D. Ventral view.

BREVIORA

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THE MOLLUSCAN FAUNA OF AN UNUSUAL BERMUDIAN POND: A NATURAL EXPERIMENT IN FORM AND COMPOSITION

Stephen Jay Gould

Abstract. Twenty-four molluscan species inhabit a landlocked marine pond of normal salinity in Hamilton Parish, Bermuda. Walsingham Pond, unusual because of its isolation and the ecologic effects thereof, can be viewed as a natural experiment. The form and composition of its molluscan fauna are compared with "control" samples from open marine environments. Composition of the fauna is similar to two modern and three fossil samples from localities similar in ecology to Walsingham Pond but directly exposed to the open sea. Isolation does not seem to affect the presence and absence of species. Walsingham Pond molluscs are, however, unique in their shell form. As demonstrated by plots of weight vs. size, the four major Pond gastropods have thinner shells than those of the same species from control samples.

It is often said that natural history is science of a lower order than experimental biology. If description and explanation are viewed as ascending orders of sophistication, this charge is valid when natural history remains at the level of "plain story"; for the very undertaking of an experiment implies a search for explanation. Yet there are a variety of natural situations that possess the essential character of experiments, even though no human manipulation of material is involved. The evolutionary phenomena of parallelism and convergence, for example, serve the same function as experimental replication; both provide the repeated occurrences upon which inductive generalizations are based (Harris and Morren, 1966). I am concerned here with another kind of "natural experiment" — the unusual situation amidst a large number of "normal" occurrences that act as controls.

Walsingham Pond in Hamilton Parish, Bermuda, is an unusual situation. Walsingham is a landlocked marine pond of nearly normal salinity maintained by tidal interchange with Castle Harbor through underground caves. Limestone walls and mangrove roots form the borders of the Pond; the bottom is covered with a soft organic mud composed primarily of decaying material, faecal pellets, and shell fragments. Dominant elements of the bottom biota are the alga *Chaetomorpha crassa*, a profusion of sponges, and, unfortunately for collectors, the jellyfish *Cassiopeia;* there are no hard corals in the Pond. Maximum water depth is 22 feet; the bottom mud layer may be several feet thick. Helz (unpublished manuscript) studied the water chemistry of Walsingham Pond. Oxygen increases steadily from top to bottom; values are consistently 1 ml/l less than those of the normal marine waters of Castle Harbor. Nitrate and phosphate show no trend with depth; values are two to three times those of Castle Harbor. This abundance is presumably related to the continuing concentration of organic matter in Walsingham Pond. After several rainless days, Pond salinity was 100-170 ppm higher than that of Castle Harbor. Surface waters were 10-50 ppm above bottom waters; mixing may occur by sinking of the denser surface water. Ten hours after a heavy rain, surface waters of the Pond were less saline than those of Castle Harbor by 1500 ppm.

Two aspects of the Pond fauna — composition and form — may be studied to find and explain differences between this unusual situation and the normal open marine habitats of Bermuda. I have confined my attention to the Mollusca, due both to personal preference and to the availability of abundant comparative material in the magnificent collection of Mr. Arthur Haycock (Bermuda Museum). Since Walsingham Pond's landlocked status is its most unique attribute, I shall concentrate on questions related to this point. We shall want to know if the Pond's isolation, of itself, influences the form and composition of its molluscan fauna. Failing such influence, we may still ask if a secondary result of isolation — an unusual condition of water chemistry attributable to curtailed mixing of Pond with ocean, for example — can be correlated with differences between the Pond fauna and "control" faunas from normal marine environments.

COMPOSITION OF THE MOLLUSCAN FAUNA

Nine thousand two hundred fifty years ago, the sea stood approximately 78 feet below its present level (A. C. Neumann, personal communication, determined this figure by dating a peat bed cored at the bottom of Harrington Sound). With a maximum depth of 22 feet, Walsingham Pond cannot be more than a few thousand years old. Entrance to the Pond can be obtained only through the channels of underground caves that connect Walsingham to

Castle Harbor; I suspect that the molluscan populations now living in the Pond owe their origin to the infrequent transport of larvae through these channels. If this isolation exerts a major control on composition, I would expect a disharmonious assemblage of molluscan species with a predominance of forms having long and highly mobile larval stages. If ecology is the major control, then neither the young age of the Pond nor its isolation should affect the distribution of species. In this case, I would expect a molluscan fauna composed of those species that characterize similar environments in open marine areas around Bermuda. This finding would carry the implication that most molluscan species had ample access to the Pond and that the composition is a function of the normal environmental preferences of species rather than of chance introductions.

I have endeavored to compile a complete listing of the molluscs in Walsingham Pond. Shells were obtained both by visual collecting and by bulk sampling with a Van Veen grab at various depths; composition does not seem to change with depth. With the exception of *Chama macerophylla,* which occur infrequently, cemented to the limestone walls, all species inhabit the muddy bottom. Some burrow into the mud (*Vermicularia spirata*), others crawl along the surface (*Nassarius ambiguus*), and still others (*Modulus modulus*) commonly live among the algal colonies of *Chaetomorpha crassa.*

Class Bivalvia
- Family Mytilidae
    - *Brachidontes exustus* (very few specimens)
- Condylocardiidae
    - *Carditopsis smithii* (one specimen)
- Lucinidae
    - *Codakia orbiculata* (most common bivalve in Pond)
- Chamidae
    - *Chama macerophylla* (infrequently on limestone walls)
- Leptonidae
    - *Lasaea bermudensis* (very common)
- Cardiidae
    - *Laevicardium laevigatum* (one immature specimen)
- Veneridae
    - *Gouldia cerina* (very common)
- Tellinidae
    - *Tellina mera* (one specimen)
- Sanguinolariidae
    - *Tagelus divisus* (rare)

Class Gastropoda
  Family Rissoidae
      Alvania platycephala (very common)
      Rissoina cancellata (one specimen)
    Vitrinellidae
      Vitrinella helicoidea (moderately common)
    Turritellidae
      Vermicularia spirata (most common mollusc in Pond)
    Caecide
      Caecum delicatulum (a few specimens)
      Caecum termes (very common)
    Modulidae
      Modulus modulus (very common)
    Cerithiidae
      Alabina cerithioides (quite common)
      Cerithium variabile (very common)
    Nassariidae
      Nassarius ambiguus (quite common)
    Marginellidae
      Hyalina avena (rare)
    Bullidae
      Bulla striata (rare)
    Atyidae
      Haminoea antillarum (rare)
    Retusidae
      Retusa candei (moderately common)
    Pyramidellidae
      Odostomia didyma (moderately common)

I was able to obtain samples of the molluscan fauna from five additional localities of similar environment (mangrove roots and muddy substrates), but situated in areas having free access to the open sea. These "controls" should serve to test the hypothesis that composition of the Walsingham Pond fauna is unusual for a mangrove-mud area because of the Pond's isolation and young age.

1. Ely's Harbour, Sandys Parish (grab sample collected at a depth of 10 feet by Robert F. Schmalz).

2. Mangrove root area on north coast of Ferry Reach, 50 yards east of Bermuda Biological station (personally collected; three Van Veen grab samples at depths of 5-7 feet).

Fortunately, three small samples of fossil shells were available to provide some temporal control on the stability of community composition during the past 10,000 years. Dried mud and mangrove root fragments were present in all samples.

TABLE 1

Composition and Relative Abundance of Macromolluscs in Mud-Mangrove Environments. (Relative abundance indicated by numerical order.)

	Vermicularia spirata	*Cerithium variabile*	*Codakia orbiculata*	*Modulus modulus*	*Nassarius ambiguus*	*Bulla striata*	*Tagelus divisus*	*Brachidontes exustus*	*Tellina mera*	*Batellaria minima*	*Chione cancellata*	*Columbella mercatoria*	*Cantharus tinctus*
I. Modern Samples													
Walsingham Pond	1	2	3	4	5	6	7	8	9				
Ely's Harbour	1	2		3	4	5							
East of Biostation	3	2	4	5	6	9	10	7		1	8	11	
II. Fossil Samples													
Pembroke Marsh	4	2	1	3	5						6		7
Longbird 4 (-71.8 feet)	2	6	3	5	4	7	8				1		
Longbird 5 (-85.5 feet)	1	5	4	3	2								

3. Pembroke Marsh, Pembroke Parish (collected by Charles Schuchert of Yale University in the 1920's). Of the five controls, only this sample cannot be identified as having been in open contact with the sea.

4. Longbird Bridge boring, 71.8 feet below present sea level.

5. Longbird Bridge boring, 85.5 feet below present sea level.

Samples 4 and 5, kindly supplied by Walter S. Newman, were obtained from the test boring made prior to construction of Longbird Bridge, St. George's Parish.

Table 1 lists all the mud-dwelling macromolluscs of Walsingham and these five localities in order of their abundance (only the rock-cementing *Chama macerophylla* is eliminated by this constraint on environment). I do not know how representative the small fossil samples are of actual diversity and abundances. The micromolluscs are not included, because several of the samples contained only the larger shells, with insufficient matrix for the screening of small species. Yet strong similarities almost surely exist between micromolluscs of Walsingham and the five controls. Several specimens of *Retusa candei*, *Caecum termes*, and *Odostomia didyma*, for example, were obtained from dried mud caking the apertures of *Vermicularia spirata* specimens in the Longbird 4 sample; all three of these micromolluscs are common in Walsingham Pond.

The similarities between Walsingham and the controls are striking. Five macromolluscs strongly dominate the Walsingham fauna — *Vermicularia spirata*, *Cerithium variabile*, *Codakia orbiculata*, *Modulus modulus*, and *Nassarius ambiguus*, in that order. Excepting the absence of *Codakia* in the Ely's Harbour sample, all of these species are present in all of the five controls. Considering the small size of several samples (20 shells in Longbird 5, for example), this correspondence seems highly significant. *Bulla striata* and *Tagelus divisus*, rare but consistently present in Walsingham, are found in three and two of the controls respectively. Of *Brachidontes exustus* and *Tellina mera*, the Walsingham "trace elements," only the first is found at one other locality.

A few unexplained discrepancies arise from species present in control samples but not in Walsingham Pond. The venerid clam *Chione cancellata* is present in three of the controls, dominant in one of these (Longbird 4) but absent from Ely's Harbour and Longbird 5 as well as from Walsingham. *Batillaria minima*, a homeomorph of *Cerithium variabile*, commonly occurs with the latter in rocky and sandy intertidal environments of the open sea (they are so associated in Castle Harbour, barely 100 yards from Walsingham Pond). *Batillaria* is absent from all but one of the mangrove-mud environments, but dominates among the mangrove roots east of the Biostation. This might argue for atypicality of the Biostation locality, but not for a lack of correspondence between Walsingham and the other controls. While it is not especially relevant to this study, the ecologic relationship of the homeomorphs *Cerithium* and *Batillaria* is a fascinating problem.[1]

Thus, the association of *Vermicularia spirata, Cerithium variabile, Codakia orbiculata, Modulus modulus,* and *Nassarius ambiguus* in Walsingham Pond is no product of accidental access, but an expression of the normal molluscan community in mangrove-mud areas. *Vermicularia* is not often thought of as an inhabitant of muddy areas, for it usually lives cemented to hard objects in clear, open water. Olsson (1951), however, found abundant specimens on the mud flats in Tampa Bay, Florida. He described them as *Vermicularia fargoi,* but I have synonymized this species with *V. spirata* elsewhere (Gould, in press). *Tagelus divisus* prefers muddy environments (Fraser, 1967). In short, the unique isolation of Walsingham Pond is not reflected in the composition of its molluscan fauna. Characteristic species of the molluscan community that inhabits mangrove-mud areas throughout Bermuda have all become established in Walsingham Pond despite the barriers to distribution.

FORM OF THE MOLLUSCAN FAUNA

Is the form of molluscan shells in Walsingham Pond different from that of the same species in open marine habitats? If such differences are found, we may again pose the question: Is the uniqueness of Walsingham molluscs attributable to the Pond's isolation *per se* or to some secondary ecologic result of that isolation? In the first instance, isolation of a small founding population maintains the distinguishing gene frequencies present, by chance, in the founding individuals or attained, without regard to adaptive significance, by genetic drift. In the second case, an unusual condition of water chemistry or bottom ecology works its influence upon the form of shells by direct phenotypic modification. A mixed case is also likely: unusual conditions establish strong selective pressures, while isolation favors the stabilization of new genotypes by

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[1] Where they occur together, distribution is not random. Patches of 20-30 individuals of one species are often found in large tracts dominated by the other. This phenomenon is particularly well seen in Coot Pond, St. George's Parish.

removing the diluting effect of gene influx from normal populations.

When a single species differs from its "control" counterparts in a unique way, it may be difficult to distinguish among the three explanations. Walsingham specimens of *Modulus modulus* are often relatively higher than is normal for the species in Bermuda. The most spectacular modification, however, is found in *Vermicularia spirata.* This gastropod customarily begins life as a normally coiled turritellid, but later cements to a hard object and uncoils its shell. In the absence of any hard substrate on the floor of Walsingham Pond, more than 95 per cent of the *Vermicularia* shells do not uncoil at all; those that do unwind slowly and regularly without a trace of the normal attachment scar. We have here the curious case of an animal reverting, functionally, to the form and habitat of its ancestor: Walsingham *Vermicularia* construct and inhabit burrows identical to those of its coiled ancestor *Turritella.* Since the Walsingham *Vermicularia* uncoil normally when provided with hard coral substrate in a laboratory tank, this striking modification may have no genetic base other than the great phenotypic plasticity permitted by the normal genotype. I have documented this case in some detail elsewhere (Gould, in press).

When many species differ from their "controls" in a similar way, some aspect of the Pond's unique ecology is probably involved in the explanation — either directly by phenotypic modification or indirectly via selection pressures. There is one general modification that affects all the major Walsingham species: Pond shells appear to be thinner than those of the same species in open marine habitats. I tested this observation by comparing plots of combined linear dimensions vs. weight for the four most common Pond gastropods (Fig. 1) with similar plots for the same species in normal marine habitats (Haycock collection, Bermuda Museum). Use of a combined linear dimension (length plus width) provides a better measure of overall size than length alone. (In *Modulus modulus,* for example, Pond shells of a given length are generally narrower — hence lighter — than are control specimens of the same length. The lower weight/length ratios of Pond *Modulus* at a given length might be due not to shell thinness [the hypothesis to be tested] but to differences in shape between Walsingham and control shells.)

In the ideal case of isometric growth, shell weight varies directly with shell volume, and shell volume increases as the cube of a single linear dimension or an added combination of such measures (using length plus width instead of length alone will modify the

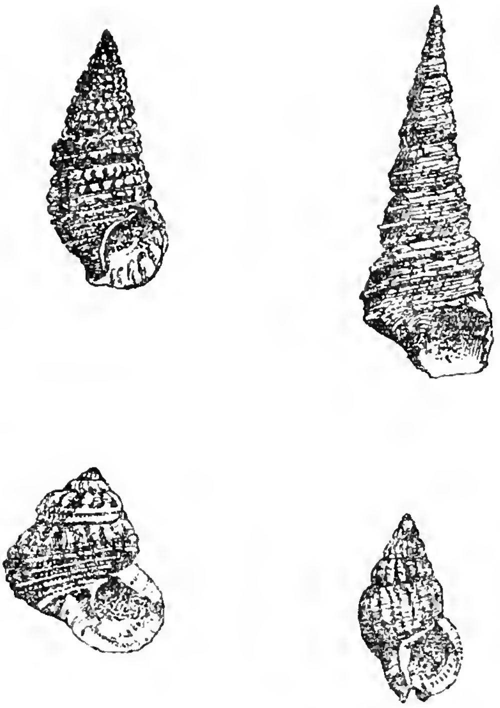

Fig. 1. The four dominant gastropods of Walsingham Pond (natural size). Upper left: *Cerithium variabile*. Upper right: *Vermicularia spirata*. Lower left: *Modulus modulus*. Lower right: *Nassarius ambiguus*.

y-intercept but not the slope of this ideal weight vs. linear dimension curve):

$$\text{weight} = \text{b (length plus width)}^3$$

Such a curve will plot as a straight line on double logarithmic paper with a slope of 3 and a y-value of b at $x = 1$. This situation is closely approached in the eight plots of Figure 2: slopes vary from 2.57 to 3.53. In three of the four pairs of plots, slopes are similar for Pond and control samples (Table 2). The high slope of Walsingham *Modulus* may be an artifact of a small and incomplete size range — see Bohlken, 1962:560. Pond b-values are lower than the control parameters in each case (Table 2), but this is not significant in itself, since $x = 1$ mm is too distant an extrapolation from the data size range to be biologically meaningful. The important point (Fig. 2) is that for *each* of the four pairs of plots, the curve for Pond snails falls *below* that for control snails over the *entire* measured size range of the samples. (The intersection of the two *Modulus* curves at a size never reached by this species is a datum devoid of biological significance; the size range of actual data should always be specified in power function plots — see White and Gould, 1965.) At any given size for which data are available, Pond snails are lighter than control snails in each of the four species.

Similar modification of at least four species suggests that some common factor of Pond ecology is involved as direct or indirect cause. Due perhaps to the vast accumulation of decaying organic matter in Walsingham, Pond pH is a good deal lower than normal marine values. Six measures from various depths made in June 1967 ranged from 7.6 to 7.7. There is some suggestion in the literature (Økland, 1964: 190) that low pH might inhibit shell formation even in the presence of sufficient dissolved calcium in the water; most Bermudian waters are supersaturated with respect to calcite (Schmalz and Chave, 1963). The lowered pH may make it metabolically more difficult to deposit available calcium; a given expenditure of energy may therefore produce a thinner shell in the Pond than in open marine habitats of normal oceanic pH. (We are, indeed, dealing with a deposition phenomenon rather than subsequent shell solution in Pond snails; only uneroded snails were used in these analyses.)

TABLE 2

Reduced Data for Weight vs. Size Relationships in Four Gastropod Species: Comparison of Walsingham and Control Samples. $\text{Weight} = b\,(\text{Height} + \text{Width})^K$

	Number of Specimens	*Slope (K)*	*b (mm)*
1. *Cerithium variabile*			
Control	20	3.24	.0123
Walsingham	10	3.14	.0115
2. *Vermicularia spirata*			
Control	20	2.65	.0356
Walsingham	15	2.58	.0348
3. *Modulus modulus*			
Control	20	3.00	.0332
Walsingham	13	3.53	.0055
4. *Nassarius ambiguus*			
Control	20	2.90	.0303
Walsingham	8	2.78	.0263

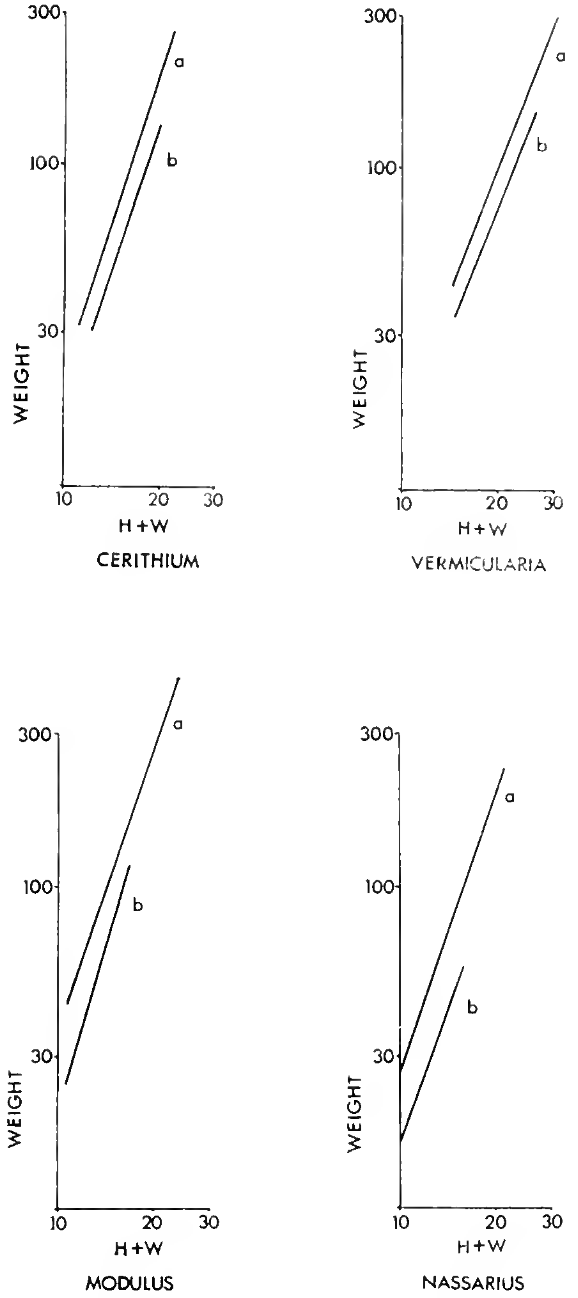

Fig. 2. Curves of weight (mg) vs. length + height (mm) for the four snails of Figure 1, both in Walsingham Pond and in normal marine habitats. Regressions marked A are for control snails, B for Pond snails. Regression lines extend only over the range of size and weight covered by actual specimens. Walsingham curves all lie below control curves, demonstrating that Walsingham shells of all species are lighter at any given weight. See Table 2 for numerical data.

I cannot state whether the thinner shells of these four species are a direct phenotypic response to unusual conditions or a result of parallel evolution, but I favor the former explanation, which is based on both the youth of Walsingham Pond and general notions of simplicity. Extreme phenotypic plasticity in shell thickness has long been recognized in land snails. By adding ground chalk to the diet of *Helix aspersa*, for example, Oldham (1934) found that shell weight increased fourfold over snails deprived of calcium.

Thus Walsingham Pond serves as a natural experiment in the form and composition of molluscan communities. The unique isolation of the Pond has no apparent effect upon the presence or absence of species but influences, in similar ways, the shell form of its dominant molluscan populations.

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VARIABILITY OF RODENT INCISOR ENAMEL AS VIEWED IN THIN SECTION, AND THE MICROSTRUCTURE OF THE ENAMEL IN FOSSIL AND RECENT RODENT GROUPS

John H. Wahlert

ABSTRACT. The microstructure in enamel of various fossil and Recent rodent incisors is described from thin sections. Measurements of enamel thickness and inclination of bands in the inner enamel layer were made from sagittal sections on large and small samples of *Rattus norvegicus* and on small samples of the Eocene forms *Paramys copei* and *Knightomys depressus*. Statistical analyses of these data show that a sample of size 10 yields an adequately close approximation to the population mean. Differences in enamel dimensions between upper and lower incisors and between incisors of different species are apparent. Thickness and inclination can be used in the identification of isolated incisors when data for other rodents have been compiled. Band width is of apparently similar utility, but small size precludes anything more than rough measurement at 430 diameters magnification. Korvenkontio's "external index" and other measurements taken from sagittal sections are deemed unreliable. Rodent species whose enamel has been studied are listed according to the kind of enamel they possess. Pauciserial enamel, found only in Eocene and Oligocene forms, appears to be the structural predecessor of uniserial and multiserial enamels, which occur in all post-Oligocene rodents examined. At present, the microstructure of incisor enamel is useful as an additional character for determining the systematic position of rodent higher taxa, but it is no touchstone.

INTRODUCTION

That incisor enamel may be useful in the classification of rodents was first suggested by the work of Tomes (1850) and later by that of Korvenkontio (1934). Tomes examined the microstructure of incisor enamel in a number of living rodents and found that within supposedly related groups the arrangement of enamel prisms is similar; his descriptions and figures showed that the enamel of modern rodents is of two basic kinds. Korvenkontio named these uniserial and multiserial. His extension of the research to other

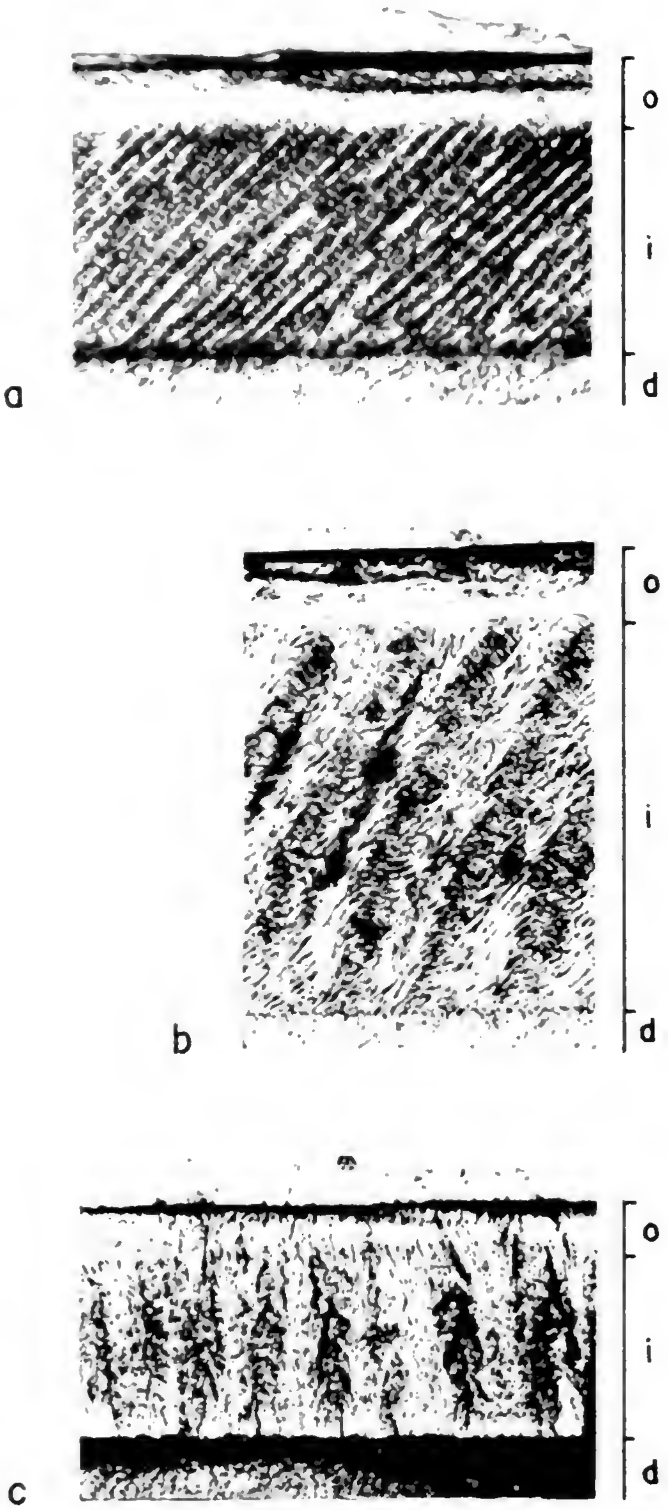

Figure 1. Sagittal sections of enamel in lower incisors: a. *Rattus norvegicus;* b. *Metaphiomys schaubi;* c. *Paramys copei.* Tips of incisors are to the right. Magnification is approximately 240 diameters. Abbreviations: o, outer enamel layer; i, inner enamel layer showing bands; d, dentine.

modern rodents and to various fossil forms greatly enlarged Tomes' work and led to the discovery of a third kind of incisor enamel structure, which he named pauciserial, among early fossil forms. In all rodents enamel covers the outer, labial side of the incisors; it may extend slightly on the mesial and distal sides.

Korvenkontio published an extensive table (1934: 116-123) giving the dimensions of various parts of the enamel and indices derived from these measurements for the incisors of all the species he examined. These suggested the possibility that some dimensions and ratios, at least, might be characteristic of low level taxa. If this should prove to be true, it would be a relatively simple matter to section, measure, and identify fossil rodent incisors, which are so frequently found separated from their jaws. Korvenkontio states (1934: 125, footnote) that in his study of 72 Recent and 33 fossil forms he used about 520 sections. He attempted to make sagittal, transverse, and frontal sections of each species wherever possible, and thus his sample size for measurement was very small.

The primary purpose of the work here reported has been to determine the variability of enamel and the sample size needed to obtain meaningful measurements. In the course of the work I have had occasion to section incisors of a number of rodents, both Recent and fossil. These are included in Table 5, which lists all species whose incisor microstructure is known.

THE KINDS OF RODENT INCISOR ENAMEL

A sagittal section of *uniserial* enamel, for example that of *Rattus norvegicus* (Fig. 1a), reveals two layers of enamel. The inner layer in this aspect appears to consist of bands one enamel prism wide that extend outward from the dentine and upward toward the tip of the tooth. On close examination each band is seen to be divided into small units, somewhat like a string of beads. Study of transverse and frontal sections reveals that each band is the cross-sectional view of a transverse lamella of enamel prisms. The width of bands and prisms is the same in sagittal section; Korvenkontio's data show a range of 2.2 to 5.0 microns for uniserial enamels. The prisms in a single lamella are parallel; they do not make a right angle with the dentine but are at some oblique angle to the sagittal plane of the tooth. A band is, therefore, the cross-section of prisms comprising a lamella. The prisms of every other lamella have the same orientation. There are two kinds of differences in orientation of prisms of adjacent lamellae. In transverse section the prisms of adjacent lamellae are seen to cross each other at a fairly constant angle. Frontal sections reveal that the prisms are tilted to one side of the sagittal plane in every other lamella and to the other in the alternating set. In the outer layer of the enamel the prisms of all lamellae are parallel, and lamination ceases; they are usually inclined more steeply toward the tip of the tooth than in the inner layer.

A sagittal section of *multiserial* enamel, for example that of *Metaphiomys schaubi* (Fig. 1b), also reveals two layers of enamel. The bands of the inner layer are many prisms wide. Korvenkontio found that band widths range from 12 to 30 microns for multiserial enamels. Prisms are directed obliquely with respect to the direction of the bands; the obliquity differs in adjoining bands but corresponds in alternate ones. Prisms of the outer layer are parallel and more steeply inclined toward the tip of the tooth, as in uniserial enamels. The three-dimensional structure is more complicated than in uniserial enamels, and for my own work I have relied on Tomes' description (1850: 552-53), which I paraphrase closely here: In an oblique transverse section parallel with the course of the enamel lamellae, the inner enamel layer looks as though the prisms were thrown into waves, the furrows of which commence at the surface of the dentine and, proceeding obliquely outwards, crop out where the prisms become parallel in the external layer. The prisms pursue a serpentine course in the inner, lamelliform portion, where they describe tolerably uniform curves. By altering the focus of the microscope it may be seen that the prisms of adjacent layers pursue a similar serpentine course, but are arranged so that the concavities and convexities point in opposite directions, thus producing a sort of figure 8.

Pauciserial enamel, for example that of *Paramys copei* (Fig. 1c), is also divided into two layers. The prisms of the inner layer may or may not be organized into lamellae. In a sagittal section the bands of lamellar enamel are seen to be of somewhat variable width, depending on the number of prisms included. Korvenkontio found that band widths of pauciserial enamels fall between 5 and 16 microns, between the ranges for uniserial and multiserial enamels, with slight overlap. The structure appears similar to multiserial enamel but lacks the uniformity of organization. Bands are usually not inclined. Prisms in the external portion are slightly inclined toward the tip of the tooth, though this is not visible in the figure. Some pauciserial enamels have fewer prisms per band, and thus the bands are narrower, suggesting uniserial enamel in appearance.

These descriptions of the kinds of enamel seen in sections of rodent incisors refer only to the vicinity of the midline of the tooth, where the structure is clearly seen. The terms uniserial, multiserial, and pauciserial apply, of course, to the inner layer of the enamel only.

MEASUREMENTS AND INDICES

Sagittal sections are the best for determining what kind of enamel is present in a given rodent incisor, and they are the easiest to make; therefore, I have considered only measurements made from them.

Total enamel thickness and thicknesses of the two enamel layers can be measured. Korvenkontio's external index, which is the percentage of total enamel thickness occupied by the outer layer, compares these dimensions. Total enamel thickness is defined as the length of a line segment normal to the enamel surface at a point, in the vicinity of the midline of the tooth, at which the enamel is thinnest. If a sagittal section contains this segment, it occurs where the enamel is unworn and thinnest. The geometry of rodent incisor enamel distribution, as seen in transverse section (Fig. 2a and b), makes underestimation of the total enamel thickness impossible in a reasonably good section.

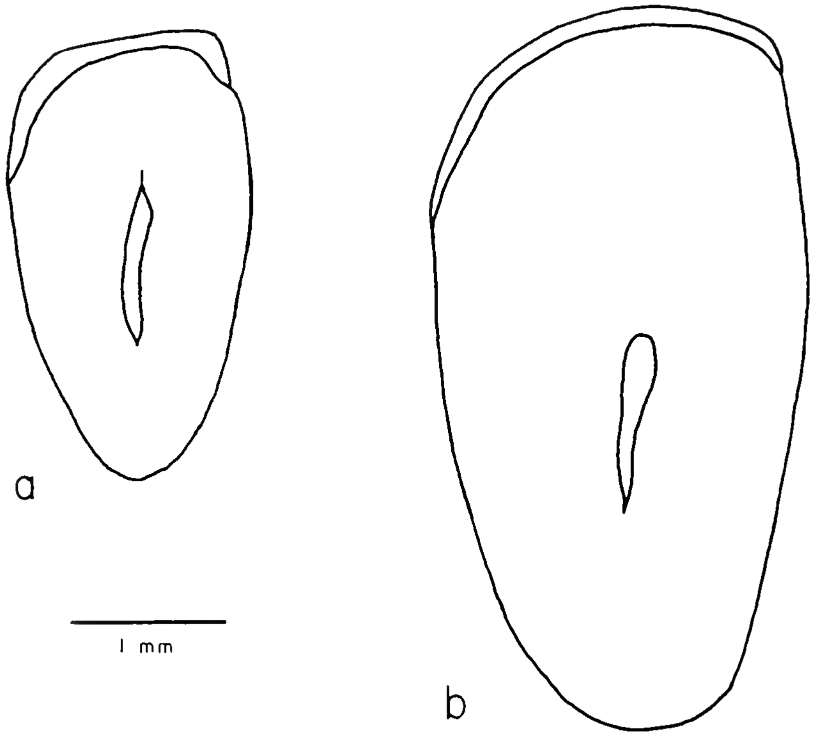

Figure 2. Transverse sections of upper incisors: a. *Rattus norvegicus;* b. *Paramys copei.* Mesial side is to the right.

Band width and inclination of bands are also measured best in sagittal section. Korvenkontio defined inclination as the angle at which bands intersect a perpendicular to the dentine in the sagittal plane.[1] When bands appear curved, a tangent to the midpoint of a band is used to determine inclination. Prisms in the external layer also have an inclination that can be measured; this is not visible in most sections, however, and I have not considered it. In this paper I use enamel thickness, external index, band width, and inclination in the internal enamel layer according to Korvenkontio's definitions for sagittal sections.

MATERIALS

Incisors of 48 individuals from a highly inbred strain of albino *Rattus norvegicus* were available to me at the beginning of this project. This is a large sample for statistical analysis by paleontological standards. The heads had been preserved in formaldehyde, and sexes were not recorded. Incisors of *Paramys copei* and *Knightomys depressus* were also available in fair quantity. These had been collected by Amherst College parties from the early Eocene Lysite member of the Wind River Formation in the Wind River Basin, Wyoming. Individual incisors from a variety of rodents were also sectioned; specimens were obtained from the collections of Amherst College, Albert E. Wood, the Museum of Comparative Zoology, the University of Texas, and the Yale Peabody Museum.

PROCEDURE

Standard sectioning techniques were used. All four incisors from each rat were sectioned on one petrographic slide. Fossil incisors and individual modern incisors were sectioned singly. Preliminary grinding was done on a water-bathed 600 grain diamond wheel that turned at approximately 100 rpm. Sections were hand held. Final polishing was done with wet 900 grain alundum on wood, and then sections were etched briefly with dilute hydrochloric acid; this step makes the enamel structure visible. When sections of modern teeth become thin, water absorption causes them to buckle. This difficulty was solved by drying the section before it became thin and then impregnating it with mineral oil which acts as a waterproofing agent.

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[1] Tomes (1850) measured inclination as the angle made by bands and the dentine surface.

Thickness measurements were made by comparing the projection of a thin section with a micrometer slide. The number of bands within a standard unit of a micrometer eyepiece divided by the length of the unit in millimeters yields the average band width. Inclination was measured on the rotating stage of a petrographic microscope. In each case 430 diameters magnification was used.

Tabulation and statistical analyses of the measurements are given in Tables 1-4. The formulae used in computation are those given by Simpson, Roe, and Lewontin (1960: 84, 90, 166). Abbreviations are as follows: N, sample size; OR, observed range;

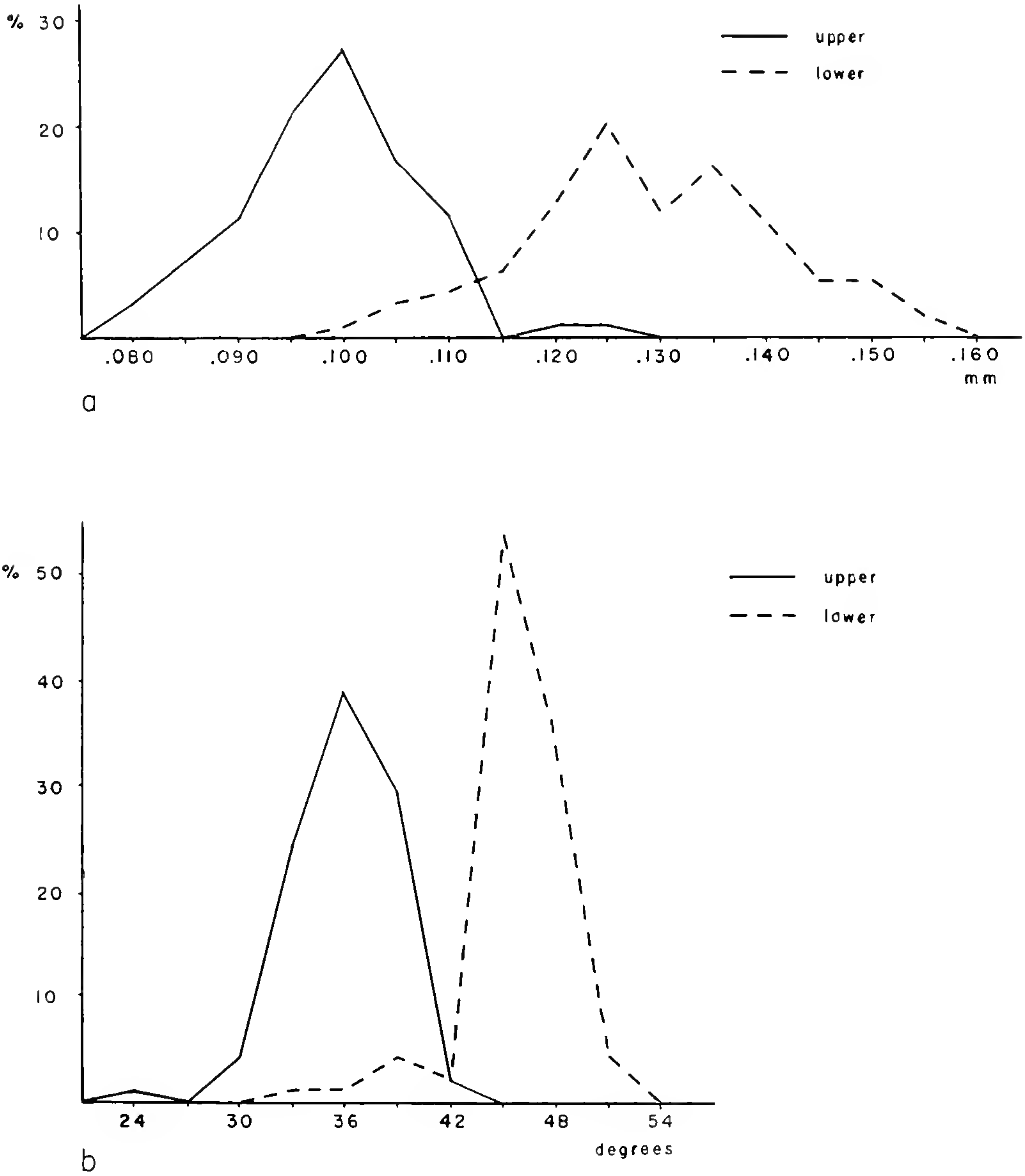

Figure 3. Frequency distributions for incisors of *Rattus norvegicus*: a. total enamel thickness; b. enamel prism inclination.

$\overline{X}$, arithmetic mean; Conf. Int., confidence interval of the mean; SD, one standard deviation unit; V, coefficient of variation. In all thickness measurements there is an error in estimation of ±.001 mm; this error is inherent in the mean. Frequency distributions for enamel thickness and inclination of bands in the large sample of albino laboratory rats appear in Figure 3a and b.

Although all four incisors of forty-eight rats were sectioned, not all individual sections were usable, and thus the sample size varies slightly. Inclination was not measured in *Paramys copei* and *Knightomys depressus* because prism bands are not well defined and are nearly perpendicular to the dentine surface. The sample size in both cases was too small for frequency diagrams to be constructed. Measurements of band widths were, at best, crude, because boundaries are not well defined and magnification was low for such small objects. Consequently, I present only average width and range under the appropriate headings.

TABLE 1

Data for albino laboratory rat incisors.

Total enamel thickness (in mm)						
				95%		
Incisor	N	OR	$\overline{X}$	Conf. Int.	SD	V
Upper	96	.080-.126	.099	±.002	.009	8.7
Lower	93	.100-.155	.129	±.003	.012	9.1
Inclination of enamel prisms (in degrees)						
Upper	95	23-42	36	±.6	3	8.3
Lower	93	32-51	46	±.6	3	6.1

DESCRIPTION OF SAMPLES

Rattus norvegicus (laboratory strain). The incisor enamel is uniserial (Fig. 1a), and the enamel thickness is greater in the lower than in the upper incisors of each individual rat, although the ranges of total enamel thickness for upper and lower incisors overlap appreciably (Table 1). In only one specimen were the measurements within the error of estimation of each other, the enamel thickness of the upper right incisor being .126 mm and of the lower left, .127 mm. The overlap of ranges shows that it is unsafe to decide whether upper or lower incisors have the thicker enamel on the basis of only one or two specimens. The frequency distribution is graphed in Figure 3a.

The 95 per cent confidence interval for the mean is quite small in relation to the total thickness. The standard deviations are greater for lower incisors than for uppers. The coefficients of variation are high for a Recent species (Simpson, Roe, and Lewontin, 1960: 92). This may be accounted for by deviation of the section from the sagittal plane and also by natural variation, such as effects of age, sex differences, and inbreeding, none of which can be excluded as a factor contributing to a high V. The distribution of enamel on the front of an upper incisor as seen in transverse section (Fig. 2a) is uneven; thus, deviation of sections from the sagittal plane could be the cause of considerable variation in thickness measurements. The enamel distribution is more uniform in lowers. Separate analysis of left and right incisors yielded the same mean in lowers and a difference of means in uppers that is within the estimated range of observational error.

The number of incisors of a single extinct species collected from one locality is usually small, on the order of ten or so. To test the reliability of enamel thickness measurements for small samples, I considered the data for forty-eight rats as representing an entire population with a known mean and took from it ten random samples of ten upper and of ten lower incisors. The results of the analyses are presented in Table 2. Although the means of these samples may be as much as five thousandths of a millimeter from the mean of the population, the ninety-five per cent confidence intervals of the means for all but one sample (upper incisors, sample 8) include it. This same sample has both the highest mean thickness and the least variability. With any two samples representing upper and lower incisors, the relative difference in enamel thickness is apparent; the smallest difference in mean enamel thickness obtainable from these results amounts to .020 mm and the largest is .039 mm.

Attempts to measure the thickness of either layer of the enamel separately were unsatisfactory, because there is no clear line of demarcation between the two. Figure 1 shows how bands of the inner layer project into the outer; it is impossible to establish a definite line that is consistently placed in each thin section. In the sample the outer enamel layer occupies *approximately* 30 per cent of the mean total thickness in uppers and 19 per cent in lowers. The observed ranges are 20 to 39 per cent for uppers and 14 to 27 per cent for lowers. In two individuals the external index of an upper and a lower incisor is the same, but in no instance in an individual is that of the lower greater. A regression analysis of these measurements of outer layer thickness versus total enamel

TABLE 2

Variability of total enamel thickness (in mm) in ten samplings, each of ten incisors selected at random from data for albino laboratory rats.

Upper incisors

Samp.	OR	x	95% Conf. Int.	SD	V
1	.085-.120	.101	±.007	.010	9.9
2	.080-.126	.099	±.009	.013	13.1
3	.085-.110	.097	±.006	.008	8.2
4	.085-.110	.099	±.005	.007	7.1
5	.092-.109	.099	±.004	.006	6.1
6	.094-.106	.100	±.003	.004	4.0
7	.080-.112	.095	±.006	.009	9.5
8	.100-.107	.104	±.001	.002	1.9
9	.085-.126	.102	±.009	.013	12.7
10	.092-.110	.101	±.004	.006	5.9

Lower incisors

Samp.	OR	x	95% Conf. Int.	SD	V
1	.110-.155	.129	±.011	.015	11.6
2	.119-.153	.134	±.008	.011	8.2
3	.110-.143	.127	±.007	.010	7.9
4	.107-.143	.128	±.007	.010	7.8
5	.111-.138	.127	±.007	.010	7.9
6	.114-.153	.129	±.008	.011	8.5
7	.111-.145	.124	±.007	.010	8.1
8	.107-.150	.131	±.011	.015	11.4
9	.107-.138	.126	±.008	.011	8.7
10	.110-.145	.129	±.008	.012	9.3

thickness was carried out within upper and lower incisors of the entire sample. The correlation coefficient for upper incisors is .27; for lowers, .18. This is extremely poor, but the gross difference between uppers and lowers remains.

Band width in sagittal section appeared nearly invariable at 450 diameters magnification. It is .0033 for both upper and lower incisors. The mean inclination of enamel prisms in the inner layer is distinctly greater in nearly all lower incisors (Table 1, Figure 3b). However, in one specimen the inclination of bands in one lower incisor was less than that of the uppers; in another, an upper and a lower incisor yielded the same angle. Thus, two teeth, even from the same individual, may not indicate the usual relationship. The standard deviation of inclination is the same for both upper and lower incisors.

TABLE 3

Data for *Paramys copei* incisors.

Total enamel thickness (in mm)				95%		
Incisor	N	OR	$\bar{x}$	Conf. Int.	SD	V
Upper	16	.088-.115	.104	±.004	.008	7.7
Lower	24	.065-.105	.088	±.004	.009	10.2

Paramys copei. The sample of incisors of *Paramys copei* from the Lysite represents a minimum of twelve individuals, all but two of the teeth being from the same locality. Enamel is pauciserial. In this species the distribution of enamel across the face of the tooth as seen in transverse section is fairly even (Fig. 2b). The error caused by the deviation of a section from the mid-plane is therefore not large when compared to the same situation in rat incisors.

The data presented in Table 3 indicate that the mean enamel thickness in upper incisors is .016 greater than in lowers, the reverse of the situation in rats. There is overlap in ranges, and examination of only a few teeth could show the opposite relationship. The standard deviations for upper and lower incisors are similar to the figure for upper incisors of rats. The sample is too small to construct a meaningful frequency distribution curve.

The mean band width and observed range are .017 mm and .013-.021 mm in upper incisors and .016 mm and .014-.023 mm in lowers. Inclination of bands is approximately zero. In any individual tooth, bands may be slightly inclined toward or away from the tip.

TABLE 4

Data for *Knightomys depressus* incisors.

Total enamel thickness (in mm)				95%		
Incisor	N	OR	$\bar{x}$	Conf. Int.	SD	V
Upper	13	.103-.150	.120	±.009	.016	13.3
Lower	6	.053-.095	.068	±.005	.005	7.35

Knightomys depressus. The sample of *Knightomys depressus* from the Lysite represents a minimum of seven individuals. Enamel is pauciserial. The data presented in Table 4 show that the mean enamel thickness is much greater in upper incisors and that the ranges for upper and lower incisors do not overlap. The lack of overlap may simply mean that the sample size is too small. The confidence interval, standard deviation, and coefficient of variation for the lower incisors seem low with regard to these figures for the other samples. They are in best agreement with those for small samples of rat upper incisors.

The distribution of enamel is similar to that in *Paramys copei*. The mean band width and observed range are .014 mm and .012-.017 mm in upper incisors and .012 mm and .009-.016 mm in lowers. Inclination of bands is approximately zero, and the boundary between inner and outer layers of enamel is again not a distinct line.

SAMPLE SIZE AND THE UTILITY OF MEASUREMENTS AND INDICES AS CRITERIA FOR IDENTIFICATION OF ISOLATED INCISORS

A sagittal thin section of a rodent incisor is sufficient to show whether the enamel is pauciserial, uniserial, or multiserial. A few sections provide a rough measure of enamel thickness. A sample of ten or more upper and ten or more lower incisors yields a mean enamel thickness with a fairly small confidence interval and shows the relationship of thicknesses. A sample of about a hundred individual upper and lower incisors is needed for graphing a frequency distribution of thickness. The inclination of bands in the inner enamel layer also yields a continuous curve when plotted for a sample of this size. The inclination of prisms in the external layer is usually not visible. A rough measure of band width may be made at a magnification of 430 diameters, but variation is not apparent.

The boundary between internal and external enamel layers is not a line, and thus the thickness of either part cannot be measured precisely. This variability and the lack of correlation between thickness of the outer layer and total enamel thickness within a sample suggests that a ratio of the two, Korvenkontio's external index, cannot be used.

At present there are few numerical data available concerning the microstructure of rodent incisor enamel. Identification of isolated incisors cannot be made on the basis of measurements alone.

DISCUSSION OF INCISOR ENAMELS

Pauciserial enamel was found by Korvenkontio to be present in ischyromyid, sciuravid, pseudosciurid, and some theridomyid rodents. I have sectioned incisors of some of the same Eocene species; these and thin sections of different ischyromyid and sciuravid species reveal pauciserial enamel. *Prosciurus relictus*, a mid-Oligocene ischyromyid has uniserial enamel. Korvenkontio found a condition transitional between pauciserial and uniserial in the Oligocene theridomyid, *Nesokerodon minor*.

Completely uniserial and multiserial enamels are first met with in incisors of early Oligocene rodents. Korvenkontio found uniserial enamel in species of this age in the Theridomyidae and Ischyromyidae, and I have observed it in *Cylindrodon fontis* of the Cylindrodontidae. Other species having uniserial enamel are listed in Table 5.

Multiserial enamel is characteristic of all caviomorph rodents so far examined. Wood and Patterson (1959: 292)[2] found it in a Deseadan (early Oligocene) incisor, very probably of *Scotamys antiquus*, and I have found it in *Cephalomys arcidens* from deposits of the same age. The early Oligocene African phiomyid rodents sectioned by me had acquired multiserial enamel; thin sections of incisors of *Phiomys andrewsi, Metaphiomys schaubi,* and a new species (Wood, in press) demonstrate this. The Recent *Thryonomys* and *Petromus,* which Lavocat (1962) and Wood (in press) associate closely with the phiomyids, also prove to have multiserial enamel. Other species possessing multiserial enamel are listed in Table 5.

Pauciserial enamel is a good structural predecessor for uniserial and multiserial enamels. It would appear to be the ancestral condition. As far as present evidence goes, it had probably been achieved by the time rodents made their first appearance in the record. It is known thus far in only a few post-Eocene rodents, and uniserial and multiserial enamels have not yet been recorded prior to the Oligocene. Presumably acquisition of two layers in which the organization of prisms is different served in some way to strengthen the enamel. The pauciserial structure, judging from the record, would appear to have been less efficient than the other two. There is no available evidence to suggest that one of the two surviving kinds is superior to the other or that one of them has ever evolved from the other. Seemingly, selection has favored increase in strengthening rather than any one method of accomplishing it.

To the possible question: could the pauciserial condition be an artifact caused by diagenetic changes in materials of greater age?

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[2] A lapsus in this paper may be corrected. The authors state (p. 292 n.): ". . . the Theridomyidae are in the process of passing from a pauciserial to a multiserial type." For "multiserial" read "uniserial."

I would reply in the negative. In none of the many slides of enamel of Eocene age that I have examined is there any indication that recrystallization has disrupted the fine structure.

The enamels of all modern rodent incisors fall into one of the two major categories, uniserial and multiserial, but there are minor differences within each of the two as regards dimensions and orientation of lamellae. Study of the internal detail of lamellar structure is needed to understand the differences and to determine how they may have evolved.

ACKNOWLEDGMENTS

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TABLE 5

Enamel structure in rodent incisors.

The initials after each species name are those of the authors who have described its incisor enamel. Species names are mainly as in Ellerman (1941); familial and generic assignments are mainly as in Simpson (1945). Where a name given in the publications of those who have described rodent incisor enamels differs from the current one, I have included it in brackets. A classification of rodents above the familial level is given by Wood (1958)

Abbreviations: B., Bohlin (1946); K., Korvenkontio (1934); T., Tomes (1850); W., Wahlert; W. and P., Wood and Patterson (1959). Eoc., Eocene; Olig., Oligocene; Mioc., Miocene; Pleist., Pleistocene; E., early; M., mid; L., late. Af., Africa; As., Asia; Eu., Europe; N.A., North America; S.A., South America. (Geologic age and location given only for fossils.)

PAUCISERIAL ENAMELS

Ischyromyidae: *Ischyrotomus petersoni* W., L.Eoc. N.A. *Knightomys depressus* W., E.Eoc. N.A. *Manitsha* sp. W., E.Olig. N.A. *Microparamys tysitensis* W., E.Eoc. N.A. *Paramys c. copei* K., W., E.Eoc. N.A. *Paramys* *c. major* K., W., E.Eoc. N.A. *Paramys delicatior* K., M.Eoc. N.A. *Paramys excavatus* K., W., E.Eoc. N.A. *Thisbemys perditus* W., E.Eoc. N.A.

Sciuravidae: *Mysops parvus* W., M.Eoc. N.A. *Sciuravus nitidus* K., M.Eoc. N.A.

Theridomyidae: *Archaeomys gracilis* K., L.Eoc.-M.Olig. Eu. *Archaeomys major* K., L.Eoc.-M.Olig. Eu. *Theridomys gregarius* K., L.Eoc.-M.Olig. Eu. *Theridomys vaillanti* K., Eoc. Eu.

Pseudosciuridae: *Pseudosciurus suevicus* K., E.Olig. Eu. *Sciuroides quercyi* K., L.Eoc.-M.Olig. Eu. *Sciuroides* sp. K., L.Eoc.-M.Olig. Eu.

UNISERIAL ENAMELS

Ischyromyidae: *Ischyromys typus* K., M.Olig. N.A. *Prosciurus relictus* W., M.Olig. N.A. *Titanotheriomys veterior* K., E.Olig. N.A.

Cylindrodontidae: *Cylindrodon fontis* W., E.Olig. N.A.

Aplodontidae: *Allomys nitens* K., L.Olig. N.A. *Aplodontia rufa* K.

Mylagaulidae: *Mesogaulus novellus* W., M.Mioc. N.A. *Mylagaulus* sp. W., L.Mioc. N.A.

Muridae: *Acomys* sp. K. *Arvicanthis* sp. K. *Conilurus [Hapalotis] albipes* T. *Hydromys chrysogaster* T. *Mus. musculus* K. *Notomys [Hapalotis] longicaudatus* T. *Otomys* sp. K. *Rattus norvegicus [Mus decumanus* T., K.*]* T., K., W. *Rattus [Mus] rattus* K.

Cricetidae: *Cricetodon minor* K., L.Mioc. Eu. *Eumys elegans* K., W., M.-L.Olig. N.A. *Eumys gracilis* K., Olig. N.A. *Sigmodon* sp. W., L.Pleist. N.A. *Akodon arenicola* K. *Arvicola amphibius* T. *Arvicola [Microtus] terrestris* K. *Clethrionomys [Arvicola* T., *Evotomys* K.*] glareolus* T., K. *Cricetulus migratorius [phaeus]* K. *Cricetus cricetus [fumentarius* T.*]* T., K. *Ellobius talpinus* K. *Gerbillus* sp. K. *Lemmus lemmus [norvegicus]* T., K. *Meriones [Gerbillus] shawi* T. *Microtus [Arvicola] nivalis* T. *Myopus schisticolor* K. *Ondatra [Fiber] zibethica* T., K. *Oryzomys flavescens [longicaudatus]* K. *Oxymycterus rufus* K. *Phyllotis [Hesperomys] darwinii* T. *Tatera* sp. K.

Spalacidae: *Spalax microphthalmus [typhlus]* T., K. *Tachyoryctes splendens* K.

Geomyidae: *Entoptychus cavifrons* K., E.Mioc. N.A. *Entoptychus* sp. K., L.Olig. N.A. Entoptychine geomyid W. M.Mioc. N.A. *Heterogeomys hispidus* K. *Thomomys [Geomys] umbrinus* T.

Heteromyidae: Heteromyid W., M.Mioc. N.A. *Dipodomys* sp. K. *Perognathus fasciatus* K. *Perognathus* sp. K. *Perognathus [Cricetodipus]* sp. K.

Eomyidae: *Adjidaumo* sp. W., M.Olig. N.A. *Paradjidaumo trilophus* W., M.Olig. N.A.

Dipodidae: *Alactaga sibirica [saliens]* K. *Jaculus jaculus [Dipus hirtipes]* K. *Jaculus [Jerboa* T., *Dipus* K.*] orientalis [aegyptius]* T. K.

Zapodidae: *Napaeozapus insignis* K. *Sicista [Sminthus] subtilis* K. *Zapus hudsonius* K.

Gliridae: *Glis [Myoxus] wetzleri* K., L.Olig. Eu. *Dryomys nitedula* K. *Eliomys quercinus* K. *Glis [Myoxus* K.*] glis* K., W. *Graphiurus ocularis [capensis]* K. *Muscardinus [Myoxus* T.*] avellanarius* T., K.

Sciuridae: *Sciurus feignouxi* K., E.Mioc. Eu. *Callosciurus [Sciurus] prevosti* K. *Citellus [Spermophilus] eversmanni* K. *Citellus parryii [Spermophilus empetra]* K. *Citellus [Spermophilus]* sp. T. *Cynomys ludovicianus* K. *Marmota caligata [Arctomys pruinosus]* T. *Marmota [Arctomys] monax [empetra* T.*]* T., K. *Marmota [Arctomys* K.*]* sp. K., W. *Petaurista volans [Pteromys russicus]* K. *Ratufa [Sciurus] macroura* K. *Sciurus niger* T. *Sciurus vulgaris* K. *Tamias sibiricus [Eutamias asiaticus]* K. *Tamias striatus [lysteri* T.*]* T., K.

Castoridae: *Steneofiber eseri* K., E.Mioc. Eu. *Steneofiber peninsulatus* K., L.Olig. N.A. *Castor fiber* T., K.

Eutypomyidae: *Eutypomys thomsoni* W., M.Olig. N.A.

Theridomyidae: *Archaeomys laurillardi* K., Olig. Eu. *Nesokerodon minor* K., L.Eoc.-M.Olig. Eu. *Sciuromys typicus* K., L.Eoc.-M.Olig. Eu.

Anomaluridae: *Anomalurus fraseri* K. *Idiurus macrotis* K.

MULTISERIAL ENAMELS

Octodontidae: *Sciamys principalis* K., E.Mioc. S.A. *Aconaemys [Schizodon] fuscus* T. *Octodon degus* T. *Spalacopus cyanus [poeppigii]* T.

Echimyidae: *Adelphomys candidus* K., E.Mioc. S.A. *Myocastor [Myopotamus* T.*] coypus* T. K.

Ctenomyidae: *Ctenomys magellanicus* K.

Abrocomidae: *Abrocoma [Habrocoma] bennettii* T.

Capromyidae: *Capromys pilorides [fournieri]* T.

Chinchillidae: *Scotamys antiquus* W. and P., E.Olig. S.A. *Perimys procerus* K., E.Mioc. S.A. *Chinchilla laniger* T. *Lagostomus maximus [trichodactylus]* K.

Dasyproctidae: *Cephalomys arcidens* W., E.Olig. S.A. *Neoreomys australis* K., E.Mioc. S.A. *Cuniculus [Coelogenys] paca* T., K. *Dasyprocta aguti* T., K. *Myoprocta [Dasyprocta] acouchy* T.

Caviidae: *Cavia aperea* T. *Cavia porcellus [cutleri]* K. *Dolichotis patagona* K. *Galea [Kerodon] flavidens* K. *Galea [Kerodon] spixii* K. *Microcavia australis [Cavia kingii]* T.

Hydrochoeridae: *Hydrochoeris hydrochaeris [capybara]* T.

Erethizontidae: *Coendou [Hystrix* T.*] prehensilis* T., K. *Erethizon dorsatum* K. *Erethizon epixanthum* K.

Ctenodactylidae: *Sayimys obliquidens* B., ?Mioc. As. *Tataromys* cf. *plicidens* B., ?Mioc. As. *Ctenodactylus gundi* K., B.

Pedetidae: *Pedetes cafer* T., K.

Hystricidae: *Atherurus africanus* K. *Hystrix cristata* T.

Phiomyidae: *Metaphiomys schaubi* W., E.Olig. Af. *Phiomys andrewsi* W., E.Olig. Af. Phiomyid W., E.Olig. Af.

Thryonomyidae: *Thryonomys* sp. W.

Petromuridae: *Petromus typicus* W.

Bathyergidae: *Bathyergus suillus [maritimus]* T. *Cryptomys mellandi* K. *Georychus capensis* K.

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A SHOVEL-TUSKED GOMPHOTHERE FROM THE MIOCENE OF KENYA

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ABSTRACT. A tusk fragment of the first recorded occurrence in Africa of *Platybelodon*, a shovel-tusked gomphothere, is described, and its relationships to the Asiatic and North American representatives of the Amebelodontinae are discussed. It is suggested that the African form represents a very early member of the group, and that Africa may have been the place of origin of the subfamily.

INTRODUCTION

In 1927, E. H. Barbour described as *Amebelodon fricki* the first specimen of a rather bizarrely specialized group of proboscideans, the shovel-tusked gomphotheres — Amebelodontinae. The geological and geographical range of this subfamily has hitherto been believed to extend from the late middle Miocene (Tortonian)[1] of Asia to the late Pliocene of North America. Osborn (1936) proposed a subfamilial separation of the North American *Amebelodon* from *Platybelodon*, which occurs in both North America and Asia, suggesting an independent origin of the two genera — *Amebelodon* in North America from a stock of the "Bunomastodontidae" and *Platybelodon* from the "Serridentidae" in Asia. Gregory (1945) considered the two genera to represent a more closely related group than did Osborn and placed them both in a single subfamily, the Amebelodontinae. This is the view subscribed to here. Until now, it has seemed likely that the shovel-tusked gomphotheres originated in Asia from a stock of the Gomphotheriidae sometime during the early to middle Miocene,

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[1] *Platybelodon danovi* Borissiak, the earliest known species, occurs in the Chokrak beds of the Kuban region in the North Caucasus, considered to be of late middle Miocene age (Tortonian of western Europe) by Nalivkin (1960).

migrating to North America during the early Pliocene. The specimen described in the present note, however, demonstrates the presence in east Africa during middle Miocene time of shovel-tusked gomphotheres very similar to the Asiatic amebelodontines.

The fragment (MCZ field number 38-64K) was collected by Mr. James G. Mead during the 1964 field season of the Museum of Comparative Zoology expeditions to east Africa[2] directed by Professor Bryan Patterson. The locality is 35° 50′ E, 02° 20′ N, approximately 4 mi. NNE of the site of the abandoned town of Loperot and 50 mi. SSE of Lodwar, in the Loperot area of southern Turkana District, northwestern Kenya (map in Joubert, 1966). Although none of the associated fauna has yet been studied in detail, the following elements have been identified: *Deinotherium hobleyi*, *Dorcatherium* sp. cf. *D. pigotti*, *Chilotherium* sp., ?*Brachyodus* sp., and hyracoid aff. *Prohyrax*.

The specimen, weathered from the Turkana Grit, was found on the surface near the top of the formation, about 20 feet below a fine-grained olivine basalt sequence. Joubert recognized three successive basaltic flows overlying the Turkana Grit in this region and on geological evidence placed the onset of the basal flow in the Lower Miocene (1966: 35). The associated fauna collected from the Turkana Grit is not wholly incompatible with this view, in that it appears to be close to those in the Rusinga series and, although less so, to that of Lothidok,[3] both usually considered to be of early Miocene age.

Although detailed faunal comparison is not possible at present, the Loperot fauna probably correlates with part of the Rusinga complex[4]; it does not appear to be equivalent to that of Lothidok. *Dorcatherium pigotti* and *Chilotherium sp.* occur on Rusinga Island.

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[2] The field work was supported by National Science Foundation Grant GP-1188.

[3] The name Losodok as used by Arambourg (1933), Whitworth (1954), and Hooijer (1966), is replaced by the name Lothidok on most current geologic maps of the area, as, for example, SK. 57 Kenya, 1:1M (Special), Survey of Kenya, 1965.

[4] As Simpson has recently emphasized (1967: 43), the stratigraphic and faunal successions at Rusinga are at present inadequately known, as are the facies and age relationships of the several other earlier Miocene faunas known from the Kavirondo Gulf region. Evidence in support of the often quoted "early Miocene" age, or indeed of any other age, for these deposits is inconclusive, although they are almost certainly older than those at Fort Ternan, for which an acceptable age (12-14 million years) is available. The

The hyracoid is close to, but lower crowned than, *Prohyrax* from Langental, South Africa (Stromer, 1926), and may be the same as *Meroëhyrax* from Rusinga (Whitworth, 1954). The Lothidok fauna includes *Dorcatherium chappuisi, Megalohyrax championi* (see Whitworth, 1954), and *Aceratherium acutirostratum.*

The lowest basalt in the Loperot sequence has been dated at 17.5 ± 0.9 million years by Geochron Laboratories, Inc., using the Potassium/Argon method (Patterson, personal communication). This date indicates a Vindobonian age for the basalt immediately overlying the fossil-bearing sediments. There does not appear to be any significant time interval between deposition of the upper part of the Turkana Grit and the basalt flow, and this age is here considered approximately correct.

The specimen under discussion is too fragmentary for positive identification, but, as far as can be determined from what remains, the form it represents was closely related to *Platybelodon.* It is therefore tentatively placed in that genus, pending further knowledge.

PLATYBELODON SP.

The specimen (Fig. 1) is a fragment from the middle of a left lower incisor, and measures 56.8 mm in maximum length. The upper surface is broadly concave and the lower convex. The two surfaces are not parallel but diverge somewhat towards the sides, so that the tooth is thicker along the medial and lateral edges than at the center. The medial edge is flattened, with a broad, shallow, concave groove along the entire length of the fragment; the two lower incisors may have been closely appressed during life, at least in this region of the tusk. The specimen tapers in all dimensions toward one end, which is probably anterior. A similar tapering toward the tip of the tusk is seen in more complete specimens of other amebelodontines, e.g., the specimen of *Amebelodon fricki*

age of 15.3 million years suggested by Evernden *et al.* (1964) as the maximum for the Rusinga series seems unlikely. The sample used for this determination was taken from a locality at the base of Kiahera Hill and, as suggested by Savage (1965) and Leakey (1967), these deposits may not be part of the Kiahera Series, supposedly the oldest formation on Rusinga Island. Until the deposits of Rusinga are better understood, correlation within the east African Miocene will remain uncertain.

The relative position of the various deposits within the Miocene depends in part on the inclusion in or exclusion from this epoch of the Aquitanian and Pontian stages.

described by Gregory (1945). The medial thickness tapers from 14.6 mm to 11.6 mm anteriorly. The lateral edge is thinner than the medial and measures 8.5 mm to 7.0 mm. In overall width, the fragment decreases from 78.5 mm to 74.5 mm.

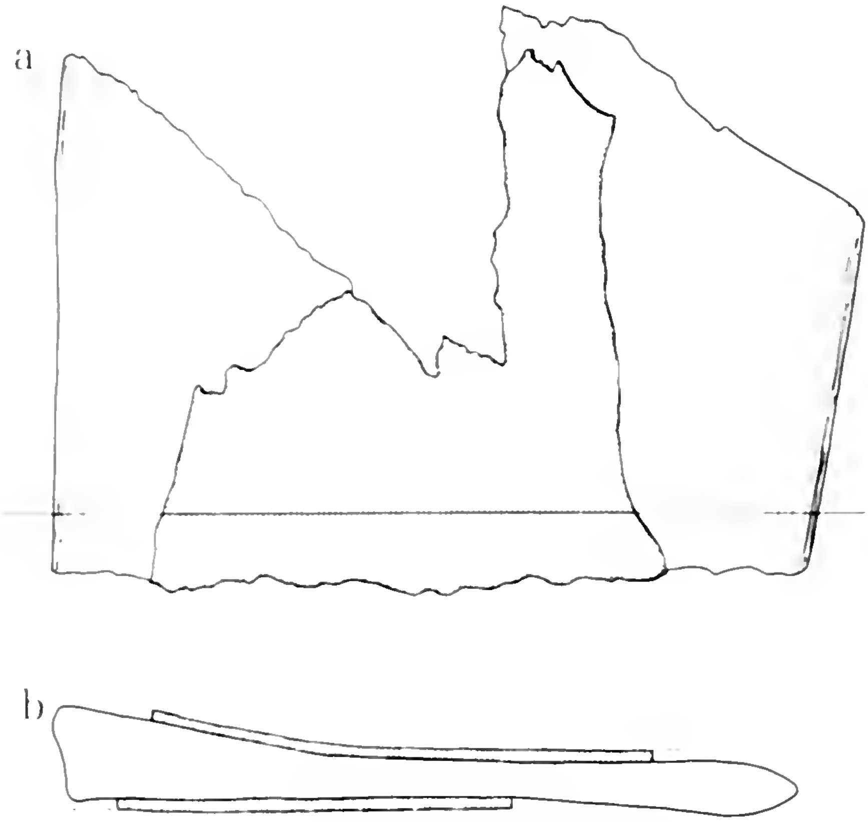

Figure 1. *Platybelodon* sp. Tusk fragment. MCZ field number 38-64K, from the Loperot area, Kenya. *a*, Dorsal view; horizontal line indicates plane of section. *b*, Anterior view of cut surface. Shaded area, investment of laminated dentine. × 1.

The broken ends reveal a complex internal structure of dentine organized into *dentinal systems*[5] or rodlike masses as in most other amebelodonts, although they have not weathered out as discrete and isolated rods, such as those described in *Platybelodon grangeri* (Osborn and Granger, 1931) and *Amebelodon fricki* (Barbour, 1941). In thin section (Fig. 2), the dentine has a fibrous texture, consisting of numerous microscopic dentinal tubules. These tubules

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[5] The term *dentinal system* was restricted by Tomes (1850) to that portion of a tooth consisting of a canal from which dentinal tubules radiate and around which there is no investment of enamel.

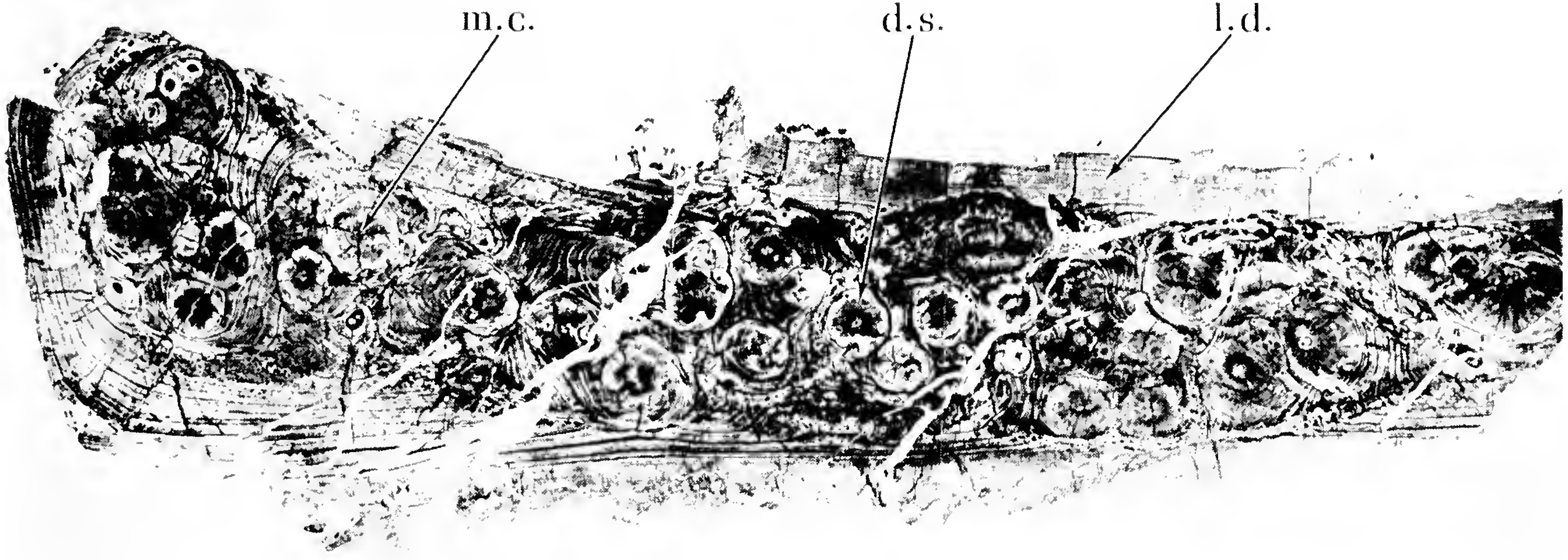

Figure 2. *Platybelodon* sp. Thin section of tusk fragment showing medial half of cross-section; composite photograph using transmitted light. *d.s.*, Dentinal systems. *l.d.*, Laminated dentine. *m.c.*, Medullary canal. ×4.

appear to radiate from the center of each dentinal system and may curve partially around its outer edge. Near the center of each dentinal system is a round to irregularly shaped canal, secondarily filled with calcite, as are the numerous small cracks which cut across the tubule boundaries. The canals probably correspond to the "small lumen" noted in the dentinal systems ("rod-cones") of *Platybelodon* by Osborn (1936: 465). The tooth is thus composed of a series of dentinal systems, each with a medullary canal as in *Orycteropus* (Tomes, 1850).

Some of the dentinal systems are closely aggregated into bundles of two or three. A laminar substance is seen to swirl around and between the systems and bundles, completely filling the spaces between them. Optically, this material resembles dentine; its structure is that of dentine and in no way resembles that of cement. Such a condition has been described by Tomes (1850) as *confluent dentinal systems*, in which "parallel dentinal systems are united to each other, throughout their length, by a thin longitudinal lamina of dentine."

The individual dentinal systems are large, about one and one-half mm in diameter, and loosely packed; there are approximately 70 visible on the complete cross-section of the tusk in the region represented by the fragment. This is in strong contrast to the very small, discrete dentinal systems found in *Platybelodon grangeri*, in which there are about 250 in the cross-section (Osborn and Granger, 1931). In a tusk referred to *Amebelodon fricki* (Colorado Museum no. 1319), Osborn and Granger noted the presence of dentinal systems ("rod-cones") "larger and much less numerous" than in *P. grangeri*, the total number being estimated at 100 to 150. Dentinal systems have not been definitely recognized in *Platybelodon danovi*, although Osborn (1936: 462) interpreted the "irregular longitudinal grooves," described by Borissiak (1928) on the upper surface of the tusk, as indicating their presence. If, however, *P. danovi* was ancestral to *P. grangeri*, or at least represented a more primitive type, we might expect the internal structure of the tusk to be less advanced and closer to that of the African form.

The outer surface of the tooth was sheathed in life by a thick (1.5 mm) layer of what appears to be strongly laminated dentine with dentinal tubules oriented perpendicular to the surface. This superficially resembles enamel, but its internal edge is seen to merge into the underlying dentine, with which the tubules are continuous, without the sharp contact and contrasting structure characteristic of dentine-enamel junctions. Its microscopic structure is also not at all like that of cement. This sheath has been broken away from much of the tooth surface, but enough remains to indicate its former presence over the entire fragment; there is no indication of enamel or cement.

In the degree of flattening, the present specimen exceeds *Platybelodon danovi* and approaches *P. grangeri,* which shows the most extreme flattening of any species of the subfamily yet described. In size, the African form, as determined from available measurements, is the smallest amebelodont, with a tusk width about 28 per cent smaller than in *P. danovi.*

DISCUSSION

The present specimen demonstrates that by Vindobonian times a shovel-tusked gomphothere was present in east Africa. The internal modifications of the dentine into discrete dentinal systems, presumably for strengthening the tusk, were in a relatively rudimentary stage as compared with those of *P. grangeri,* being large, loosely compacted, and generally poorly defined. Yet if the degree of flattening can be used to infer the degree of adaptation to a relatively specialized ecological role, we must conclude that the present form had already reached a degree of specialization with respect to tusk shape equal to that of *P. grangeri,* despite the relatively primitive organization of the dentinal systems.

It appears reasonable to suggest that the present form represents (with *P. danovi*) an early specialization toward the adaptations that were to characterize the later amebelodonts. Its exact relationship to the Asiatic representatives of this genus is uncertain, but in view of its similarity to those species, as far as can be determined from this specimen, a close relationship to *P. danovi* may be suggested, both forms being among the earliest members of the subfamily.

The question arises as to the place of origin of the Amebelodontinae. The mere presence of this group in east Africa during the Miocene does not, of course, positively answer this question. However, unless the African form proves, on further evidence, to be an independent adaptation to this particular ecological situation, the existence of this group in Africa and Asia at roughly the same time suggests a possible African origin for the subfamily. This view becomes more probable when one considers the long prior evolutionary history of the Gomphotheriidae in Africa and their relatively late appearance in Eurasia during the early Miocene. It is to be hoped that further specimens will be unearthed and also that among the isolated gomphothere teeth and bones from the African Miocene in museum collections additional remains of this group will be recognized.

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TABLE 1

Comparative measurements of *Platybelodon* species from Asia with *Platybelodon* from Africa, in mm

	P. danovi[1] Type	AMNH 26200 P. grangeri[1] Type	MCZ 38-64K[2]	MCZ 38-64K[3]
width	110	166	79.5	74.5-78.5
medial thickness	30	33	16.1	11.6-14.6
lateral thickness	15	25	10.8	07.0-08.5
$\frac{\text{medial thickness}}{\text{width}}$	0.272	0.199	0.224	—
$\frac{\text{average thickness}}{\text{width}}$	0.201	0.175	0.169	—

[1] Measurements for *P. danovi* and *P. grangeri* taken from Osborn and Granger (1931, p. 2).

[2] Estimated mean measurements corrected for missing outer layer of laminated dentine.

[3] Actual measurements of specimen.

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THE GENERA APENESIA AND DISSOMPHALUS IN ARGENTINA AND CHILE (HYMENOPTERA, BETHYLIDAE)

Howard E. Evans

Abstract. *Apenesia* and *Dissomphalus,* two of the three genera of Pristocerinae occurring in Argentina and Chile, have been known from those countries from only a few specimens representing 5 species. Recent use of Malaise traps has greatly increased the available material and has made a further study of these genera desirable. In *Apenesia,* 12 species are here reported from Argentina, 6 of them new; 2 species are reported from Chile, 1 of them new. In *Dissomphalus,* 9 species are reported from Argentina, 8 of them new; this genus has not been collected in Chile. Keys to species are presented and important taxonomic features are illustrated.

This is a supplement to two papers published in the Bulletin of the Museum of Comparative Zoology.[1] It covers recently collected material of two of the three genera of the subfamily Pristocerinae occurring in southern South America. The remaining genus, *Pseudisobrachium,* has been treated elsewhere.[2]

Most of the material reported on here was taken by Dr. Lionel Stange in Malaise traps in the province of Tucumán, Argentina. The value of these traps as faunal samplers is shown by the fact that *Apenesia* was previously known from Argentina from two species represented by 7 specimens; in the present paper 12 species are reported, 6 of them new, these species known from over 150 specimens. *Dissomphalus* was previously known from Argentina from 3 species; 9 additional species are here reported from that country, 8 of them new. The figures for *Pseudisobrachium* are even more impressive: previously known from Argentina from only 4 species, each represented by only one or a few specimens, this genus is now

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[1] Bull. Mus. Comp. Zool., 130: 249-359 (1963).
Bull. Mus. Comp. Zool., 132: 1-222 (1964).

[2] Acta Zoologica Lilloana (in press).

known from 22 species, represented in all by several hundred specimens. Altogether, the number of known species of Pristocerinae in Argentina has been increased from 9 to 48, the number in Chile from 0 to 3. Material quite recently collected by Dr. Stange near Tucumán and by Charles C. Porter in several localities has consisted wholly of these same species, suggesting that a fairly high percentage of the species occurring in the areas sampled is now known.

A discussion of the terminology employed will be found in the papers cited earlier. The abbreviations used are listed here for the sake of ready reference:

DAO: diameter of anterior ocellus (transversely)
HE: height of eye (maximum, lateral view)
LFW: length of fore wing
LH: length of head (frontal view, including clypeus but not mouthparts)
OOL: ocello-ocular line (minimum distance between lateral ocelli and nearest eye margin)
WF: width of front (at minimum point, between eyes)
WH: width of head (full frontal view, including eyes)
WOT: width of ocellar triangle (including lateral ocelli).

All the material discussed in this paper is in the collections of the Instituto Miguel Lillo, Tucumán, Argentina, and of the Museum of Comparative Zoology, Cambridge, U.S.A. All holotypes have been deposited in the Instituto Miguel Lillo.

GENUS *APENESIA* WESTWOOD

This genus has been known from 35 species in South America, to which 7 more species are added here. All South American species are presently known from only one sex, and this unfortunate situation will prevail until these insects are reared in series from their hosts or taken in copula. No females of the genus *Apenesia* are as yet recorded from Argentina or Chile. In the treatment that follows, arrangement of the species-groups follows my 1963 revision.

KEY TO MALE *Apenesia* KNOWN FROM ARGENTINA AND CHILE

1. Pronotal disc without a transverse carina anteriorly 2
Pronotal disc with a transverse carina anteriorly 10
2. Eyes glabrous; clypeus with a median lobe, not prominent on the sides (Figs. 10-13) 3

Eyes hairy; clypeus large, well developed on sides, and without a distinct median lobe (Figs. 7-9) (*dissomphaloides* group) 8

3. Abdomen with a distinct, moderately long petiole; LFW 2.1-2.4 mm (*laevigata* group) . . . . 9. *crenulata* (Kieffer)

Abdomen sessile; LFW exceeding 3 mm 4

4. Propodeum with no evidence of a transverse carina margining the disc behind; pronotum very short, strongly sloping (*exilis* group) . . . . 8. *chilena* Evans

Propodeum with a transverse carina margining the disc behind; pronotum longer and with a more or less flat dorsal surface 5

5. Antennae with erect setae on the under surface, which stand out strongly above the pubescence (most noticeable on segments 4-7) (*pilicornis* group) 6

Antennae with erect setae sparse and standing out slightly if at all above the prominent, bristling pubescence (*columbana* group) 7

6. Transverse carina of propodeum complete, median carina also complete and reaching transverse carina; LFW 3.3-3.5 mm . . . . 1. *angusticeps* Evans

Transverse carina of propodeum obsolescent in middle, median carina not nearly reaching posterior margin of disc; LFW 4.0-5.6 mm . . . . 2. *reducta* Evans

7. Ocelli of moderate size; OOL at least as great as WOT; head about as wide as high . . . . 3. *flammicornis* Evans

Ocelli greatly enlarged; OOL about half WOT; head considerably wider than high . . . . 4. *photophila* (Ogloblin)

8. Mandibles broad, with four teeth (Fig. 23); clypeus with a sharp median tooth but no additional processes (Fig. 9); notauli present only on anterior half of mesoscutum . . . . 7. *pygmaea* n. sp.

Mandibles slender, with two or three teeth; clypeus with a small median tooth flanked by two rounded processes (Figs. 7, 8); notauli complete 9

9. Mandibles bidentate (Fig. 21); punctures of front small but quite distinct; legs testaceous . . . . 5. *lilloana* n. sp.

Mandibles tridentate (Fig. 22); front obscurely punctate; coxae and femora medium brown . . . . 6. *simulata* n. sp.

10. Abdomen sessile, first tergite broadly reaching articulation with propodeum; mandibles with three large teeth (Fig. 24); inner margin of volsella with only a few setae just below cuspis (*mexicana* group) . . 11

Abdomen short-petiolate, first tergite not reaching extreme base; mandibles with 4 or 5 teeth (Figs. 25, 26); inner margin of volsella setose for a considerable distance (*brasiliensis* group) 12

11. Clypeus broadly subangulate (as in Fig. 12); antennae elongate, the pubescence short and subappressed; head and thorax polished, nonalutaceous . . . . 10. *laevicornis* n. sp.

Clypeus truncate or bidentate apically (Fig. 10); antennae shorter, with suberect pubescence; head and thorax somewhat alutaceous . . . . 11. *inca* Evans

12\. Clypeus short, broadly truncate (Fig. 13); mandibles with four teeth (Fig. 26); front polished, non-alutaceous, strongly punctate .... 14. *spinipes* n. sp.

Clypeus more prominent, subangulate (Figs. 11, 12); mandibles with five teeth (Fig. 25); front somewhat alutaceous, punctures small and widely spaced 13

13\. Ocelli enlarged, DAO .20-.22 × WF, OOL .80-.95 × WOT; mesoscutum evenly alutaceous; parameres not highly modified (Fig. 4) .... 12. *spatulata* n. sp.

Ocelli not or but slightly enlarged, DAO .16 to .20 × WF, OOL at least slightly exceeding WOT; mesoscutum not or obscurely alutaceous, at least medially; parameres each divided into two separate lobes (Fig. 5) .... 13. *lacerata* n. sp.

1. *Apenesia angusticeps* Evans

This species has been known from one male from Santa Cruz, Bolivia. Five Argentinian males are similar to the type in color and sculpture. However, the antennae are somewhat shorter (segment three 1.6-1.9 × as long as wide, segment eleven about twice as long as wide) and the front is somewhat broader (WF 1.1-1.3 × HE). LFW varies from 3.2 to 3.8 mm.

Specimens examined. — ARGENTINA: 1 ♂, Horco Molle, Tucumán, 3-10 April 1966 (L. Stange); 2 ♂♂, Horco Molle, Oct., Dec. 1967 (C. C. Porter); 1 ♂, 11 km W Las Cejas, Tucumán, 1-21 Feb. 1968 (L. Stange); 1 ♂, San Pedro Colalao, Tucumán, Nov.-Dec. 1967 (L. Stange).

2. *Apenesia reducta* Evans

This species has been known from a single male from Chapada, Brazil. Twenty-three males now before me key well to this species if allowance is made for the fact that in about half the specimens the very small fourth mandibular tooth is altogether absent. In some specimens the tip of the abdomen is weakly suffused with brown, while in others the last two segments are rufous as in the type. All these specimens are larger than the type (LFW 4.2-5.6 mm) except for the two from Tucumán, which are slightly smaller (LFW 3.6-3.9 mm). Throughout this series, the propodeum is broader than in the type (disc 1.2-1.4 × as wide as long), although similar in sculpturing.

Specimens examined. — ARGENTINA: 2 ♂♂, 11 km W Las Cejas, Tucumán, Jan.-Feb. 1968 (L. Stange); 5 ♂♂, Oran, Abra Grande, Salta, 29 Jan.-7 Feb. 1967 (R. Golbach); 4 ♂♂, Rio Pescado, Salta, 19-25 Nov. 1967 (C. Porter, E. Willink). PARAGUAY: 12 ♂♂, Carumbé, 1 Feb.-8 March 1966 (R. Golbach).

3. *Apenesia flammicornis* Evans

This species was described from Santa Cruz, Bolivia, and later reported from Jujuy, Argentina.[3] Nine additional males from northern Argentina compare favorably with the type, but some are smaller (LFW 4.0-5.5 mm), and there is considerable variation in some standard measurements (OOL 1.05-1.40 × WOT; WF 1.05-1.20 × HE).

Specimens examined. — ARGENTINA: 7 ♂♂, Oran, Abra Grande, Salta, 29 Jan.-7 Feb. 1967 (R. Golbach); 2 ♂♂, Rio Pescado, Salta, 19-25 Nov. 1967 (C. Porter, E. Willink).

4. *Apenesia photophila* (Ogloblin)

This species is known from a series from Loreto, Misiones, Argentina. It is closely related to the preceding, but has much larger ocelli and a reddish abdomen. I redescribed the species in my 1963 revision of this genus.

5. *Apenesia lilloana* NEW SPECIES

Holotype. — ♂, ARGENTINA: Horco Molle, San Xavier Mts., Tucumán, 1-7 May 1966 (L. Stange).

Description of type. — Length 2.6 mm; LFW 2.4 mm. Head black; thorax and propodeum fusco-castaneous; abdomen castaneous, irregularly banded with light brown, base of first segment piceous; mandibles in large part testaceous; first two antennal segments testaceous, remainder of antenna dark brown; legs testaceous, coxae and femora weakly suffused with darker brown; wings subhyaline, with dark setulae, veins and stigma brown. Head, thoracic dorsum, venter, and basal parts of legs clothed with dense, short hair. Mandibles slender, bidentate (Fig. 21). Clypeus large, well developed in front of antennal sockets, below which there are large. semicircular depressions; median carina sharply defined, nearly straight in profile, forming a small median tooth at its terminus, this tooth flanked by two small, rounded processes, so that the clypeus is weakly tridentate (Fig. 7). Antennae very slender, scape elongate, first four segments in a ratio of about 3:1:1:1, segments three and eleven each nearly 3 × as long as wide; flagellar pubescence erect, bristling, setulae nearly as long as width of flagellum. Eyes hairy, somewhat protuberant; WH .97 × LH; vertex broadly rounded, nearly straight in middle; distance from eye tops to vertex crest somewhat less than eye height. WF 1.25 × HE; ocelli not notably enlarged, in a compact triangle, the front angle less than

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[3] Evans, H. E., Acta Hymenopterologica, 2: 103 (1966).

a right angle; OOL 1.3 × WOT. Front strongly alutaceous, weakly shining, with an abundance of shallow but well-defined punctures. Thoracic dorsum wholly alutaceous, obscurely punctate; pronotum short, without a transverse carina; notauli linear, complete, curved somewhat mesad posteriorly. Propodeum of moderate length, with a somewhat irregular transverse carina along the top of the declivity, the median carina not quite reaching this transverse carina; surface strongly reticulate basally, polished apically; disc measuring 1.1 × as long as wide. Mesopleura alutaceous, without a well-defined callus. Fore wing with the discoidal vein strongly pigmented for a distance greater than length of basal vein. Abdomen very slender at base, subpetiolate; subgenital plate broadly truncate; genitalia with the aedoeagus terminating in two simple lobes, the parameres with a lateral, digitiform process (Fig. 1).

Paratypes. — 4 ♂♂, same data as type except various dates March-July 1966, 1967 (L. Stange).

Variation. — The paratypes vary slightly in size (LFW 2.3-3.2 mm); WH/LH varies from .92 to .98, WF/HE from 1.15 to 1.25, OOL/WOT from 1.15 to 1.25. There is no noteworthy variation in color or sculpture.

Remarks. — I would assign this species to the *dissomphaloides* species-group, previously known from Mexico and the southwestern United States, although it will not run to that group in my revision of *Apenesia* (1963) because of the presence of a transverse carina on the propodeum. However, the hairy eyes, tridentate clypeus, and male genitalia all suggest that it belongs in that group. The two species that follow are closely related to *lilloana* and these remarks apply equally well to them.

6. *Apenesia simulata* NEW SPECIES

Holotype. — ♂, ARGENTINA: Horco Molle, San Xavier Mts., Tucumán, 4-12 Jan. 1966 (L. Stange).

Description of type. — Length 3.0 mm; LFW 2.6 mm. Head, thorax, and base of first abdominal segment black; remainder of abdomen dark castaneous, irregularly banded with light brown; mandibles in large part testaceous; clypeus dull ferruginous; first two antennal segments testaceous, remainder of antenna dark brown; legs medium brown except trochanters, tarsi, and femorotibial joints paler; wings subhyaline, with dark setulae, veins and stigma brown. Head, thoracic dorsum, venter, and basal parts of legs clothed with short, brownish hair. Mandibles slender, tridentate (Fig. 22). Clypeus much as in *lilloana*, but the median tooth very small and flanked by two fairly large, rounded processes (Fig. 8).

First four antennal segments in a ratio of about 16:5:6:5, segments three and eleven each about 2.5 × as long as wide; flagellar pubescence erect, bristling, setulae nearly as long as width of flagellum. Eyes hairy, strongly protuberant; WH .96 × LH; sides of head roundly convergent behind eyes; occipital carina unusually strong, readily visible for a considerable length when head is viewed from front. Front broad, WF 1.4 × HE; ocelli small, in a compact triangle far above eye tops, OOL 1.55 × WOT. Front moderately alutaceous, somewhat shining, punctures small and shallow, separated by 2-4 × their own diameters. Thoracic dorsum alutaceous, obscurely punctate; notauli strong, complete. Propodeal disc slightly longer than wide, with a well-defined transverse carina behind; sculpturing similar to that of preceding species. Features of mesopleura and wings as in *lilloana,* and abdomen subpetiolate as in that species. Subgenital plate broadly emarginate apically; genitalia similar to those of *lilloana* but the parameres simple, the aedoeagus with prominent ventral rami and with elongate apical lobes which are serrate on their inner margins (Fig. 2).

Paratypes. — 6 ♂♂, same data as type except various dates Jan.-May 1966 (L. Stange).

Variation. — LFW varies from 2.2 to 2.9 mm, WH/LH from .95 to .97, WF/HE from 1.30 to 1.45, OOL/WOT from 1.3 to 1.6. In the majority of specimens the propodeal disc is about as long as wide.

7. *Apenesia pygmaea* NEW SPECIES

Holotype. — ♂, CHILE: Queb. de la Plata, Rinconada Maipú, Santiago Prov., 510 meters, 26 Dec. 1966 (L. Stange).

Description of type. — Length 1.8 mm; LFW 1.6 mm. Head and thorax dark brown, abdomen somewhat lighter brown except base of first tergite black; apical half of mandibles light brown; antennae dark brown except second segment testaceous; legs brown, tarsi and apices of tibiae somewhat lighter than remainder; wings hyaline, with dark setulae, veins and stigma brown. Head and thorax dorsum with rather dense short, brownish setae. Mandibles with a large apical tooth and three small, sharp teeth above it (Fig. 23). Clypeus large, well developed in front of antennal insertions, with a median tooth but no additional irregularities; median carina very strong basally, then abruptly declivous to apex (Fig. 9). Antennae very slender, first four segments in a ratio of about 7:4:3:4, segments three and eleven each about 3 × as long as wide; flagellar pubescence suberect, bristling, setulae about as long as width of flagellum. Eyes small but strongly convex, hairy;

WH .97 × LH; vertex broadly rounded, distance from eye tops to vertex crest subequal to eye height. WF 1.25 × HE; ocelli small, widely spaced, front angle of ocellar triangle less than a right angle; OOL 1.3 × WOT. Front alutaceous although rather strongly shining, obscurely punctate. Thoracic dorsum also alutaceous, somewhat shining; pronotum unusually short, without a transverse carina; mesoscutum with a few small punctures medially, notauli strong on anterior half, absent behind; scutum longitudinally depressed on each side. Propodeum elongate, with a weak, incomplete carina margining the disc behind; disc 1.3 × as long as wide, with a long median carina and several short, radiating carinae basally. Features of mesopleura and wings as in preceding species; subgenital plate truncate as in that species; genitalia not studied.

Remarks. — I have seen only one specimen of this minute species, but since it is the second species of the genus known from Chile, it seems worth describing at this time. The other Chilean species, *chilena*, is much larger and has a very different clypeus, glabrous eyes, larger ocelli, and several other prominent differences.

8. *Apenesia chilena* Evans

I described this species from one specimen from Pichinahuel, Arauco, Chile.[4] I have seen no additional specimens, nor have I seen other South American species closely related to it. I assigned the species tentatively to the *exilis* group, known otherwise from the southern United States.

9. *Apenesia crenulata* (Kieffer)

This very distinctive species has been known only from the type, from Pará, Brazil. Two specimens before me agree well with the type but are both slightly smaller (LFW 2.1-2.2 mm) and have the ocelli less far removed from the eyes (OOL 1.1-1.2 × WOT); both have propodeal sculpturing generally similar to that of the type, but the median carina is well defined.

Specimens examined. — ARGENTINA: 1 ♂, Oran, Abra Grande, Salta, 29 Jan.-7 Feb. 1967 (R. Golbach). BRAZIL: 1 ♂, Nova Teutonia, Santa Catarina, Feb. 1964 (F. Plaumann).

10. *Apenesia laevicornis* NEW SPECIES

Holotype. — ♂, ARGENTINA: 11 km W Las Cejas, Tucumán, 13 July-2 Aug. 1967 (L. Stange).

Description of type. — Length 3.8 mm; LFW 3.2 mm. Head and thorax black; abdomen dark castaneous, irregularly mottled

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[4] Proc. Ent. Soc. Washington, 69: 271 (1967).

with lighter brown; mandibles black except suffused with dull ferruginous on apical third; antennae very dark brown; legs dark brown except tarsi somewhat paler; wings hyaline, with pale setulae, veins and stigma brown. Body setae relatively sparse and long. Mandibles with three large apical teeth (Fig. 24). Clypeus broadly subangulate, median part somewhat tectiform but not carinate (as in Fig. 12). Antennae slender, first four segments in a ratio of about 14:4:9:8, segment three 3 × as long as wide, segment eleven 3.5 × as long as wide; flagellar pubescence short, subappressed, a few slightly longer, erect setulae standing above it. Eyes with scattered short setae, only slightly protuberant; vertex broadly rounded off well above eye tops; WH .97 × LH. Front broad, WF 1.47 × HE; ocelli small, widely spaced, in a right triangle; OOL 1.25 × WOT. Front strongly polished, non-alutaceous, punctures strong, rather irregularly spaced, mostly separated by 5-8 × their own diameters. Thoracic dorsum also wholly non-alutaceous, strongly polished, sparsely punctate; pronotum with a transverse carina on the anterior slope; notauli and parapsidal furrows strong, nearly complete. Propodeal disc as long as wide, with a complete median carina and a rather irregular transverse carina; basal part of disc alutaceous and with strong reticulations, apical part smooth and shining. Mesopleura wholly polished, non-alutaceous, very sparsely punctate. Discoidal vein of fore wing very weakly developed, arising a short distance down on transverse median vein. Abdomen sessile; subgenital plate arcuately emarginate; aedoeagus complex although nearly parallel-sided; ventral arms of cuspides narrowly rounded; parameres with a rounded apical enlargement (Fig. 3).

Remarks. — This unusual species is known from a single specimen. It is a member of the *mexicana* group, similar to *neotropica* Evans in many details, but with longer and smoother antennae, a much broader and more polished front, and smaller ocelli.

11. *Apenesia inca* EVANS

This distinctive species was described from Peru and Ecuador in 1963; in 1966 I recorded it from two localities in eastern Brazil. Nineteen Argentinian males have the usual tridentate mandibles and bidentate clypeus (Fig. 10), as well as genitalia resembling those of the type closely. LFW varies from 2.7 to 3.8 mm, WF from 1.0 to 1.2 × HE; in the majority of specimens OOL is subequal to or even slightly less than WOT.

Specimens examined. — ARGENTINA: 19 ♂♂, 11 km W of

Las Cejas, Tucumán, Sept., Nov., Dec., Jan., Feb., 1967-68 (L. Stange).

12. *Apenesia spatulata* NEW SPECIES

Holotype. — ♂, ARGENTINA: Horco Molle, Tucumán, 7-26 March 1967 (L. Stange).

Description of type. — Length 4.8 mm; LFW 4.0 mm. Head, thorax, and abdominal petiole black; remainder of abdomen dark castaneous with irregular banding with lighter brown; apical half of mandibles testaceous, teeth rufous; antennae medium brown except second segment light brown; legs entirely testaceous; wings subhyaline, with dark setulae, vein and stigma dark brown. Mandibles broad, with five strong teeth (Fig. 25). Clypeus broadly subangulate, its median line tectiform but not carinate (Fig. 11). First four antennal segments in a ratio of about 20:7:10:10, segment three 2.5 × as long as wide, segment eleven 3 × as long as wide; flagellar pubescence pale, suberect, majority of setulae about .7 as long as width of flagellum. Eyes large, somewhat protuberant, glabrous; WH 1.03 × LH; vertex forming a broad, even arc above eye tops. WF 1.1 × HE; ocelli large, less than their diameters apart, front ocellus located on an imaginary line drawn between eye tops; DAO .22 × WF; OOL .85 × WOT. Front wholly alutaceous, weakly shining, punctures small but sharply defined, separated for the most part by 3-5 × their own diameters. Pronotal disc margined in front by a transverse carina, weakly alutaceous and with scattered, minute punctures; mesoscutum also weakly alutaceous, shining, with punctures slightly stronger than on pronotum; notauli nearly complete. Propodeum elongate, the disc margined behind by a series of fine transverse ridges, disc measuring slightly longer than wide; median carina complete, disc also reticulate medio-basally. Mesopleurum wholly weakly alutaceous, obscurely punctate anteriorly. Middle tibiae strongly spinose above. Discoidal cell of fore wing weakly outlined, the discoidal vein itself strongly pigmented for a distance about equal to basal vein. Abdomen petiolate, but the petiole very short; subgenital plate truncate; aedoeagus complex; ventral lobes of cuspides spatulate, narrowly rounded apically, parameres with a broad, subquadrate lobe which is directed mesad (Fig. 4).

Paratypes. — 20 ♂♂, same data as type but various dates Jan.-July 1966 (L. Stange).

Variation. — In the paratypes, LFW varies from 3.2 to 4.1 mm, WH from 1.03 to 1.06 × LH, WF from 1.05 to 1.20 × HE, OOL from .80 to .95 × WOT, DAO from .20 to .22 × WF. There is no noteworthy variation in other characters.

Remarks. — This species is a member of the *brasiliensis* group, apparently related to *angustata* (Evans). The species name refers to the large, spatulate lobes of the cuspis.

13. *Apenesia lacerata* NEW SPECIES

Holotype. — ♂, ARGENTINA: 11 km. W of Las Cejas, Tucumán, 16-29 April 1967 (L. Stange).

Description of type. — Length 3.3 mm; LFW 3.0 mm. Head, thorax, and abdominal petiole piceous; remainder of abdomen dark castaneous, irregularly banded with lighter brown; mandibles testaceous, darker at extreme base and apex; antennae testaceous basally, grading into medium brown beyond segment three; legs wholly testaceous; wings hyaline. Mandibles with five teeth (as in Fig. 25); clypeus broadly subangulate, tectiform medially (Fig. 12). First four antennal segments in a ratio of about 18:5:10:9, segment three 3 × as long as wide, segment eleven 3.5 × as long as wide; flagellar pubescence suberect, nearly as long as width of flagellum. Eyes weakly hairy, slightly protuberant; WH 1.03 × LH; vertex forming a broad, even arc above eye tops. WF 1.22 × HE; ocelli slightly enlarged, DAO .17 × WF; front ocellus slightly above a line connecting eye tops; OOL 1.1 × WOT. Front wholly alutaceous, somewhat shining; punctures small, separated by 3-5 × their own diameters. Pronotum strongly polished, non-alutaceous, the disc margined in front by a transverse carina; mesoscutum strongly polished, very weakly alutaceous laterad of the very strong, complete notauli. Propodeal disc as wide as long, sculptured exactly as in the preceding species. Mesopleurum shining, barely alutaceous, strongly punctate in front. Discoidal vein of fore wing very weakly outlined by pigmented lines. Abdominal petiole very short; subgenital plate subtruncate; genitalia of unusual form in that the ventral arms of the cuspides are very long and pointed, the parameres deeply divided into a slender process and an enlarged mesal lobe (Fig. 5).

Paratypes. — 17 ♂♂, same data as type but various dates July-Nov. 1967 and Jan., Feb., May 1968 (L. Stange).

Variation. — LFW varies from 3.0 to 3.3 mm, WH from .98 to 1.03 × LH, WF from 1.12 to 1.30 × HE, DAO from .16 to .20 × WF, OOL from 1.1 to 1.2 × WOT. In the majority of paratypes the propodeal disc is longer than wide. In a few specimens the front coxae and femora are suffused with brown. In two specimens the mesoscutum is somewhat alutaceous, even medially.

Remarks. — This species resembles the preceding closely, and I would be inclined to consider the two conspecific if it were not for the distinctive genitalia. The name *lacerata* refers to the greatly dissected parameres of the genitalia of this species.

14. *Apenesia spinipes* NEW SPECIES

Holotype. — ♂, ARGENTINA: 11 km W of Las Cejas, Tucumán, 3-19 June 1966 (L. Stange).

Description of type. — Length 4.3 mm; LFW 3.5 mm. Head and thorax black, abdomen dark castaneous with lighter markings along margin of first tergite as well as apically; mandibles testaceous except teeth rufous; antennae wholly testaceous, legs also of this color except coxae and femora suffused with brown; wings hyaline, veins and stigma dark brown. Mandibles with four large apical teeth (Fig. 26). Clypeus very short, broadly truncate (Fig. 13). First four antennal segments in a ratio of about 4:1:2:2, segments three and eleven each about 3 × as long as wide; flagellar pubescence erect, pale, setulae about one third as long as width of flagellum. Eyes very weakly hairy; vertex forming a broad, even arc above eye tops, distance from eye tops to vertex crest nearly equal to HE. WH 1.02 × LH; WF 1.2 × HE; ocelli small, in a compact triangle, OOL 1.4 × WOT. Front polished, non-alutaceous, with strong punctures which are separated by only 1-2 × their own diameters. Thoracic dorsum polished, non-alutaceous; pronotal disc with a strong transverse carina in front, its surface covered with small punctures except along a median band. Mesoscutum with scattered, sharply defined punctures; notauli strong, complete; scutellar disc impunctate medially. Propodeal disc 1.2 × as wide as long, the transverse carina weak although complete, median carina also complete; disc reticulate medio-basally, elsewhere strongly polished and smooth; posterior face shining, with a few punctures and some medial roughening, but no median carina. Mesopleurum in large part smooth and polished, the callus convex. Middle tibiae very strongly spinose. Discoidal cell of fore wing weakly outlined by pigmented lines, the subdiscoidal vein more heavily pigmented than the discoidal vein. Abdomen short-petiolate; subgenital plate truncate; genitalia with the aedoeagus narrowed subapically, with a pair of curved apical processes; ventral arms of cuspides large, rounded; parameres with broad mesal lobes (Fig. 6).

Paratypes. — 41 ♂♂, same data as type except various dates May, Aug., Oct., Dec., 1967; Jan., Feb., 1968 (L. Stange).

Variation. — Several specimens have the coxae and femora more heavily infuscated than in the type, and the apical third of the antennae may also be somewhat infuscated. LFW varies from 2.7 to 4.2 mm, WH/LH from 1.01 to 1.05, WF/HE from 1.10 to 1.25, OOL/WOT from 1.20 to 1.45.

Remarks. — This species runs to *brasiliensis* (Kieffer) in my 1963 key, although the transverse carina of the propodeum is not as strong. The genitalia are very different from those of *brasiliensis* and the sculpturing of the basal triangle of the propodeum quite different.

GENUS *DISSOMPHALUS* ASHMEAD

Seventeen species of this genus have so far been described from South America, and 8 more are added here. I would estimate that there are at least 2 to 4 times that many species on that continent, even though some synonymy will be discovered when the sexes are properly associated. The following three species are known from Argentina from the female sex and are not treated here: *attaphila* (Bruch), *azarai* (Ogloblin), and *platensis* (Bruch). This genus has not yet been found to occur in Chile

KEY TO MALE *Dissomphalus* KNOWN FROM ARGENTINA

1. Second abdominal tergite with two large, pubescent pits close together medially and sharing a common depression (Figs. 16, 17) 2
   Second abdominal tergite not as above, containing two medium-sized to minute pits, marks, or processes which are separated by much more than their own length (Figs. 18-20) 3
2. Pronotum with a strong transverse ridge; second tergite with four pits, the two middle ones very large, the tergite swollen and distorted behind them (Fig. 16) ....1. *deformis* n. sp.
   Pronotum without a transverse ridge; second tergite with two somewhat smaller pits medially, the tergite not swollen and distorted behind them (Fig. 17) ....2. *ulceratus* n. sp.
3. Notauli absent on posterior two-thirds of mesoscutum; mandibles with four teeth (Fig. 31) ....6. *teren* n. sp.
   Notauli complete; mandibles with 2 or 3 teeth 4
4. Second tergite with fairly large, round pits with raised rims (Fig. 18); subgenital plate with a large, V-shaped apical emargination; WF not exceeding HE ....3. *puteolus* n. sp.
   Second tergite with minute pits, slits, or processes; subgenital plate without a V-shaped emargination: WF exceeding HE 5
5. Clypeus tapering to a long, sharp median point (Fig. 15); WH only .9 X LH; second tergite with a pair of small, spatulate processes anteromedially ....8. *bispinulatus* n. sp.

Clypeus not so strongly pointed apically and WH subequal to HE; second tergite not modified as above 6

6. Second tergite smooth, with a pair of pale, roughened spots at extreme anterior margin laterally, but no other modifications; clypeus with a median process, not or very indistinctly tridentate..9. *incomptus* Evans

Second tergite with small pits, slits, or processes not nearly so close to anterior margin (Figs. 19, 20); clypeus strongly tridentate (as in Fig. 14) 7

7. Modifications of second tergite in the form of oblique slits (Fig. 20); propodeal disc short, 1.7 × as wide as long ......7.*infissus* n. sp.

Modifications of second tergite in the form of minute pits or hair pencils (Fig. 19); propodeal disc 1.0-1.3 × as wide as long..............8

8. LFW 1.8 mm; eyes and ocelli small, WF 1.2 × HE, OOL 1.05 × WOT; wings pale, discoidal vein unpigmented, basal vein suberect ....4. *mendicus* n. sp.

LFW 2.6 mm; eyes and ocelli rather large, WF 1.1 × HE, OOL only .8 × WOT; wings with dark veins and stigma, discoidal vein a short, brown streak, basal vein strongly oblique ......5. *microstictus* n. sp.

1. *Dissomphalus deformis* NEW SPECIES

Holotype. — ♂, ARGENTINA: Oran, Abra Grande, Salta, 8-15 Feb. 1967 (R. Golbach).

Description of type. — Length 2.7 mm; LFW 2.4 mm. Head and thorax black; abdomen dark brown, suffused with lighter brown on parts of basal and apical segments; mandibles largely testaceous; antennae testaceous, suffused with brown on apical half; coxae and femora dark brown, hind tibiae medium brown, legs otherwise testaceous; wings hyaline. Mandibles tridentate, the middle tooth the smallest (Fig. 27). Clypeus tridentate, median carina strong, straight in profile (Fig. 14). First four antennal segments in a ratio of about 3:1:1:1, segment three 1.5 × as long as wide, segment eleven twice as long as wide. Head as wide as high, the eyes large, convergent below; WF 1.1 × HE; ocelli widely spaced, front angle of triangle less than a right angle; OOL 0.9 × WOT. Front alutaceous although somewhat shining, covered with shallow punctures. Thoracic dorsum strongly alutaceous, obscurely punctate; pronotal disc crossed anteriorly by a very strong carina; notauli strong, complete. Propodeal disc 1.2 × as wide as long, disc and declivity wholly coarsely reticulate. Discoidal vein of fore wing barely indicated. First tergite short, with a strong median groove for much of its length; second tergite with two very large, pubescent, elliptical pits close beside the midline, the tergite strongly gibbous behind and slightly laterad of these pits; second tergite also with a pair of much smaller pits in addition, so that there are four pits in a transverse series; tergite with a median band of small setae behind the pits (Fig. 16). Subgenital plate broadly concave apically; parameres large, triangular in lateral view, subacute apically.

Paratypes. — 3 ♂♂, same data as type.

Variation. — The paratypes are all slightly larger than the type (LFW 2.5-2.7 mm) and all have the propodeal disc slightly shorter and wider (1.25-1.35 × as wide as long). There is no noteworthy variation in standard measurements or in the remarkable configuration of the second tergite.

2. *Dissomphalus ulceratus* NEW SPECIES

Holotype. — ♂, ARGENTINA: Horco Molle, San Xavier Mts., Tucumán, 1-7 May 1966 (L. Stange).

Description of type. — Length 2.0 mm; LFW 1.9 mm. Dark brownish-fuscous, sides of basal abdominal segments suffused with light brown; mandibles testaceous on apical half; mandibles dark brown except second segment somewhat lighter than remainder; coxae and femora dark brown, legs otherwise testaceous; wings hyaline. Mandibles tridentate, the uppermost tooth the smallest (Fig. 28). Clypeus with a strong median angulation and two small, rounded teeth beside it (much as in Fig. 7); median carina straight in profile. Third antennal segment 1.5 × as long as wide. Head as wide as high, eyes not convergent below, front broad, WF 1.3 × HE; ocellar triangle compact, OOL 1.2 × WOT. Front alutaceous, somewhat shining, covered with shallow punctures. Thoracic dorsum alutaceous although somewhat shining; pronotum short, without a transverse carina; notauli complete. Propodeum short, disc measuring 1.35 × as wide as long; disc mostly reticulate, but with a smooth area behind. Discoidal vein of fore wing present as a long but weakly pigmented streak. First tergite more rounded behind and with a shorter median groove than in *deformis,* and the second tergite not gibbous behind the pits as in that species; pits large, narrowly separated medially, sharing a common bowl-shaped depression, the tergite without other pits and with only a few scattered setae (Fig. 17). Subgenital plate broadly truncate.

Paratype. — 1 ♂, same data as type except 3-10 April 1966 (L. Stange).

Variation. — In the paratype, LFW is 2.0 mm, WF 1.4 × HE. This specimen is closely similar to the type in every respect.

3. *Dissomphalus puteolus* NEW SPECIES

Holotype. — ♂, ARGENTINA: 11 km W of Las Cejas, Tucumán, 13-27 May 1967 (L. Stange).

Description of type. — Length 2.5 mm; LFW 2.1 mm. Head and thorax black; abdomen dark brown, with paler markings toward base and apex; mandibles in large part testaceous; scape medium brown, flagellum light brown; coxae and femora dark brown, remainder of legs light brown; wings hyaline. Mandibles with three strong apical teeth, the most basal tooth somewhat rounded (Fig. 29). Clypeus with a projecting median lobe which is tridentate (much as in Fig. 14). First four antennal segments in a ratio of about 10:4:3:3, segment three only slightly longer than wide, segment eleven 1.5 × as long as wide. WH 1.02 × LH; eyes large, strongly convergent below, WF only .93 × HE; ocelli widely spaced, OOL only .8 × WOT. Front alutaceous and strongly roughened by punctures which are separated by less than their own diameters. Thoracic dorsum alutaceous; pronotum short, without a transverse carina; mesoscutum somewhat shining, with numerous small punctures, notauli complete. Propodeal disc unusually short and broad, 1.7 × as wide as long, surface reticulate except smooth over a small area behind. Discoidal vein of fore wing absent. First tergite relatively longer and second tergite shorter and less convex than in preceding two species; second tergite with a pair of fairly large, circular pits dorso-laterally, each pit in a depression, with a raised rim and giving rise to a small tuft of setulae; second tergite with numerous setae, especially laterad of the pits (Fig. 18). Subgenital plate with a strong, V-shaped apical emargination; parameres broad, tapering to an acute apex.

Paratypes. — 5 ♂♂, same data as type except various dates Jan., March, April, June, 1966-1968 (L. Stange).

Variation. — The paratypes are very similar to the type; LFW varies from 1.9 to 2.1 mm; all have the basal flagellar segments testaceous, contrasting with the darker apical segments; in two the propodeum is not quite as short as in the type, the disc measuring 1.6 × as wide as long.

4. *Dissomphalus mendicus* NEW SPECIES

Holotype. — ♂, ARGENTINA: 11 km W of Las Cejas, Tucumán, 17 June-12 July 1967 (L. Stange).

Description of type. — Length 2.1 mm; LFW 1.8 mm. Head and thorax dark brownish-fuscous except pronotal collar medium brown; abdomen dark castaneous except first tergite bordered with light brown, second tergite light brown on extreme sides; mandibles in large part testaceous; antennae dull brown except second segment and adjacent parts of first and third segments testaceous; legs brown, tarsi and femoro-tibial joints straw-colored; wings hyaline, with pale setulae and pale veins and stigma. Mandibles tridentate, the basal two teeth small (much as in Fig. 28). Clypeus as described for the preceding species. First four antennal segments in a ratio of about 5:2:2:2, segments three and eleven both about 1.5 × as long as wide. WH and LH subequal; eyes weakly converging below, WF 1.2 × HE; ocelli small, front angle of ocellar triangle less than a right angle, OOL 1.05 × WOT. Front moderately alutaceous, shining, the punctures small and shallow, separated by 2-4 × their own diameters. Thoracic dorsum alutaceous although somewhat shining; pronotum short, without a transverse carina; mesoscutum weakly punctate, notauli complete. Propodeal disc 1.25 × as wide as long, surface reticulate. Discoidal vein of fore wing distinct for a short distance although barely pigmented. First tergite rounded behind, with a strong median groove; second tergite with a pair of minute lateral pits with raised rims, the pits occupying very shallow depressions and flanked by several setae (much as in Fig. 19). Subgenital plate broadly truncate apically.

Remarks. — This small but distinctive species is known from a single specimen.

5. *Dissomphalus microstictus* NEW SPECIES

Holotype. — ♂, ARGENTINA: 11 km W of Las Cejas, Tucumán, 3-19 June 1966 (L. Stange).

Description of type. — Length 3.0 mm; LFW 2.6 mm. Head black; thorax dark brownish-fuscous; abdomen dark castaneous, with paler markings basally and apically; mandibles in large part testaceous; antennae medium brown except segments two and three and apex of one testaceous; legs straw-colored except front and hind femora weakly suffused with brown; wings hyaline, with dark veins and stigma. Mandibles with two strong apical teeth (Fig. 30). Clypeus with a tridentate median lobe (much as in Fig. 14). Third and eleventh antennal segments both about twice as long as wide. WH and LH subequal; eyes prominent, short-haired, inner orbits subparallel on lower half; WF 1.1 × HE; ocelli slightly enlarged, in about a right triangle, OOL only .8 × WOT. Front wholly strongly alutaceous, weakly shining, punctures very shallow, separated by 1-3 × their own diameters. Thoracic dorsum alutaceous although less strongly so than front; pronotum short, without a transverse carina; mesoscutum with scattered small punctures, notauli complete. Propodeal disc elongate, barely wider than long, disc smooth and shining behind, the median carina not reaching the transverse carina. Discoidal vein of fore wing lightly pigmented for a considerable distance. First tergite elongate, median groove confined to basal half; second tergite with a pair of widely spaced very small pits with raised rims, these pits in very shallow, broad depressions and flanked by a few setae (Fig. 19). Subgenital plate broadly, shallowly emarginate; parameres twisted mesad apically.

Paratypes. — ARGENTINA: 53 ♂♂, same data as type except various dates Nov.-Dec. 1967, Jan.-May 1968; 1 ♂, San Pedro Colalao, Tucumán, Jan. 1968 (L. Stange).

Variation. — LFW varies from 2.1 to 3.6 mm. The legs vary from wholly straw-colored to almost wholly brown. WF varies from 1.1 to 1.3 × HE. The ocelli of some of the smaller specimens are only slightly enlarged, and in these specimens OOL is only slightly less than WOT. There is little variation in the form of the second tergite in this long series.

6. *Dissomphalus teren* NEW SPECIES

Holotype. — ♂, ARGENTINA: Horco Molle, San Xavier Mts., Tucumán, 3-11 June 1966 (L. Stange).

Description of type. — Length 1.8 mm; LFW 1.6 mm. Dark brownish-fuscous, including mandibles and antennae; legs dark brown except tarsi testaceous; wings hyaline, veins and stigma dark. Mandibles with four teeth, basal two teeth connate (Fig. 31). Clypeus tridentate, with a strong median carina (much as in Fig. 14). First four antennal segments in a ratio of about 10:4:3:3, segments three and eleven each about 1.5 × as long as wide. Head elongate, vertex broadly rounded off far above eye tops; WH .93 × LH; WF 1.25 × HE; front angle of ocellar triangle less than a right angle, OOL 1.3 × WOT. Front weakly alutaceous, moderately shining, punctures small and shallow. Thoracic dorsum smooth, somewhat shining, obscurely punctate; pronotum without a transverse carina; notauli present on anterior third of mesoscutum, absent behind. Propodeal disc 1.3 × as wide as long, with a transverse polished band posteriorly. Discoidal vein of fore wing weakly pigmented. First tergite rounded apically, with a median groove on the basal .6; second tergite smooth except for scattered small setae and a pair of curved hair-pencils which arise from slightly elevated bases, these located dorsally but separated by about twice the length of one of the hair-pencils. Subgenital plate unusually broad, arcuately emarginate; parameres very slender apically, their tips directed mesad.

Remarks. — This species possesses a number of unique features: the 4-tooth mandibles, reduced notauli, and broadly emarginate subgenital plate. It is known only from the type specimen.

7. *Dissomphalus infissus* NEW SPECIES

Holotype. — ♂, ARGENTINA: Oran, Abra Grande, Salta, 16-23 Feb. 1967 (R. Golbach).

Description of type. — Length 3.2 mm; LFW 2.6 mm. Dark brownish-fuscous; mandibles in large part testaceous; antennae medium brown, dark brown beyond basal .4; front coxae, all femora, and hind tibiae dark brown, remaining coxae, trochanters, femora-tibial joints, middle and front tibiae, and all tarsi testaceous; wings subhyaline, with dark setulae and dark veins and stigma. Mandibles tridentate (much as in Fig. 28). Clypeus with a tridentate median lobe (much as in Fig. 14). First four antennal segments in a ratio of about 3:1:1:1, segments three and eleven each about 1.5 × as long as wide. Head about as wide as high; front broad, WF 1.2 × HE; vertex slightly emarginate behind ocellar triangle, the latter about a right triangle, OOL 1.15 × WOT. Front strongly alutaceous, covered with shallow punctures which are separated by only 1-2 × their own diameters. Pronotum short, roughened but not carinate along anterior margin of disc; mesoscutum somewhat shining, with scattered small punctures; notauli strong, complete. Propodeal disc short, 1.7 × as wide as long, covered with coarse reticulations. Discoidal vein of fore wing interstitial with media, pigmented for a distance exceeding basal vein. First tergite rounded apically, with a strong median groove on basal half; second tergite with a pair of dorso-lateral slits with raised rims, each slit flanked by a group of setae (Fig. 20). Subgenital plate broadly truncate.

8. *Dissomphalus bispinulatus* NEW SPECIES

Holotype. — ♂, ARGENTINA: Oran, Abra Grande, Salta, 16-23 Feb. 1967 (R. Golbach).

Description of type. — Length 1.7 mm; LFW 1.5 mm. Dark brownish-fuscous; mandibles testaceous apically; antennae medium brown except basal three segments light brown; legs straw-colored except front coxae, all femora, and hind tibiae medium brown; wings hyaline, with dark setulae and dark veins and stigma. Mandibles with a large apical tooth and two minute teeth above it. Clypeus tapering medially to a long, acute process which is at the terminus of a strong median ridge (Fig. 15). First four antennal segments in a ratio of about 9:4:3:3, segments three and eleven each about 1.5 × as long as wide. Head elongate, WH only .90 × LH; eyes glabrous, inner orbits slightly diverging above and below middle; WF 1.17 × HE; ocelli small, in an acute triangle, OOL 1.3 × WOT. Front shining, weakly alutaceous, obscurely punctate. Pronotum much expanded from front to rear, sides concave as seen from above, without a transverse carina; mesoscutum weakly alutaceous, obscurely punctate, notauli complete. Propodeal disc 1.2 × as wide as long, most of its posterior half smooth and shining, median carina not nearly reaching transverse carina. Discoidal vein of fore wing strongly pigmented for a considerable distance. First tergite rounded apically, with a median groove on basal half; second tergite with a pair of small, spatulate processes close behind the margin of the first tergite, these separated medially by about twice their own length; second tergite also with a pair of roughened spots anterolaterally. Subgenital plate very broadly truncate apically.

9. *Dissomphalus incomptus* Evans

I described this species from eight males from Santa Catarina, Brazil, in my 1964 synopsis. Its presence in Paraguay and in two provinces of Argentina suggest that it is widely distributed and not uncommon in southern South America. The specimens before me key readily to this species in my 1966 paper[5] and agree with the type series in most details, including the genitalia. They average somewhat larger (LFW 1.9-2.6 mm) and show minor variation in head measurements (WF 1.1-1.3 × HE, OOL 1.15-1.30 WOT). The sinuations beside the median process of the clypeus vary in development, such that in some specimens the clypeus may be said to be indistinctly tridentate.

Specimens examined. — PARAGUAY: 1 ♂, Carumbé, 1 Feb.-8 March 1966 (R. Golbach). ARGENTINA: 2 ♂ ♂, Oran, Abra Grande, Salta, 1 Jan.-7 Feb. 1967 (R. Golbach); 12 ♂ ♂, Horco Molle, San Xavier Mts., Tucumán, Jan.-June 1966 (L. Stange), Dec. 1967 (C. C. Porter).

(Received 7 October 1968.)

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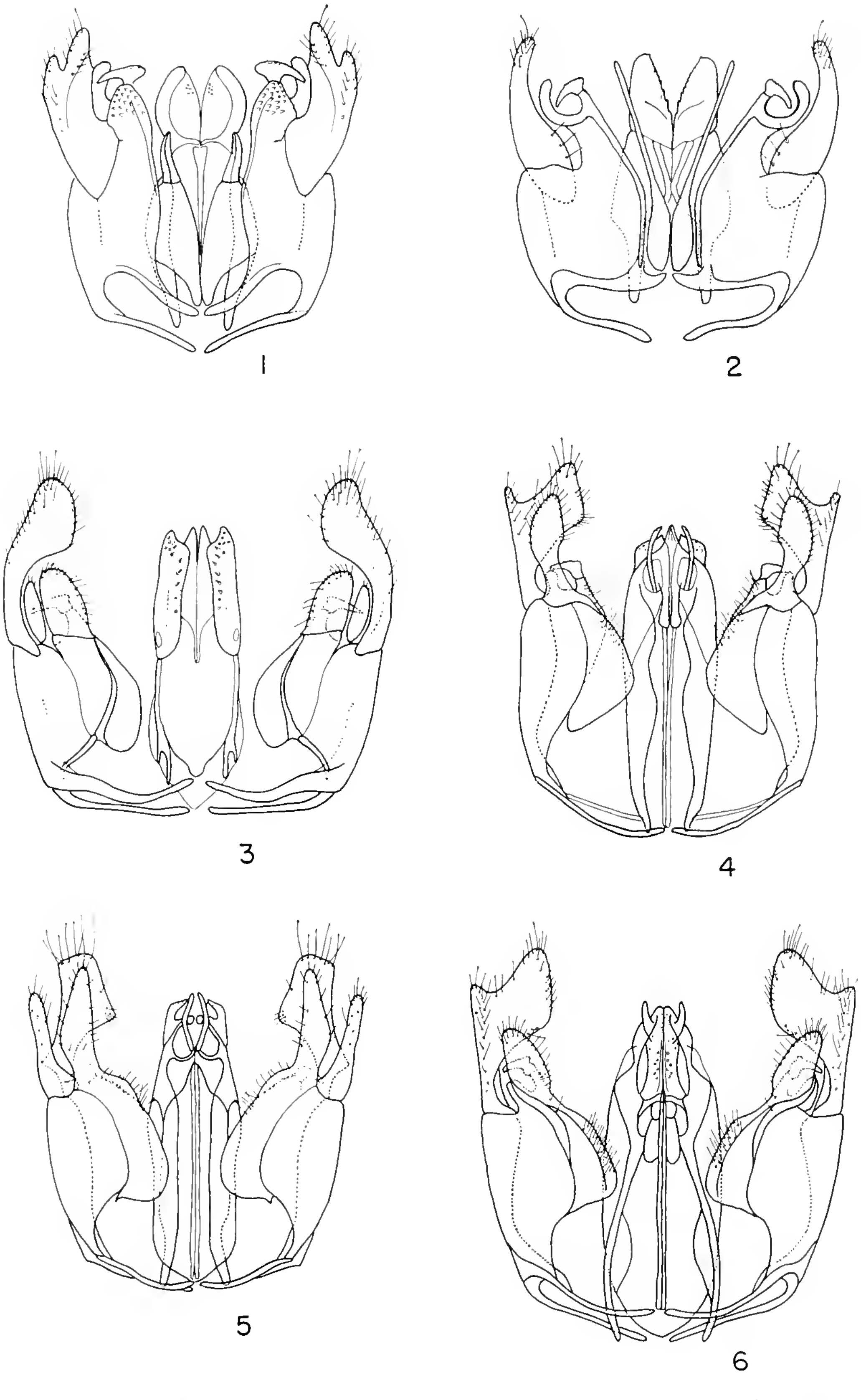
[5] Acta Hymenopterologica, 2: 110.



Figs. 1-6. Male genitalia of *Apenesia* spp., ventral aspect. Fig. 1., *A. lilloana* n. sp. Fig. 2., *A. simulata* n. sp. Fig. 3., *A. laevicornis* n. sp. Fig. 4., *A. spatulata* n. sp. Fig. 5., *A. lacerata* n. sp. Fig. 6., *A. spinipes* n. sp.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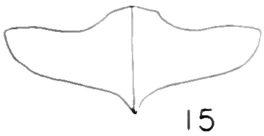
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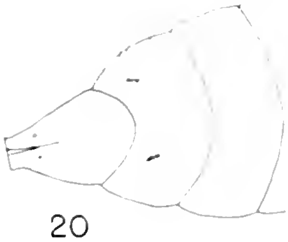
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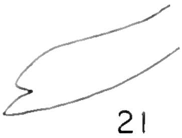
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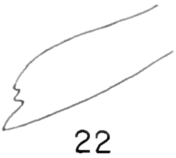
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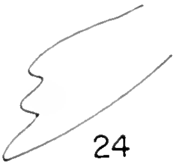
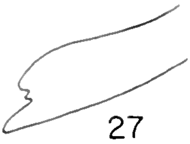
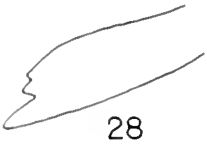
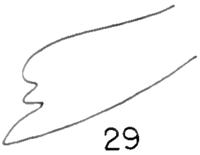

24


25


26


27


28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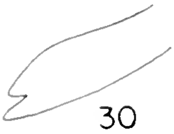
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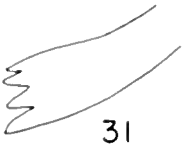
31

Figs. 7-15. Clypeus of male *Apenesia* and *Dissomphalus.* Fig. 7., *A. lilloana* n. sp. Fig. 8., *A. simulata* n. sp. Fig. 9., *A. pygmaea* n. sp. Fig. 10., *A. inca* Evans. Fig. 11., *A. spatulata* n. sp. Fig. 12., *A. lacerata* n. sp. Fig. 13., *A. spinipes* n. sp. Fig. 14., *D. deformis* n. sp. Fig. 15., *D. bispinulatus* n. sp.

Figs. 16-20. Base of abdomen of male *Dissomphalus,* dorsal view. Fig. 16., *D. deformis* n. sp. Fig. 17., *D. ulceratus* n. sp. Fig. 18., *D. puteolus* n. sp. Fig. 19., *D. microstictus* n. sp. Fig. 20., *D. infissus* n. sp.

Figs. 21-31. Mandibles of male *Apenesia* and *Dissomphalus.* Fig. 21., *A. lilloana* n. sp. Fig. 22., *A. simulata* n. sp. Fig. 23., *A. pygmaea* n. sp. Fig. 24., *A. laevicornis* n. sp. Fig. 25., *A. spatulata* n. sp. Fig. 26., *A. spinipes* n. sp. Fig. 27., *D. deformis* n. sp. Fig. 28., *D. ulceratus* n. sp. Fig. 29., *D. puteolus* n. sp. Fig. 30., *D. microstictus* n. sp. Fig. 31., *D. teren* n. sp.

BREVIORA

Museum of Comparative Zoology

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ECOLOGICAL OBSERVATIONS ON *ANOLIS OCCULTUS* WILLIAMS AND RIVERO (SAURIA, IGUANIDAE)

T. Preston Webster

ABSTRACT. Recent observations indicate that the structural niche of *Anolis occultus* on Puerto Rico is the peripheral foliage of the montane forests from which it has been recorded; probably best considered a canopy species, it descends to ground level only at the few localities where trail-edge vegetation merges with the tree crowns. Structurally, behaviorally, and in coloration it is very well adapted for a life on twigs and leaves. As expected from other studies of *Anolis* ecology, the spatial preferences of *occultus* show little overlap with those of the other species recorded from the same locality.

In 1963 the first specimen of the very distinctive species *Anolis occultus* was captured by day at Cerro La Punta in Puerto Rico's Cordillera Central. Subsequent collecting produced about 40 additional specimens from all areas of higher montane forest on the island. All but two of these specimens were collected by Richard Thomas at night along forest trails where the trail-edge vegetation merged more or less intimately with the foliage of the canopy. Thomas suggested (Williams, Rivero, and Thomas, 1965) that *occultus* is a canopy species with a preference for exposed areas of bare twigs and vines, although after further collecting he suggested that "their habitat requirements may not be as narrow as my first experience with the species indicated" (Thomas, personal communication, March, 1968). As Thomas observed only a single specimen during the day, the diurnal ecology of this elusive lizard remained a mystery.

Recently 15 additional specimens were obtained 13.6 kilometers south of Palmer, Puerto Rico, in the Sierra de Luquillo. The species was first sought at night; nine specimens were easily located the night of April 7th. Four slept on long, exposed twigs, two slept on twigs near leaves, and one slept across the upper surface of a broad, stiff leaf. Twigs selected for sleeping perches were a quarter inch in diameter or less. Thomas's observations were confirmed; *occultus* clings tightly to its perch while asleep, may squeak loudly when handled, and can grip the twig strongly with its prehensile tail. Sleeping specimens are a light grey and stand out clearly in the beam of a headlamp. The two remaining anoles, asleep in the same small clump of vegetation, one across a leaf, the other on a bare twig, were left for observation in the morning.

Both lizards were found asleep at 6:15 A.M. One became active at 6:30, moving sluggishly to a nearby perch that seemed to offer greater exposure to the sun. The second became active a half hour later, but neither moved far for at least an additional hour. While both were in view, a third specimen was discovered when it became backlighted; far more active, it seemed to drink from raindrops on two occasions and prowled with frequent long pauses over an area of largely bare and exposed twigs, eventually wandering upward and out of sight. The remaining two also disappeared in the vegetation, but with the appearance of new individuals or the reappearance of those previously seen a total of six were observed, at least one staying in sight at all times. Movements were slow, cautious, and generally along twigs of small diameter, although occasionally the anoles crossed leaves or used larger branches to ascend or descend through the vegetation; after seemingly great deliberation, quick and agile leaps from twig to twig and twig to leaf were undertaken. Movement for more than a few inches at a time was infrequent; during the intervening pauses the lizard generally lay flush with a twig or leaf. Much more rapid and extensive changes of perch occurred when the foliage was briefly disturbed by a gust of wind. At 10:15 the three specimens remaining in sight were captured without difficulty.

When the locality was revisited about noon, an *occultus* was soon located on a dead twig in a pile of cut branches. It showed the same alternation of pauses with slow movements over short distances observed earlier. After extensive wandering among the twigs it leaped to the upper surface of a fern frond, where it remained for perhaps a half hour; although this small brown lizard was difficult to distinguish on a substrate of bare twigs, on the frond it was always conspicuous, and the two pale orange spots at the base of the tail were displayed. Eventually, after a little maneuvering on its leaf, the lizard jumped to another tangle of dead twigs and disappeared.

That evening intensive searching yielded six additional specimens in an hour and a half; three were on living twigs near leaves, one was on a long dead twig, one was at the tip of a very long descending branch, and a juvenile was on a dead fern.

On Puerto Rico the genus *Anolis* is represented by 10 species. All share adaptations for an active, diurnal, arboreal life, are primarily insectivorous, and in many cases are of similar size. Rand (1964) used the concept of a structural niche, which for arboreal *Anolis* is a combination of perch height and diameter as determined by quantitative observation, to separate into three ecological groupings seven of the eight Puerto Rican *Anolis* recognized at the time. Temperature preference provided an additional niche dimension that permitted Rand to separate the species within each grouping. It is of interest to relate the structural niche of *occultus* to those of other Puerto Rican species, especially those recorded from the same locality.

Anolis occultus appears to be an inhabitant of the peripheral foliage. Branches and bushes along trails have characterized all the productive collecting localities discovered to date; these somewhat artificial conditions give the collector access to vegetation continuous with the more or less high canopy characteristic of Puerto Rico's montane forests. Thomas's (1965) hypothesis that *occultus* is normally an occupant of the canopy is probably statistically correct, as suitable conditions near the ground occur only infrequently. There is no indication, however, that areas of dead branches and climbing plants are preferred; the specimens observed in this study showed a preference for fairly dense vegetation by day and no well-defined selection of dead or living twigs for sleeping perches. The sleeping positions selected in thin foliage or on dead twigs are probably optimal for early morning sunning; one of the two specimens observed to awaken was asleep in moderately dense foliage, but moved early to a more exposed position where it remained motionless for a long time.

Rand (1964) has provided a detailed study of the structural niches for the three common Puerto Rican *Anolis* present at the La Mina area in the Sierra de Luquillo. Of the three species present at La Mina, *A. evermanni* uses almost exclusively perches of several inches or more diameter. *A. gundlachi,* which shows somewhat greater preference for shade than *evermanni,* perches lower but also on tree trunks and branches of large diameter. *A. krugi,* while primarily found on grasses and similar plants, occasionally perches low in bushes on branches of moderate diameter. Although *evermanni* and *krugi* were common, *gundlachi* uncommon, and *cristatellus* rare at the locality of the recent *occultus* collection, the only species showing any overlap of structural niche with *occultus* in early April was *evermanni.* Juvenile *evermanni* were occasionally seen on twigs and small branches, although in general they seem to prefer perches of large diameter. This overlap is probably over-emphasized by an examination of trail-margin conditions; although, as Rand noted, studies of *Anolis* ecology are biased by the restriction of accurate observation to the lowest level of the forest, the available evidence indicates that *evermanni* lives below the canopy, while *occultus* is largely a species of the canopy. If the observations of as many as six *occultus* in a small clump of vegetation can be considered indicative of the population density at this locality, *occultus* is much commoner than juvenile *evermanni*, only one of which was noticed. Thomas recorded *gundlachi*, *cristatellus*, *krugi*, and *evermanni* from localities where he took *occultus*.

Anolis occultus seems well-adapted structurally, in coloration, and behaviorally for a cryptic existence in the peripheral foliage of trees and bushes. Long and slender, with a downward tapering snout, resting specimens merge easily with the outline of a twig and cast little or no shadow; from the distance of only a few feet a human observer finds the blending of outline of lizard and twig very deceptive. Although its use has only been observed at night, a prehensile tail is presumably of some diurnal advantage to *occultus*, if only to hold it firmly flush with a perch. Thomas (1965) described the coloration of live *occultus* in detail. Specimens observed in the present study by day were grey or brown, the degree of patterning variable; although individuals crossed leaves on several occasions, and one lingered for a considerable length of time on a fern frond, the green phase recorded by Thomas was not observed. The orange spots at the base of the tail are conspicuous in some postures; they may be eye spots to ward off predation or possibly function in intraspecific communication. Motion is slow and continuous over only short distances. The tendency for *occultus* to be most active when the vegetation is in general motion suggests that the species seeks to remain inconspicuous at all times. The selection of exposed surfaces for sleeping may, by warming the lizard as early as possible on cool mornings, maximize the number of daylight hours during which *occultus* is alert and active.

ACKNOWLEDGMENTS

Field work was in part supported by National Science Foundation Grant GB6944 to Ernest E. Williams. Thanks are due to Dr. Williams, who sponsored this collection of Puerto Rican reptiles and expressed particular interest in the *occultus* problem; to

Mr. Richard Thomas, who supplied information on collecting in Puerto Rico; and to Dr. Williams and Mr. Thomas Schoener, who read and provided valuable criticism of this paper.

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BREVIORA

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LOUIS AGASSIZ'S NUMBERS FOR STEAMER *BLAKE* STATIONS OF 1877-78, 1878-79

Myvanwy M. Dick

ABSTRACT. Correct *Blake* station numbers corresponding to Roman numerals used by Louis Agassiz for specimens collected by the *Blake*, 1877-1878, 1878-1879.

Eschmeyer (1965) demonstrated that frequent errors in locality data for fishes taken during *Blake* expeditions, 1877–1879, have been included in several major published works on fishes and in the fish catalogue, U. S. National Museum. These errors were caused by interpreting as station numbers Roman numerals included with the specimens — numerals intended for other purposes. For example, Goode and Bean (1896: 296–297) reported *Callionymus himantophorus* from *Blake* Station XXX and used data for that station for the station list. "XXX," however, is a number applied to the specimen, apparently by L. Agassiz, the correct station number being 274. Eschmeyer's account of these errors and their perpetuation is excellent and correct, but as no catalogue relating Agassiz's Roman numeral designation to true *Blake* Station numbers was known to exist, the resulting specific published errors could be corrected only with difficulty and in many instances not at all.

In collating early papers and catalogues relating to the Fish Department of the Museum of Comparative Zoology, a special catalogue of deep sea fish from the *Blake* expedition was found. Judging by the handwriting, this was prepared by Louis Agassiz. This contains the Roman numerals, which had been incorrectly interpreted as *Blake* Station numbers, and corresponding *Blake* Stations and localities. Each number was apparently intended to apply to a specific fish. Occasionally, in the *Blake* catalogue of 1878–1879, the same number is given in pencil as "Duplicate," with a different *Blake* Station. Presumably this would indicate fish of the same species but a different locality. This presents the possibility of questionable localities for specimens having just the Agassiz numbers, such as "Agassiz V," which would allow seven localities under "duplicate Agassiz V."

In the Agassiz catalogue of the *Blake* expedition of 1877 1878 the Roman numeral is not always accompanied by a *Blake* Station number; however a locality is given, except in a very few instances where there are entries with "no locality."

Several specimens from the *Blake* collections were sent to Steindachner in Vienna for examination. These were assigned numbers from the Agassiz catalogue with their locality, but the *Blake* Station numbers were omitted. Hence material described by Dr. Steindachner would have the Agassiz number and correct locality but would not include a *Blake* Station number.

In general, however, Agassiz's holograph catalogue can be used to relate his Roman numeral designations to *Blake* Station numbers and hence to the correct data as published by Pierce and Patterson (1870), Agassiz (1881), and Smith (1889). Agassiz's catalogue is reproduced below.

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(Received 6 December 1968.)

CAT. DEEP SEA FISH BLAKE EXP. 1878-79

Present Number	*Dredge Number*	*Depth fms.*	*Localities*	*Number of Specimens*
I	276	94	off Barbados	1
II	278	69	off Barbados	1
III	230	464	off St. Vincent	1
IV	274	209	off Barbados	1
IV dup.	147	250	off St. Kitts	1
V	240	164	off Grenadines	1
V dup.	264	416	off Grenada	1
V dup.	153	303	off Montserrat	1
V dup.	222	422	off St. Lucia	1
V dup.	258	159	off Grenada	1
V dup.	260	291	off Grenada	1
V dup.	150	375	off Nevis	1
V dup.	185	333	off Dominica	1
VI	290	73	off Barbados	1
VII	148	208	off St. Kitts	1
VIII	262	92	off Grenada	1
VIII dup.	116	150	off Jamaica	1
VIII dup.	290	73	off Barbados	1
IX	281	288	off Barbados	1
IX dup.	274	209	off Barbados	6
IX dup.	275	218	off Barbados	1
IX dup.	148	208	off St. Kitts	1
X	290	78	off Barbados	1
X dup.	297	123	off Barbados	1
XI	210	191	off Martinique	1
XII	142	27	off Flannegans Passage	1
XIII	248	161	off Grenada	1
XIV	176	391	off Dominica	1
XIV dup.	227	573	off St. Vincent	1
XIV dup.	285	159	off Grenada	1
XIV dup.	236	1591	off Bequia	2
XV	148	208	off St. Kitts	1
XVI	281	288	off Barbados	1
XVII	275	218	off Barbados	1
XVIII	274	209	off Barbados	1
XVIII dup.	274	209	off Barbados	1
XIX	297	123	off Barbados	1
XX	142	27	Flannegans Passage	1
XXI	167	175	off Guadeloupe	1
XXII	147	250	off St. Kitts	1
XXIII	147	250	off St. Kitts	1
XXIV	191	108 to 250	off Dominica	1
XXV	293	82	off Barbados	1

Present Number	*Dredge Number*	*Depth fms.*	*Localities*	*Number of Specimens*
XXVI	220	116	off St. Lucia	1
XXVII	231	95	off St. Vincent	1
XXVIII	293	82	off Barbados	1
XXIX	293	82	off Barbados	1
XXX	274	209	off Barbados	1
XXX dup.	281	288	off Barbados	1
XXX dup.	274	209	off Barbados	7
XXX dup.	258	159	off Grenada	1
XXX dup.	291	200	off Barbados	3
XXXI	273	103	off Barbados	1
XXXII	261	340	off Grenada	1
XXXIII	132	115	off Santa Cruz	1
XXXIV	253	92	off Grenada	1
XXXV	136	508	off Santa Cruz	1
XXXV dup.	221	423	off St. Lucia	1
XXXV dup.	284	347	off Barbados	1
XXXVI	280	221	off Barbados	1
XXXVII	151	365	off Nevis	1
XXXVIII	212	317	off Martinique with parasite	1
XXXIX	121	2393	off Santa Cruz	1
XL	200	472	off Martinique	1
XLI	185	333	off Dominique	1
XLII	211	357	off Martinique	1
XLII dup.	222	422	off St. Lucia	3
XLII dup.	212	317	off Martinique	1
XLII dup.	151	365	off Nevis	3
XLII	288	399	off Barbados	1
XLII dup.	260	291	off Grenada	2
XLII dup.	221	423	off St. Lucia	1
XLII dup.	260	291	off Grenada	4
XLII dup.	150	375	off Nevis	3
XLII dup.	261	340	off Grenada	1
XLIII	266	461	off Grenada	1
XLIV	248	161	off Grenada	1
XLV	104	500	Old Bahama Channel	3
XLV dup.	104	500	Old Bahama Channel	10 ±
XLVI	271	458	off Bequia	1
XLVII	188	372	off Dominica	3
XLVIII	227	573	off St. Vincent	1
XLIX	221	423	off St. Lucia	1
XLIX dup.	221	423	off St. Lucia	1
XLIX dup.	190	524	off Dominica	2
L	227	573	off St. Vincent	1
LI	148	208	off St. Kitts	1

LII	275	218	off Barbados	1
LII dup.	275	218	off Barbados	2
LII dup.	147	250	off St. Kitts	1
LII dup.	281	288	off Barbados	1
LIII	295	180	off Barbados	2
LIII dup.	295	180	off Barbados	20
LIII dup.	281	288	off Barbados	14
LIII dup.	291	200	off Barbados	3
LIII dup.	274	209	off Barbados	4
LIII dup.	275	218	off Barbados	2
LIV	283	237	off Barbados	1
LV	262	92	off Grenada	1
LVI	231	95	off St. Vincent	1
LVII	132	115	off Santa Cruz	1
LVII dup.	132	115	off Santa Cruz	2
LVIII	129	314	off Santa Cruz	1
LIX	281	288	off Barbados	1
LX	297	123	off Barbados	1
LXI	249	262	off Grenada	1
LXII	274	209	off Barbados	1
LXIII	274	209	off Barbados	1
LXIII dup.	275	218	off Barbados	2
LXIII dup.	274	209	off Barbados	2
LXIII dup.	172	62 to 108	off Guadeloupe	1
LXIV	297	123	off Barbados	1
LXV	297	123	off Barbados	1
LXV dup.	297	123	off Barbados	2
LXVI	235	1507	off Bequia	1
LXVII	222	422	off St. Lucia	1
LXVII	222	422	off St. Lucia	1
LXVIII	160	393	off Guadeloupe	1
LXVIII dup.	137	625	off Santa Cruz	1
LXVIII dup.	151	365	off Nevis	1
LXIX	161	583	off Guadeloupe	1
LXX	163	769	off Guadeloupe	1
LXX dup.	163	769	off Guadeloupe	2
LXXI	163	769	off Guadeloupe	1
LXXII	230	464	off St. Vincent	1
LXXIII	200	472	off Martinique	1
LXXIV	295	180	off Barbados	1
LXXIV dup.	291	200	off Barbados	1
LXXV	281	288	off Barbados	1
LXXV dup.	281	288	off Barbados	1
LXXV dup.	260	291	off Grenada	1
LXXVI	265	576	off Grenada	1
LXXVI dup.	265	576	off Grenada	1
LXXVI dup.	288	399	off Barbados	1

Present Number	*Dredge Number*	*Depth fms.*	*Localities*	*Number of Specimens*
LXXVII	151	365	off Nevis	1
LXXVII dup.	151	365	off Nevis	1
LXXVII dup.	222	422	off St. Lucia	1
LXXVII dup.	260	291	off Grenada	1
LXXVII dup.	150	375	off Nevis	3
LXXVII dup.	135	450	off Santa Cruz	2
LXXVII dup.	185	333	off Dominica	1
LXXVIII	291	200	off Barbados	1
LXXVIII dup.	291	200	off Barbados	1
LXXIX	274	209	off Barbados	1
LXXIX dup.	274	209	off Barbados	1
LXXIX dup.	291	200	off Barbados	1
LXXIX dup.	193	169	off Martinique	1
LXXIX dup.	149	60 to 180	off St. Kitts	1
LXXIX dup.	146	245	off St. Kitts	1
LXXX	200	472	off Martinique	1
LXXX dup.	200	472	off Martinique	1
LXXX dup.	175	618	off Dominica	1
LXXX dup.	227	573	off St. Vincent	1
LXXX dup.	135	450	off Santa Cruz	1
LXXX dup.	163	769	off Guadeloupe	1
LXXX dup.	227	573	off St. Vincent	1
LXXXI	151	365	off Nevis	1
LXXXI dup.	151	365	off Nevis	1
LXXXII	205	334	off Martinique	1
LXXXII dup.	205	334	off Martinique	1
LXXXII dup.	130	451	off Santa Cruz	1
LXXXII dup.	186	333	off Dominica	3
LXXXII dup.	222	422	off St. Lucia	1
LXXXIII	154	164	off Grenada	1
LXXXIV	182	1131	off Dominica	1
LXXXV	151	365	off Nevis	1
LXXXVI	180	982	off Dominica	1
LXXXVI dup.	180	982	off Dominica	1
LXXXVII	196	1030	off Martinique	1
LXXXVIII	214	476	off Martinique	1
LXXXVIII dup.	200	472	off Martinique	1
LXXXVIII dup.	163	769	off Guadeloupe	1
LXXXIX	205	334	off Martinique	1
XC	258	159	off Grenada	1
XC dup.	283	237	off Barbados	1
XC dup.	275	218	off Barbados	3
XCI	180	982	off Dominica	1

XCII	265	576	off Grenada	1
XCII dup.	161	583	off Guadeloupe	1
XCII dup.	135	450	off Santa Cruz	1
XCII dup.	185	333	off Dominica	2
XCII dup.	200	472	off Martinique	1
XCII dup.	227	573	off St. Vincent	1
XCII dup.	130	451	off Santa Cruz	1
XCII dup.	195	501	off Martinique	1
XCII dup.	188	399	off Barbados	1
XCII dup.	239	338	off Grenadines	1
XCIII	260	291	off Grenada	1
XCIV	100	250-400	off Moro Castle, Cuba	1
XCV	185	333	off Dominica	1
XCVI	163	769	off Guadeloupe	1
XCVI dup.	162	734	off Guadeloupe	2
XCVI dup.	227	573	off St. Vincent	4
XCVII	274	209	off Barbados	2
XCVII dup.	274	209	off Barbados	31
XCVIII	227	573	off St. Vincent	1
XCVIII dup.	227	573	off St. Vincent	3
XCVIII dup.	143	298	off Montserrat	1
XCVIII dup.	257	553	off Grenada	1
XCIX	262	90	off Grenada	3
XCIX dup.	262	90	off Grenada	30
C	132	115	off Santa Cruz	1
CI	231	95	off St. Vincent	1
CII	142	27	Flannegans Passage	1
CIII	142	27	Flannegans Passage	1
CIV	295	180	off Barbados	1
CI dup.	291	200	off Barbados	2
CI dup.	297	123	off Barbados	1
CV	150	375	off Nevis	1
CVI	190	524	off Dominica	1
CVII	291	200	off Barbados	1
CVIII	148	208	off St. Kitts	1
CIX	188	372	off Dominica	1
CX	258	159	off Grenada	1
CXI	300	82	off Barbados	1
CXII	243	82	off Barbados	1
CXIII	151	365	off Nevis	1
CXIV	290	73	off Barbados	1
CXV	243	82	off Barbados	1
CXVI	276	94	off Barbados	1
CXVII	276	94	off Barbados	1
CXVIII	290	78	off Barbados	1
CXIX	243	82	off Barbados	1
CXX	253	92	off Grenada	1

Present Number	*Dredge Number*	*Depth fms.*	*Localities*	*Number of Specimens*
CXXI	128	180	off Santa Cruz	1
CXXII	142	27	Flannegans Passage	1
CXXIII	142	27	Flannegans Passage	1
CXXIV	142	27	Flannegans Passage	2
CXXV	271	458	off Bequia	1
CXXVI	278	69	off Barbados	1
CXXVII	243	82	off Barbados	1
CXXVIII	300	82	off Barbados	1
CXXIX	132	115	off Santa Cruz	1
CXXX	220	116	off St. Lucia	1
CXXXI	276	94	off Barbados	1
CXXXII	104	500	Old Bahama Channel	1
CXXXIII	241	163	off Cariacou	1
CXXXIV	293	82	off Barbados	1
CXXXV	104	500	Old Bahama Channel	1
CXXXV dup.	104	500	Old Bahama Channel	1
CXXXVI	104	500	Old Bahama Channel	1
CXXXVII	104	500	Old Bahama Channel	1
CXXXVI dup.	104	500	Old Bahama Channel	1
CXXXVIII	104	500	Old Bahama Channel	1
CXXXIX	109	1554	off Caya de Moa	1
CXL	111	1200	lat. 19°07′N, lon. 74°52′W	1
CXLI	150	375	off Nevis	1
CXLII	288	399	off Barbados	1
CXLIII	150	375	off Nevis	1
CXLIV	256	370	off Grenada	1
CXLV	284	347	off Barbados	1
CXLVI	283	237	off Barbados	1
CXLVII	205	surface	off Martinique	2
CXLVIII	201	565	off Martinique	2
CXLVIII dup.	201	565	off Martinique	3
CXLIX	212	317	off Martinique	2
CL	204	476	off Martinique	2
CLI	217	398	off St. Lucia	1
CLII	217	398	off St. Lucia	1
CLIII	222	422	off St. Lucia	1
CLIV	124	580	off Santa Cruz	1
CLV	207	826	off Martinique	1
CLVI	182	1131	off Dominique	1
CLVII	190	524	off Dominique	1
CLVIII	190	524	off Dominique	2
CLIX	185	333	off Dominique	1
CLIX dup.	185	333	off Dominique	1
CLIX dup.	188	372	off Dominique	4

CLX	188	372	off Dominique	1
CLXI	236	1591	off Bequia	1
CLXII	180	982	off Dominica	1
CLXIII	173	734	off Guadaloupe	2
CLXIV		769	off Guadaloupe	1

Blake Exp. 1877–78

CLXV	29	955	lat. 24°36′n, lon. 84°05′w	1
CLXVI	29	955	lat. 24°36′n, lon. 84°05′w	1
CLXVII	12	36	lat. 24°46′n, lon. 83°16′w	1
CLXVIII	36	84	lat. 23°13′n, lon. 89°10′w	1
CLXIX	12	36	lat. 24°46′n, lon. 83°16′w	1
CLXX	29	955	lat. 24°36′n, lon. 84°05′w	1
CLXXI	11	37	lat. 24°43′n, lon. 83°25′w	5
CLXXII	29	955	lat. 24°36′n, lon. 84°05′w	2
CLXXIII	29	955	lat. 24°36′n, lon. 84°05′w	1
CLXXIV	31	1850	lat. 24°33′n, lon. 84°23′w	1
CLXXV	186	88	off Alligator Keys	1
CLXXVI	37	35	Alacran Shoals, Yucatan	9
CLXXVII	37	35	Alacran Shoals, Yucatan	1
CLXXIX	47	321	lat. 28°42′n lon. 88°40′w	4
CLXXX	6	137	lat. 24°17.5′ n lon. 82°09′w	1
CLXXXI	47	321	lat. 28°42′n lon. 88°40′w	1
CLXXXII		135	off Key West	1
CLXXXIII		270	Santaren Channel	1
CLXXXIV		128 to 240	Two miles off Havana	1
CLXXXV	45	101	lat. 25°33′n lon. 84°21′w	1
CLXXXVI	32	95	lat. 24°52′n lon. 88°05′w	1
CLXXXVII		177	off Havana	1
CLXXXVIII		40	off Cary's Fort Reef	1
CLXXXIX	29	955	lat. 44°36′n lon. 84°05′w	5
CXC	46	888	lat. 25°43′n lon. 84°47′30″	1
CXCI	44	539	lat. 25°33′n lon. 84°35′w	1
CXCII	36	84	lat. 23°13′n long. 84°16′w	25
CXCIII	36	84	lat. 23°13′n long. 84°16′w	25
CXCIV		175	off Havana	1
CXCV		40	off West Reef	1
CXCVI		98	"off Panfii Reef"	1
CXCVII		42	"W. of Tortugas"	1
CXCVIII		117	Illegible	1
CXCIX		37	W. of Tortugas	1
CC		306	W. of Tortugas	1
CCI		68	W. of Tortugas	1

Present Number	*Dredge Number*	*Depth fms.*	*Localities*	*Number of Specimens*
CCII		37	W. of Tortugas	1
CCIII		118	off Alligator Reef	1
CCIV	31	1920	lat. 24°33′ lon. 84°23′	1
CCV	43	339	lat. 24°08′ lon. 82°51′	1
CCVI	35	804	lat. 23°54′-46″ lon. 88°58′	1
CCVII	37	35	4 miles w. of whale rock w. of Alacran Reefs	1
CCVIII	29	955	lat. 24°36′ lon. 84°05′	1
CCIX	11	37	lat. 24°43′ lon. 83°25′	1
CCX		45	off French Reef	1
CCXI		35	off Cargofort Reef	1
CCXII		320	off Cargofort Reef	1
CCXIII		413	off Cape San Antonio	1
CCXIV		96	loc?	1
CCXV		35	W. of Tortugas	1
CCXVI		119	lat. 26°31′ lon. 85°03′	1
CCXVII	13	742	3½ N. W. off Havana	1
CCXVIII	47	321	lat. 28°42′ lon. 88°40′	1
CCXIX	30	968	lat 24°33′ lon. 84°05′	6
CCXX	29	955	lat. 24°36′ lon. 84°05′	1
CCXXI	29	955	lat. 24°36′ lon. 84°05′	1
CCXXII	47	321	lat. 28°42′ lon. 88°40′	1
CCXXIII	36	84	lat. 23°13′ lon. 89°10′	1
CCXXIV	11	37	lat. 24°43′ lon. 83°25′	1
CCXXV	47	321	lat. 28°42′ lon. 88°40′	1
CCXXVI	12	36	lat. 24°34′ lon. 83°16′	1
CCXXVII	12	36	lat. 24°34′ lon. 83°16′	2
CCXXVIII	12	36	lat. 24°34′ lon. 83°16′	1
CCXXIX	14	850	lat. 23°18′ lon. 82°21′	1
CCXXX	36	84	lat. 23°13′ lon. 89°10′	2
CCXXXI	29	955	lat. 24°36′ lon. 84°05′	1
CCXXXII	37	35	Alacran Shoals, Yucatan	1
CCXXIII	29	955	lat. 24°36′ lon. 84°05′	1
CCXXXIV	10	37	lat. 24°44′ lon. 83°00′	5
CCXXXV	3	243 to 450	off Havana	1
CCXXXVI	36	84	lat. 23°13′ lon. 89°10′	1
CCXXXVII	12	36	lat. 24°34′ lon. 83°16′	1
CCXXXIII	29	955	lat. 24°36′ lon. 84°05′	1
CCXXXIX	10	37	lat. 24°44′ lon. 83°00′	5
CCXL	29	955	lat. 24°36′ lon. 84°05′	3
CCXLI	36	84	lat. 23°13′ lon. 89°10′	1
CCXLII	36	84	lat. 23°13′ lon. 89°10′	1
CCXLIII	11	37	lat. 24°43′ lon. 83°25′	2
CCXLIV	36	84	lat. 23°13′ lon. 89°10′	1

CCXLV	3	450 to 243	off Havana	1
CCXLVI	29	955	lat. 24°36′ lon. 84°05′	1
CCXLVII	12	36	lat. 24°34′ lon. 83°16′	9
CCXLVIII	36	84	lat. 23°13′ lon. 89°10′	1
CCXLIX	11	37	lat. 24°43′ lon. 83°25′	1
CCL	11	37	lat. 24°43′ lon. 83°25′	1
CCLI	37	35	Alacran Shoals, Yucatan	5
CCLII	37	35	Alacran Shoals, Yucatan	2
CCLIII	11	37	lat. 24°43′ lon. 83°25′	1
CCLIV	37	35	Alacran Shoals, Yucatan	1
CCLV	36	84	lat. 23°13′ lon. 89°10′	9
CCLVI	47	321	lat. 28°42′ lon. 88°40′	1
CCLVII	36	84	lat. 23°13′ lon. 89°10′	1
CCLVIII	11	37	lat. 24°43′ lon. 83°25′	1
CCLIX	36	84	lat. 23°13′ lon. 89°10′	2
CCLX	36	84	lat. 23°13′ lon. 89°10′	3
CCLXI	36	84	lat. 23°13′ lon. 89°10′	1
CCLXII	14		lat. 23°18′ lon. 82°21′	2
CCLXIII	11	37	lat. 24°43′ lon. 83°25′	1
CCLXIV	36	84	lat. 23°13′ lon. 89°10′	2
CCLXV	29	955	lat. 24°36′ lon. 84°05′	1
CCLXVI	29	955	lat. 24°36′ lon. 84°05′	1
CCLXVII	29	955	lat. 24°36′ lon. 84°05′	1
CCLXVIII	29	955	lat. 24°36′ lon. 84°05′	1
CCLXIX			no loc.	1
CCLXX	31	1850	lat. 24°33′ lon. 84°23′	1
CCLXXI			no loc.	1
CCLXXII			no loc.	1
CCLXXIII			no loc.	1
CCLXXIV				
CCLXXV				
CCLXXVI				

BREVIORA

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THE CRANIAL ANATOMY OF THE PERMIAN AMPHIBIAN PANTYLUS

Alfred Sherwood Romer

ABSTRACT. A detailed description is given of the skull structure of the early Permian tetrapod *Pantylus*, using both whole specimens and a skull serial sectioned and reconstructed in wax plates. This study definitely proves that *Pantylus*, often thought to be a reptile, is a microsaurian amphibian, and furnishes further proof that microsaurs cannot be considered reptilian ancestors.

INTRODUCTION

Pantylus, known in the past mainly from a heavily-built, heart-shaped skull carrying a powerful dentition, is an early Permian tetrapod from the Texas red beds whose systematic position has been open to considerable doubt. Cope, who obtained the first materials of this animal, originally considered it to be a batrachian (1881), but later classed it among the Reptilia (1892, 1896), as did a long series of later workers, including Case (1911, 1912, 1915), Huene (1913), Broom (1913), Williston (1916a, 1916b, 1925), and Wilson (1951). Two decades or so ago, however, in considering the nature of the Paleozoic microsaurs, it became obvious to me that it was, as far as known, basically similar in structure to members of the microsaurian family Gymnarthridae, and hence should be placed in the order Microsauria (Romer, 1950). My conclusion has, I think, been generally accepted by recent workers (cf., for example, Dechaseaux, 1955; Gregory, Peabody, and Price, 1956; Tatarinov, 1964). However, it seems important to add as much as possible to our present inadequate knowledge of its structure in order to attempt to fix its systematic position.

But the importance of such study goes further. Most microsaurs are very poorly known anatomically. If (as I hope to demonstrate) *Pantylus* is a true microsaur, a study of its cranial structure may prove of value in fixing the phylogenetic position of that group as a whole. Microsaurs have often been claimed to be related to the captorhinomorph cotylosaurs and to be possibly ancestral to the reptiles, or to at least part of that class (cf., for example, Williston, 1908; Westoll, 1942a, 1942b; Olson, 1947; Huene, 1948; Vaughn, 1960, 1962; Brough and Brough, 1967).

Another possibility that has been suggested is that the microsaurs may be ancestral to modern amphibians, particularly the urodeles (Romer, 1950, etc.), although this suggestion is far from generally accepted (cf., for example, Parsons and Williams, 1963). The pedigree of the microsaurs is in doubt. I have, since 1933, somewhat arbitrarily combined the microsaurs with the aistopods and nectrideans in the Lepospondyli, in an expanded use of that term. But the interrelationships of the three groups are far from certain. And while the derivation of the Labyrinthodontia from the rhipidistian crossopterygians seems clear, there has been little evidence to tie any of the three lepospondyl orders into this evolutionary series.

Previous studies; materials. Cope's original materials consisted of two imperfect skulls; from these he was able to describe much of the roof pattern and part of the palate. Later studies of these specimens by Case (1911) and Huene (1913) added little; however, here, as frequently, Broom (1913) was able to give greater depth to analysis of the specimens available to him. Mehl, in 1912, described a fragmentary skull collected for the University of Chicago in 1908 by Paul C. Miller, but added little of interest. The latter collector, in expeditions of 1913 to 1916, obtained a series of specimens, including several skulls and some postcranial materials, from the Mitchell Creek locality; Williston (1916a) described much of this material, giving an adequate account of the skull roof (except the temporal region), some further data on the lower jaw and palate, and a few scattered details regarding the braincase and postcranial skeleton.

No further materials were found until, in 1939, Mr. A. Witte of Henrietta, in charge of a WPA group under the auspices of the Texas Bureau of Economic Geology, came upon a "nest" of specimens near Windthorst, Archer County, Texas; this suite, now entered as No. 40,001 (1-8) in the Texas Memorial Museum, Austin, includes several skulls and considerable postcranial materials. In Mr. Witte's possession is a further small skull from this locality. Post-war trips to Texas from the Harvard Museum of Comparative Zoology (abbreviated as MCZ below) yielded further specimens — two skulls from the Archer City bonebed, a partial skull from Montague County, and two incomplete crania from southern Archer County.

Study of this newer material, together with re-examination of older Chicago specimens, now makes it possible to give a nearly complete account of the skeletal anatomy of *Pantylus*. The postcranial skeleton is now being studied by Dr. Robert L. Carroll of McGill University. Both Dr. Carroll and I are much indebted to Drs. E. C. Olson and R. Zangerl of Chicago, Drs. John A. Wilson and Wann Langston, Jr., of Austin, and Mr. Witte for the loan of materials. Also, I gratefully acknowledge financial aid for the preparation of material from National Science Foundation Grant GB 500.

For cranial anatomy, some of the older Chicago and American Museum specimens were restudied. Valuable were, as noted, Harvard skulls MCZ 2040 and 3302. The latter is incomplete and broken, but the parts preserved show excellent detail, including some braincase structure. MCZ 2040 is complete, except that the roof is broken off posteriorly on one side. It shows surface structures perfectly, and the break is valuable in that it reveals much of the braincase. Several of the Texas Memorial Museum specimens show aspects of skull anatomy. Most important was No. 40,001 (1), which, with the consent of Prof. John A. Wilson, was serially sectioned and reconstructed, enlarged × 6, in wax plates. The surfaces of each section were preserved by the cellulose "peel" method, and at each grinding two peels were taken. Although this sectioned specimen was extremely valuable in revealing internal structure, and is the main "document" on which Figures 3 - 12 are based, it proved disappointing in two regards. (1) Subsequent to burial, it was invaded by calcite, obviously crystallized out of ground water. This crystallization caused multiple small fractures in the skull, which have rendered details of sutures in the dermal bones difficult to determine. (2) Before burial, the skull received one or more violent blows, which, apart from shattering a fraction of the roof (a matter of small moment), jarred loose the vomers, the epipterygoids, the basisphenoid plus parasphenoid, and most of the otico-occipital elements of the braincase. For the most part, these elements are still present in the specimen, lying, disarticulated and more or less battered, between the lower jaws. Their restoration and proper positioning in the braincase and palate presented obvious difficulties. Fortunately, most needed data on these disarticulated or demolished elements are available in MCZ 2040 and 3302.

Stratigraphy and systematics. Cope's original specimens were collected by Jacob Boll in 1880 from the "Big Wichita." In his first expedition, two years earlier, Boll had explored no higher in the Texas beds than exposures in the Belle Plains Formation of the

Wichita Group, between the site of the modern Diversion Dam on the Big Wichita River and the exposures along the Little Wichita south of Dundee. In 1880, however, he went somewhat further west, and there is reason to suppose that he collected at the Mitchell Creek locality from which Paul C. Miller later collected many valuable amphibian specimens for S. W. Williston (Romer, 1928, 1935). This locality lies high in the Clyde Formation, very generally regarded as the uppermost formation of the Wichita Group except for the overlying Leuders limestones. Miller's 1908 specimen, described by Mehl, is entered merely as from the "Big Wichita" but is probably from Mitchell Creek. His later materials, described by Williston in 1916, are all definitely from Mitchell Creek.

All the early described specimens, thus, are probably from a single locality and horizon near the summit of the Wichita Group. The newer materials extend the range stratigraphically and topographically. With two exceptions, all are from the Putnam Formation, considerably lower in the Wichita Group (and in early days thought by many to be part of the Cisco Group of the Carboniferous). The Texas Museum specimens, and the individual later collected by Mr. Witte, were found in an exposure in Section 55, Block 3, of the Clark and Plumb Subdivision, about 4 miles north of Windthorst, Archer County; the horizon is about the middle of the Putnam Formation. One Harvard specimen, MCZ 2041, is from the J. J. Prather Survey, about 5 miles northwest of Stoneburg, Montague County; this is at about the same horizon as that of the Texas Museum specimens. Harvard skulls MCZ 2040 and 3302 are from a bonebed about a mile southwest of Archer City, Archer County, which is close to the summit of the Putnam Formation. Two final specimens, MCZ 1913 and 3610, are a poorly preserved skull and a snout fragment from Section 1834, Texas Emigration and Land Co., north of the West Fork of the Trinity River in south-central Archer County and just below the presumed boundary between the Moran Formation and the overlying Putnam. It now appears, hence, that *Pantylus* was in existence for at least most of Wichita time.

Cope's original specimens were given the name *Pantylus cordatus;* no other species properly pertaining to the genus has been described. Cope in 1896 described as *Pantylus coïcodus* a fragmentary specimen, mainly a tooth row, from Coffee Creek in the Arroyo Formation of the Clear Fork Group. However, these teeth are bulbous, pointed structures, quite unlike those of other *Pantylus* specimens. As various later writers have noted, they do not appear to belong to *Pantylus* (Case, 1911; Gregory *et al.,* 1956), and the specimen is perhaps a caseid. A jaw fragment from Coffee Creek to which Cope gave the manuscript name *Pantylus tryptichus* is probably a captorhinid (Cummins, 1908; Case, 1911; Gregory *et al.*, 1956). Williston in 1913 gave the name *Ostodolepis brevispinatus* to a series of small vertebrae from Coffee Creek. In 1916 he noted the similarity of these vertebrae to those of *Pantylus*. *"Ostodolepis,"* as described by Case (1929), is a gymnarthrid microsaur of a different nature, but as noted by Carroll and Baird (1968), there is no guarantee that Case's specimen is related to the type.

It is possible that the stratigraphically lower Putnam and Moran materials are specifically distinct from the earlier described specimens from the Clyde. There is some variation in skull size, in general amounting to about 20 per cent, most skulls ranging in measured or estimated length from 72 to 90 mm; but this variation may be related to age or sex. The Witte specimen has an estimated length of about 36 mm, and one Chicago specimen from Mitchell Creek is but 39 mm long; but these are surely young individuals, presumably cospecific with the larger individuals found with them. There are dental differences, in the description and figures of earlier writers, regarding the number of teeth in the marginal rows, noted later, and the pattern of toothplate teeth. But one may strongly suspect that the patterns figured are in some cases diagrammatic and not entirely trustworthy. Quite surely age (and sex?) factors enter into variations in toothplate dentition. There may be individual differences, as well. For example, the skull sectioned by me has a large central tooth in both upper and lower toothplates, but Williston mentions a specimen in which such a tooth was present above but not below, and figures (how accurate I do not know) of other specimens show no such enlarged tooth in either upper or lower dentition.

DESCRIPTION

Skull roof (Figs. 1, 2, 7, 12). The skull of *Pantylus* is very massively built, and very broad and low — its width, which, from a rounded snout, spreads out greatly in the cheek region, is nearly as great as the length. There is no otic notch. The cheek in the jugal region extends downward so as to cover externally a considerable area of the lower jaw. Skull height, even allowing for the depth of the overhanging cheek region, is little more than a third of the length. The broad roof is nearly flat, although bending sharply downward at the margins of the "table," and there is a somewhat overhanging snout. The roof bears, as in most early or primitive amphibians, patterns of ridges and intervening valleys radiating from the ossification centers of the dermal elements. There is no evidence of grooving for lateral line canals. The small skull in Mr. Witte's collection shows nearly straight sutures between roofing

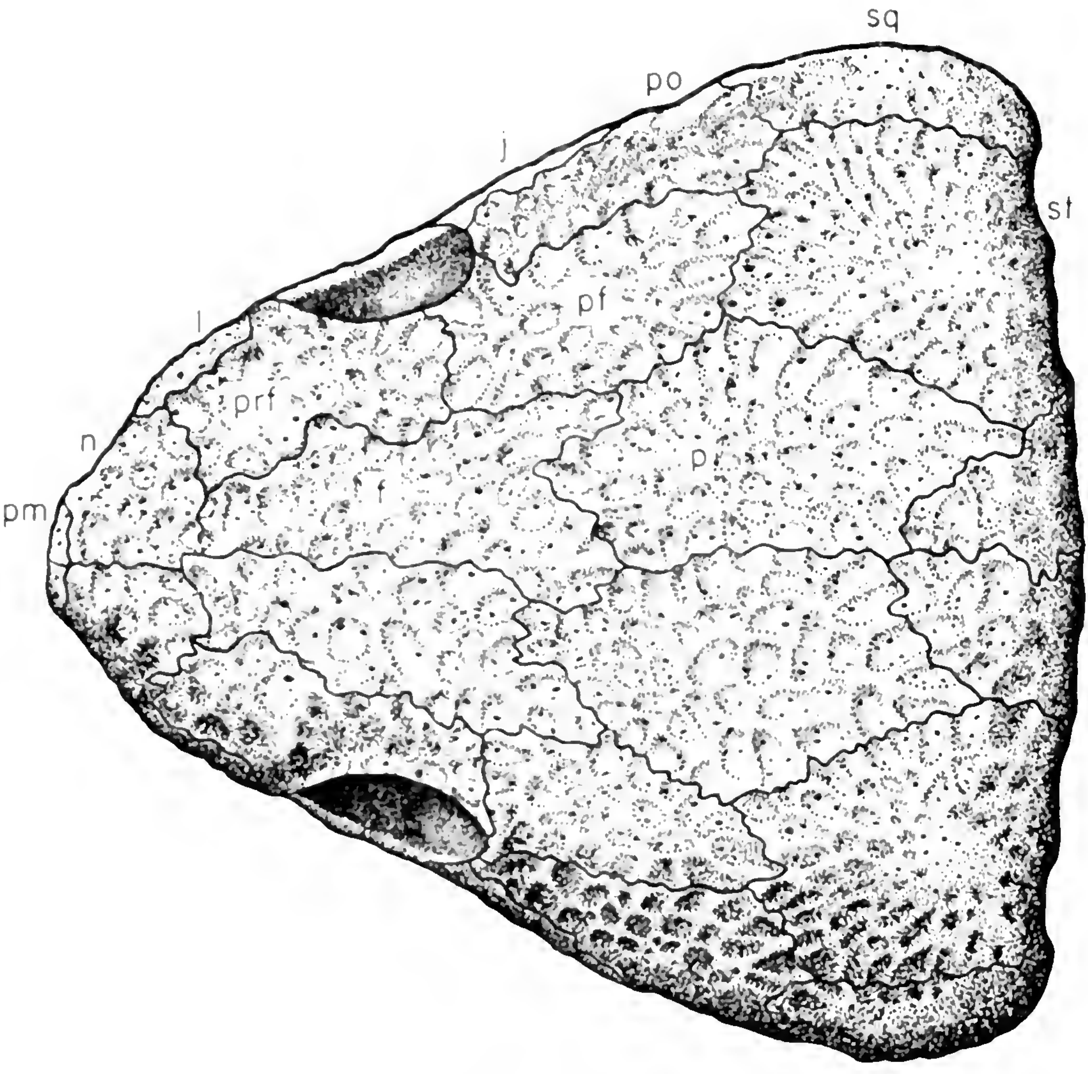

Fig. 1. Dorsal surface of skull, based on MCZ 2040; right posterior area restored, × 1½. Abbreviations for this and following figures: *a*, angular; *ar*, articular; *asp*, anterior splenial; *ba*, basal articulation of braincase with palatal structures; *bo*, basioccipital; *bs*, basisphenoid; *c*, coronoid; *ch*, choana, *d*, dentary; *e*, epipterygoid; *en*, external naris; *eo*, exoccipital; *f*, frontal; *fo*, fenestra ovalis; *fv*, foramen for transverse vein in pituitary region; *j*, jugal; *l*, lacrimal; *m*, maxilla; *n*, nasal; *op*, opisthotic; *p*, parietal; *pal*, palatine; *par*, prearticular; *pf*, postfrontal; *pm*, premaxilla; *po*, postorbital; *pp*, postparietal; *pr*, prootic; *prf*, prefrontal; *ps*, parasphenoid; *psp*, posterior splenial; *pt*, pterygoid; *q*, quadrate; *qj*, quadratojugal; *sa*, surangular; *se*, sphenethmoid; *sm*, septomaxilla; *soc*, supraoccipital; *sq*, squamosal; *st*, supratemporal; *v*, vomer; *I*, *II*, *V*, *X*, foramina for cranial nerves.

elements. With growth, however, the superficial portions of the roofing bones tend to interosculate, producing, as generally in Paleozoic amphibians, a series of zig-zag sutures. For the most part, the pattern is a bilaterally symmetrical one, although (as generally) four-square meetings of bones are not to be found. However, in the skull figured, the right frontal has invaded and taken over an area properly belonging to the right parietal.

The premaxilla is thick externo-internally, but short; it covers mainly the "overhang" anteriorly leading down to the tooth row between the external nares. It extends backward laterally below the naris to include the region of the base of the lateral premaxillary teeth. The nasals are likewise short, but broad, extending down laterally to the upper border of the nares. Frontals and parietals are long. There is no parietal foramen.

The external naris, facing laterally, is large and subcircular in outline. The premaxilla forms most of its anterior border, the maxilla the lower margin, the nasal the upper boundary, while the lacrimal extends broadly forward to a point close to the posterior margin. However, the lacrimal and, to a lesser extent, the maxilla and nasal are excluded from the narial margin by a highly-developed septomaxilla. This forms a narrow external rim along the posterior half of the narial opening and then turns inward to form a posterior wall and partial floor and medial wall to the nasal passage inside the narial opening. Evidently the air passage turned sharply upward inside the external narial opening to reach a dorsally placed nasal capsule. The anterior opening of the lacrimal duct pierces the septomaxilla just internal to the narial opening.

The lacrimal is well developed, extending from the orbit to the narial region; ventrally it is overlapped to some degree by the maxilla, but dorsally it extends high up on the side of the face, and posteriorly it extends, in a slender process, well back to a point below the orbit. Sections (Fig. 3) show that the lacrimal is essentially a cylindrical mass of bone surrounding the lacrimal duct and is, so to speak, cradled below by the maxilla. The thickness of the lacrimal bone produces a swelling of the generally smooth internal surface of the dermal roof anterior to the orbit; this swelling is continuous with a thickened anterior margin of the orbit which extends upward and backward along the prefrontal. The posterior opening of the lacrimal duct lies just inside the orbital margin.

The orbit, facing essentially laterally, is a large and somewhat oval opening, its highest point being considerably posterior to the lowest point in its ventral margin. The prefrontal is well developed, occupying a large portion of the extended dorsal and anterodorsal margins of the orbit; dorsally it extends forward between frontal and lacrimal to reach the nasal. The postfrontal, abutting posteriorly on the prefrontal, is large and extends far backward lateral to the frontal and parietal; it has, however, only a very short posterodorsal boundary on the rim of the orbit. The postorbital is likewise highly developed and elongate, the postfrontal and postorbital between them occupying much of the area which in labyrinthodonts is occupied by the "temporal" elements. The arrangement along the orbital margin is of interest. The postfrontal (as in *Tuditanus*) pushes downward posteriorly to take over a portion of the orbital margin which should properly be occupied by the postorbital; the latter bone, in turn, extends downward along the orbital margin to encroach upon the area properly pertaining to the jugal. A thickened ridge runs downward and forward inside the posterior orbital margin along the postorbital and jugal.

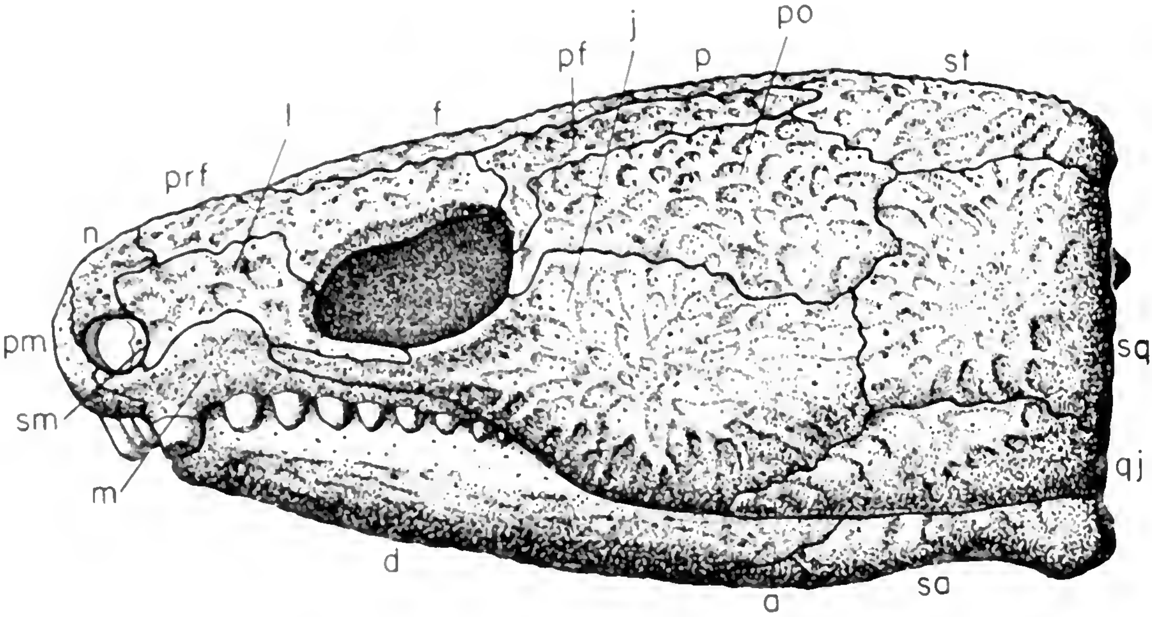

Fig. 2. Laterial view of skull and jaw, based on MCZ 2040, × 1½.

The jugal is a very large bone. It borders the posterior portion of the lower orbital margin, and sends a narrow extension far forward between lacrimal above and maxilla below. Back of the orbit it occupies a broad expanse of cheek, and forms most of a prominent flange extending downward, external to the posterior end of the tooth row and concealing the upper part of the lower jaw posteriorly.

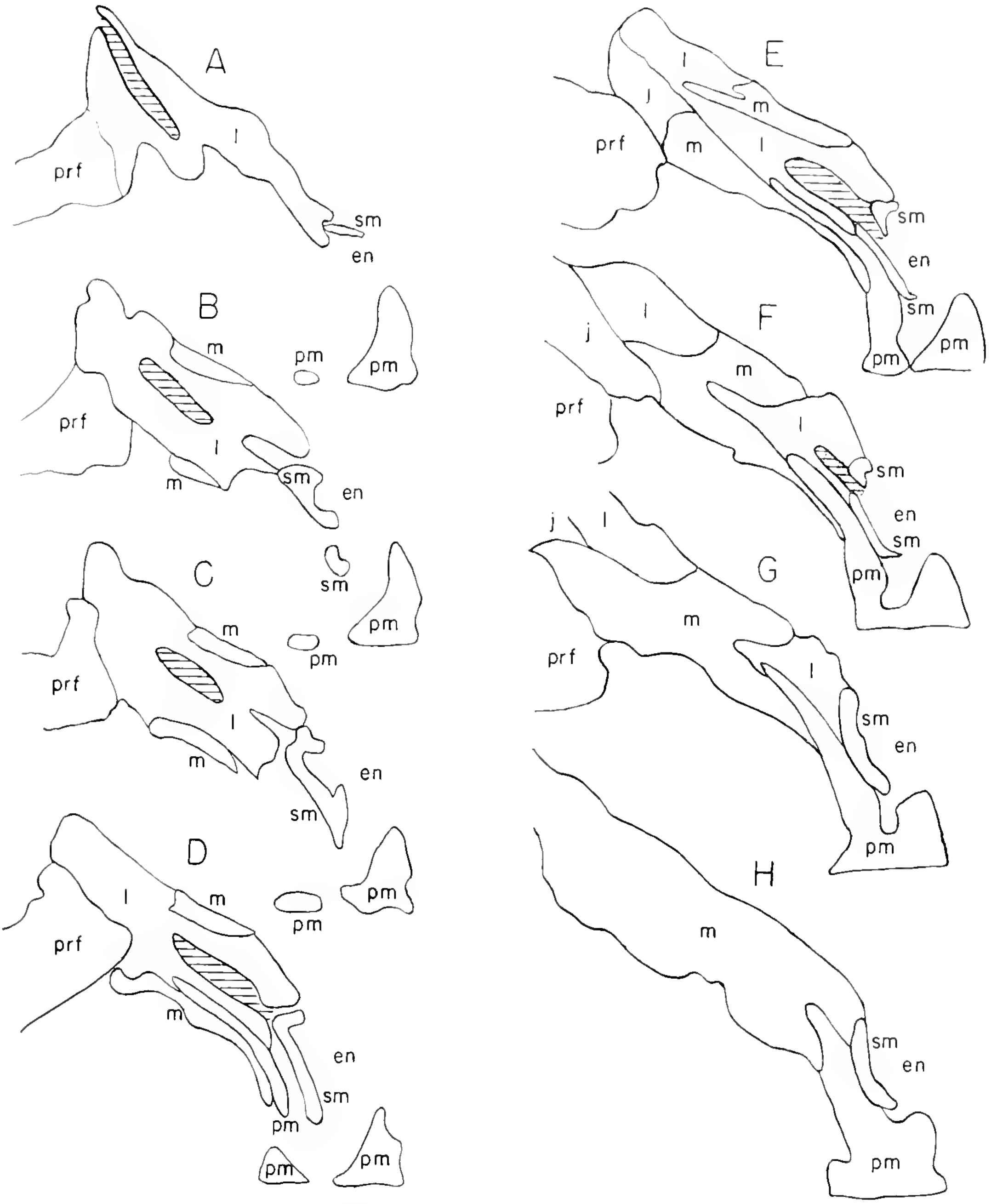

Fig. 3. A series of sections, in a horizontal plane, of the region anterior to the left orbit, in dorsoventral order, to show the relations of the lacrimal duct to the surrounding bones. From the sectioned skull, × 3. The lacrimal duct is hatched. The duct is seen leaving the orbit in section A; by E it enters the narial area through a foramen in the septomaxilla, which forms posterior and medial walls to the naris. From B downward, the maxilla is seen to bound the lacrimal medially as well as laterally.

The maxilla is stout mediolaterally, to contain the roots of the marginal teeth, but has only a limited facial exposure, except anteriorly above the large "canine." It is partly excluded from the naris by the septomaxilla, rimming it only for a short distance between premaxilla and lacrimal. Posteriorly, at the end of the lateral tooth row, the maxilla is covered externally by the jugal.

The posterior rim of the skull roof is formed by the paired postparietals, "supratemporals," squamosals, and quadratojugals. This series, as noted below, extends broadly on to the occipital surface. The postparietals are of modest size and are somewhat triangular in shape, in dorsal view, narrowing anteriorly. The large bone that may be provisionally termed the "supratemporal" is bounded by the postparietal and parietal medially, the squamosal and postorbital laterally, thus occupying essentially the position of the tabular and supratemporal of labyrinthodonts; it is in contact anteriorly with the postfrontal. The squamosal is likewise of considerable size in external exposure. The quadratojugal extends well forward along the lower margin of the cheek flange formed more anteriorly by the jugal; externally, it is narrow dorsoventrally, but the sectioned skull indicates that it underlaps the squamosal to a considerable degree internally. As noted below, it turns inward posteriorly to take part in the jaw joint.

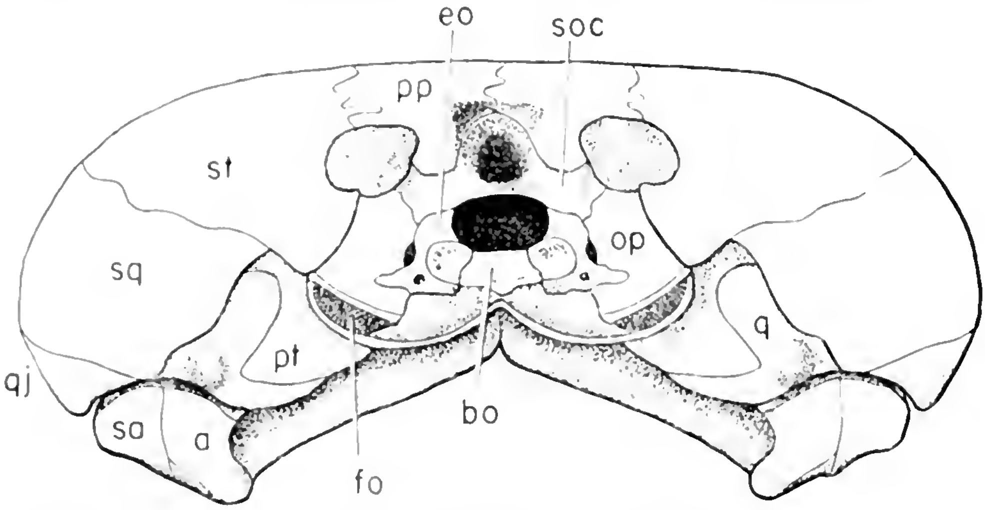

Fig. 4. Posterior view of skull, based mainly on MCZ 2040, × 1½.

Palate (Figs. 4, 5; 8-11 in part). Part of the palate could be made out in earlier described specimens. In the sectioned specimen, nearly the entire palatal structure can be accurately determined. The epipterygoids and vomers were disarticulated postmortem; however, these structures were found preserved between the lower jaws and could be readily restored to position.

The pterygoids are always long and highly developed in primitive tetrapods; here, the development is exceptional, for they extend almost the entire length of the skull. Anterior to the area of the basal articulation there is a narrow interpterygoid vacuity; this, however, extends forward little more than half the distance from basal articulation to naris. Anterior to this point, the two pterygoids meet in a median suture; this suture is of some thickness between the anterior halves of the palatines, but thins between the nares. Anterior to the region of the basal articulation, the pterygoids, as seen in ventral view, appear as a pair of rounded ridges, which bear two or three irregular rows of small teeth and are separated by a deep groove from the palatines lateral to them. Anteriorly, these ridges gradually narrow but continue to bear teeth to a point between the vomers, rather forward of the level of the posterior margins of the nares.

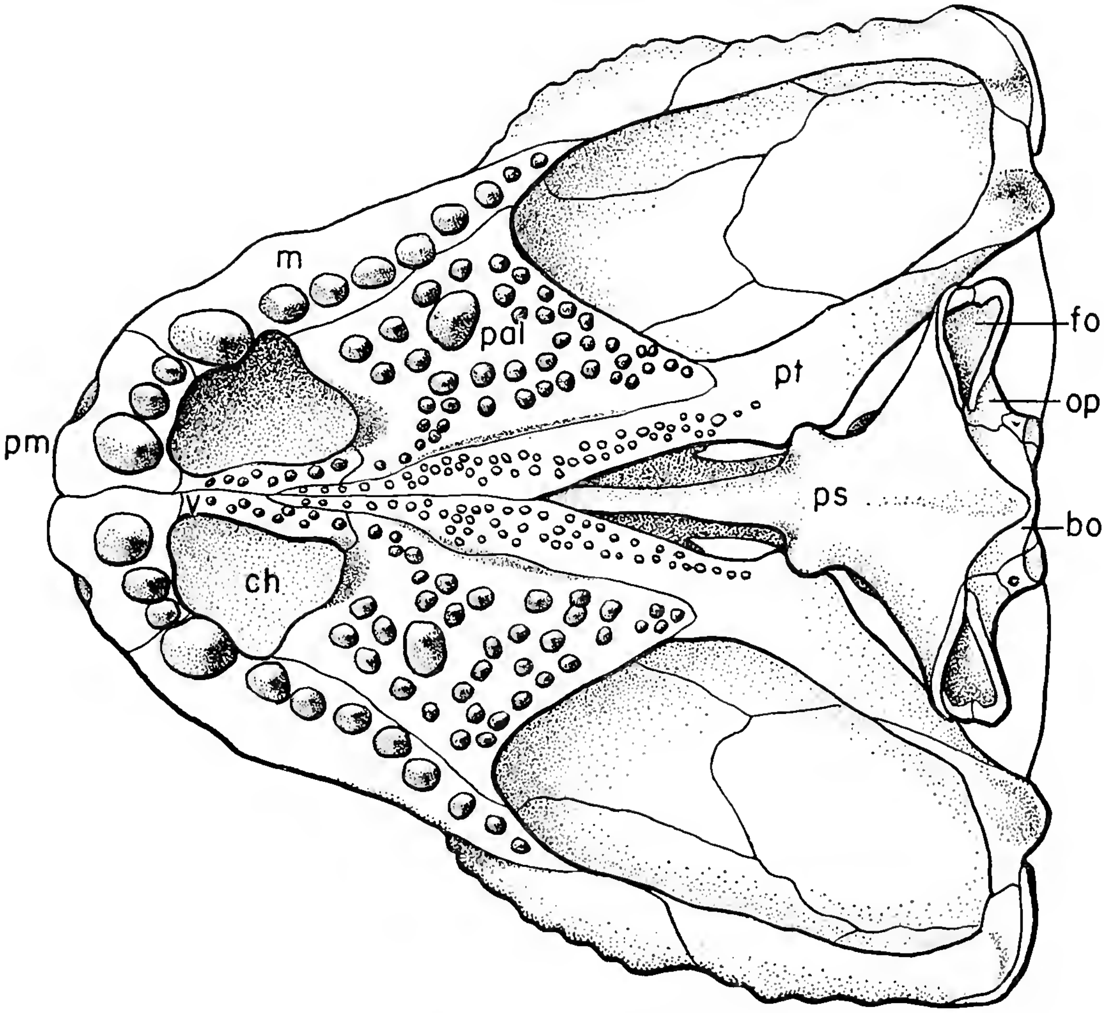

Fig. 5. Palatal view of skull, based on the sectioned specimen, × 1½.

The tooth-bearing surface of this most anterior region was broken off, together with the vomers, in the sectioned skull; but as preserved, the specimen shows a further forward continuation of the pterygoids dorsally as a pair of narrow but obviously stout little rods which reach nearly to the level of the anterior margins of the nares. For most of the broad palate, the pterygoids are covered ventrally, lateral to their median ridges, by the palatines; in dorsal view, however, the pterygoids are seen to extend laterally above (and to strengthen) the palatines, to gain contact laterally with the jugals. I have found no sutural evidence for the presence of an ectopterygoid, although such a bone may have persisted in an area internal to the posterior rim of the orbit.

The bony choanal openings are very large. They are separated from one another only by the narrow vomers, with, above them, the anterior tips of the pterygoids. Anteriorly and laterally they reach close to the bases of the premaxillary and anterior maxillary teeth, and are bounded posteriorly by the curved anterior margins of the palatines. Only the posterior parts of these openings, however, are truly choanal, for (as shown by the sectioned specimen) the large anterior teeth of the lower jaw extended upward into the anterior part of these openings when the jaws were closed.

The vomers were displaced in the sectioned skull, but other specimens show them in proper position. They are narrow tooth-bearing elements bounding the choanae medially. They are appressed medially to the slender anterior ends of the pterygoids, except that anteriorly the two vomers are in contact ventrally below the tips of the pterygoids. Anteriorly, the vomers articulate with the premaxillae; this articulation, however, is well above the level of the rim of the upper jaw; stout paired processes of the premaxillae rise dorsoposteriorly to make this contact (Figs. 8-11).

The palatines, in correlation with the powerful dentition they bear, are greatly expanded as essentially quadrilateral plates. Medially the palatine is separated from the pterygoid on the ventral surface by a longitudinal groove, deep anteriorly but fading posteriorly. The anterior, choanal, border is concave in outline. Medially the anterior margin of the bone is somewhat convex ventrally in transverse section, forming a ridge continued anteriorly by the vomer. Lateral to this, the surface is somewhat concave ventrally at the choanal margin, the concavity fading out posteriorly. Posteriorly the margin is concave in outline, the medial margin extending well posteriorly, underlain dorsally by the pterygoid. There is no development of the transverse pterygoid flange characteristic of all primitive reptiles.

Approaching, posteriorly, the region of the basal articulation, the pterygoid, as in all primitive tetrapods, narrows in transverse width and twists to a vertical plane, to form the quadrate ramus of the bone. Just in front of the articular region it sends upward a sharp spur, which aids in the support of the epipterygoid. Behind this spur the upper edge of the pterygoid is gently concave on its medial aspect, to form the lower part of the articular surface for the basipterygoid process. The posterior, quadrate ramus of the pterygoid rapidly develops into an extensive plate, thin from side to side

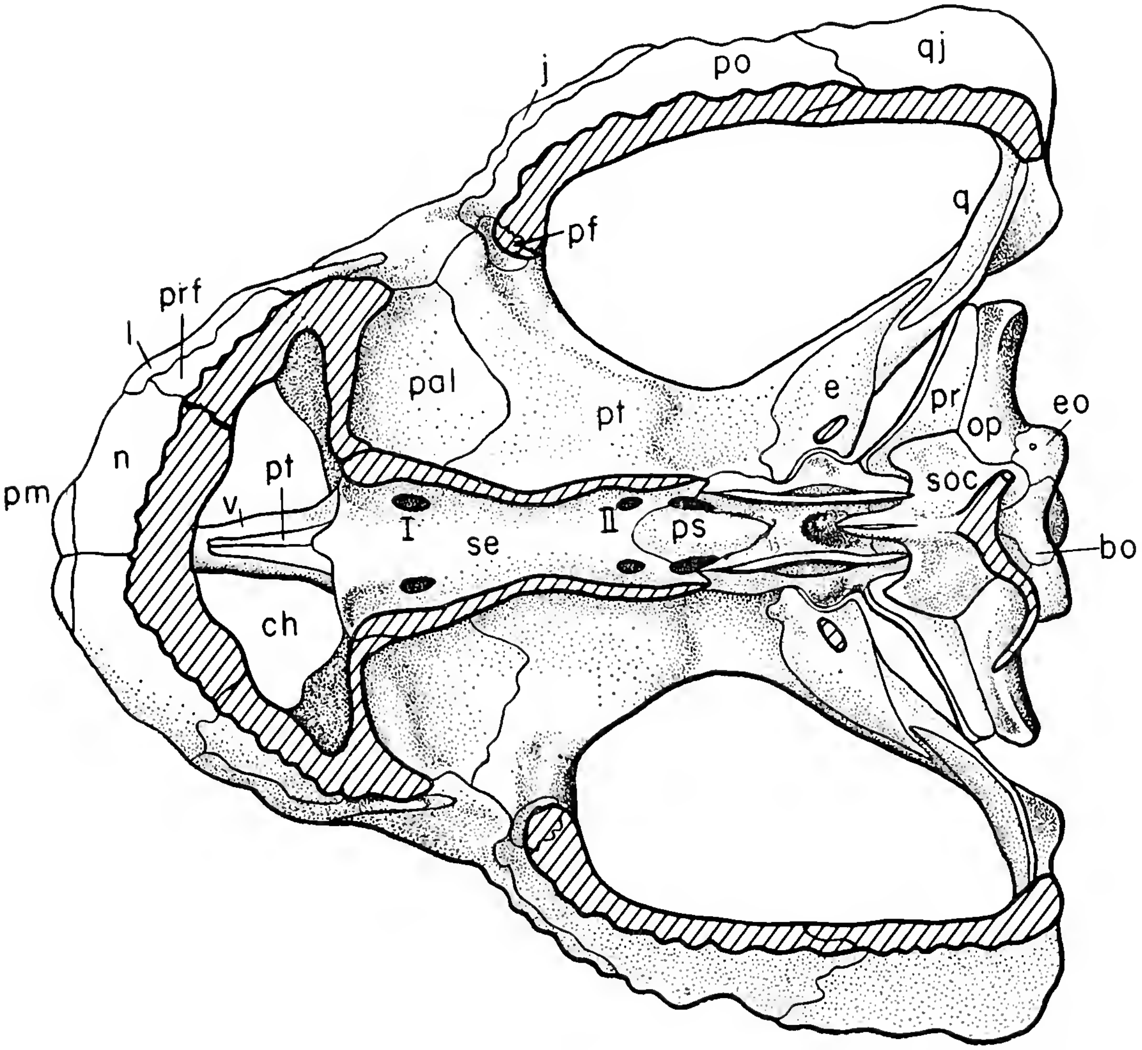

Fig. 6. Skull roof diagrammatically removed to show palate from above. Dermal roof sectioned horizontally through level of middle height of orbit; sphenethmoid and ascending ramus of epipterygoid sectioned at same level, but dorsal flange of sphenoid complete. Postparietals and tabular removed; supraoccipital shown as complete except for removal of dorsolateral flange on right; based on sectioned specimen, × 1½.

but of considerable height. It extends ventrally to about the level of the bottom of the cheek flange of the jugal and quadratojugal, and runs back nearly to the region of the jaw articulation. Above this posteroventral point, it contracts somewhat in posterior extent; meanwhile, however, the dorsal margin of the ramus has risen rapidly, and the upper blade of the ramus extends far upward, backward, and laterally, to terminate high up within the temporal region, close to, but not in direct contact with, the squamosal.

The epipterygoids had been jarred loose in the sectioned specimen and had fallen down between the jaws, where they lodged with but little damage. They can be replaced without difficulty in approximately natural position, although with some slight doubt as to dorsal orientation. Below, the bone is expanded into a flat plate applied closely to the lateral surface of the quadrate ramus of the pterygoid over a considerable area, mainly below and posterior to the basal articular area and extending only modestly anterior to that point. At the level of the upper margin of the pterygoid, the epipterygoid thickens considerably; a pair of ridges extends medially to form a socket for much of the basipterygoid process. The anterior margin of the bone here is notched to receive the supporting spur of the pterygoid mentioned above. Dorsally, the bone slims out to a slender blade, which reaches far toward the skull roof.

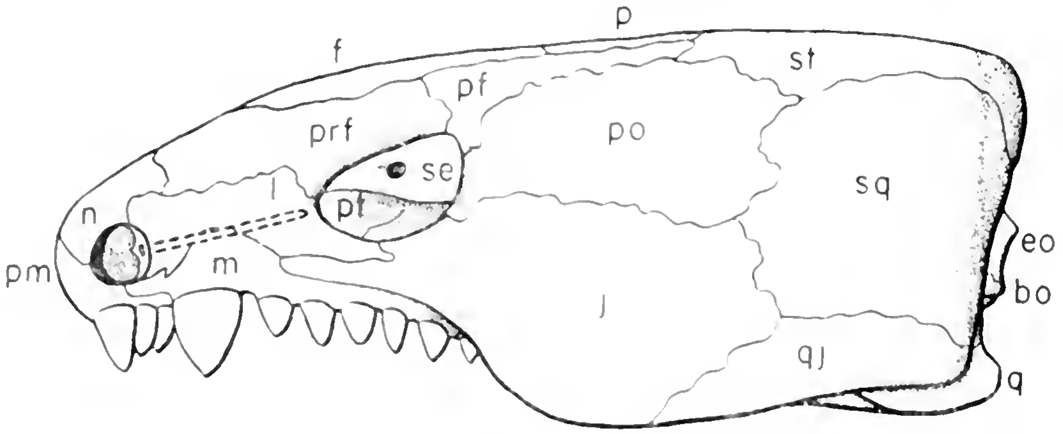

Fig. 7. First of a series of "dissections" in lateral view, based on the sectioned skull. This figure comparable to Fig. 2. The course of the lacrimal duct is shown in broken line. × 1½.

The quadrate is well developed. The articular surface for the lower jaw is broad mediolaterally, relatively narrow anteroposteriorly, and but slightly convex. The quadratojugal turns medially in a flange which is of considerable thickness ventrally; on its lower surface this forms approximately a third of the articular area. Above the articulation, the quadrate is thickened but gradually thins dorsally. Medial to the articulation, the quadrate is very stoutly developed and extends ventrally and posteriorly beyond the ventral and posterior limits of the "roofing" bones. There is a posteromedial swelling just above the articular region, presumably for a muscular or tendinous attachment. Anteriorly, the quadrate forms a very extensive plate applied closely to the outer surface of the pterygoid and extending far forward toward the epipterygoid. Dorsally, the plate, with the accompanying pterygoid, reaches far dorsally and posteriorly beneath the squamosal.

Occipital surface (Fig. 4). In the absence of an otic notch, the skull roof exhibits in posterior view an even, essentially semicircular, curved margin. In contrast to conditions in most lower tetrapods is the great extension onto the occipital surface of the posterior elements of the dermal roof. The postparietals send a flange of modest size down over part of the supraoccipital on either side. The "supratemporal" sends a broad sheet of bone downward and medially; in the fashion of a labyrinthodont tabular, there is an articulation of the supratemporal with the otic region of the braincase. The attachment is a broad one, meeting both prootic and opisthotic above the fenestra ovalis, and is far more ventrally placed than that of a typical labyrinthodont. There is a normal posttemporal fenestra, bounded mainly by "supratemporal" and postparietal, but ventrally and ventromedially by the otic elements and, to a slight degree medioventrally, the supraoccipital.

Much in the fashion of the "supratemporal," the squamosal sends a broad, thin sheet of bone downward and medially over a considerable lateral area of the occipital surface. Dorsally, this sheet underlies the occipital flange of the "supratemporal" to some extent; ventrally it sheathes the occipital surface of the quadratojugal. It ends freely ventromedially.

Centrally, on the occipital surface is seen the posterior aspect of the braincase. The usual ring of occipital elements — supra-, basi-, and small, paired exoccipitals — surrounds the foramen magnum. Above the foramen magnum the supraoccipital is deeply excavated by a pit, presumably for ligamentous connection with the column. The otic capsule is seen to extend outward far laterally (somewhat as in *Seymouria*) rather than dorsolaterally, as in the paroccipital process of typical labyrinthodonts. Beneath the lateral part of this process the fenestra ovalis is visible; more medially, between opisthotic and a lateral extension of the exoccipital, is the jugular foramen for the vagus nerve (as well as, presumably, nerve IX and the "jugular" vein). A hypoglossal foramen is present ventrally, and possibly a second hypoglossal opening may be present more dorsally. The occipital condyle is a broad, somewhat concave, and essentially tripartite structure comparable to that of such rhachitomes as *Eryops*.

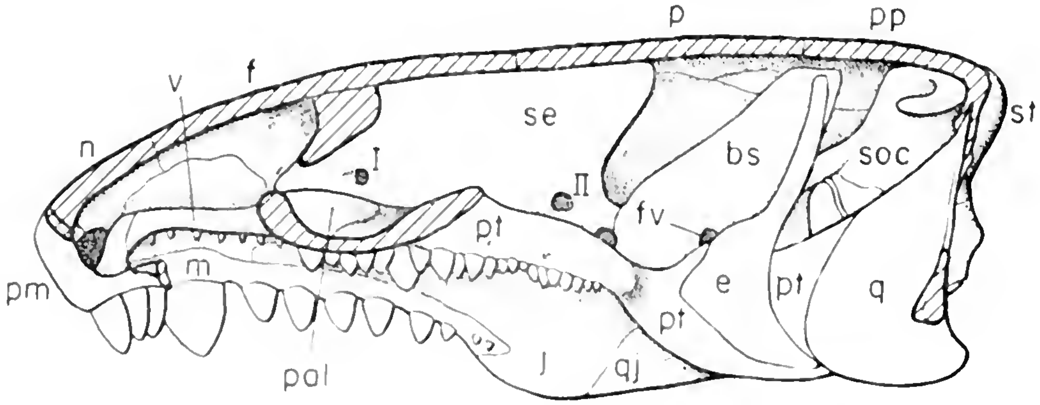

Fig. 8. As Fig. 7, but dermal bone of left side removed (except for premaxilla), to show the palatal structures in lateral view. Sutures with bones removed indicated by hatched areas. At anterior end of sphenethmoid is seen the lateral process of that bone, which is tightly fused to prefrontal; below are shown the surfaces of palatine and pterygoid, which join the lacrimal and jugal. Posteriorly is seen the area of contact between quadratojugal and quadrate.

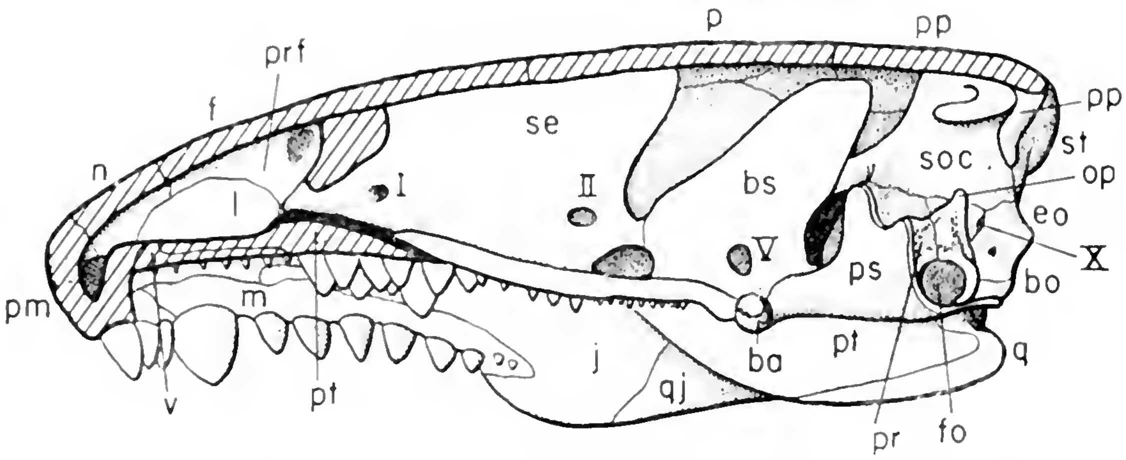

Fig. 9. As Fig. 8, but palatal structures of left side and left premaxilla removed to show lateral view of braincase. Below the anterior part of the sphenethmoid and to the front are seen the medial contacts between the pterygoids and vomers and the ascending processes of the premaxillae, which meet the vomers. The rugose area on the otic bones above the fenestra ovalis is the area of contact with the "supratemporal."

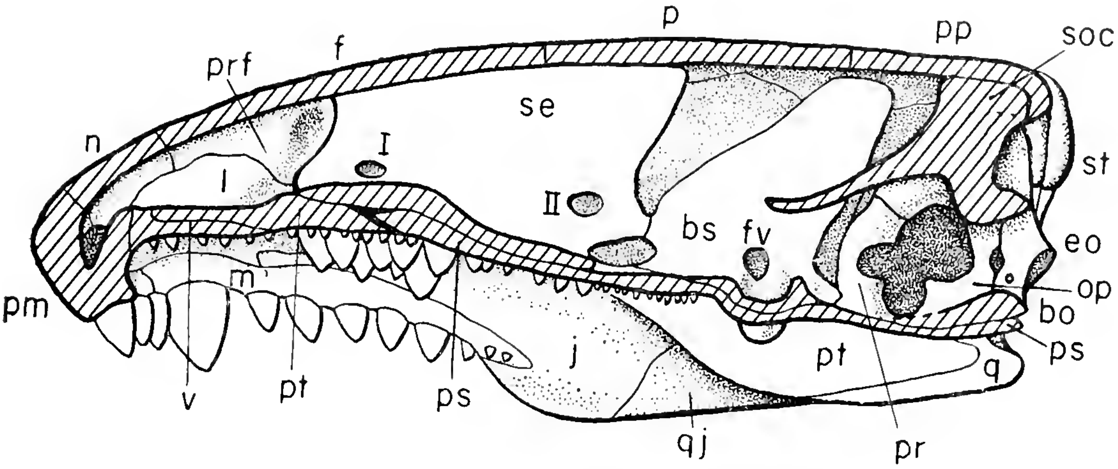

Fig. 10. As Fig. 9, but sectioned through middle of braincase, to show internal structure. Inner surface in otic region restored with doubt.

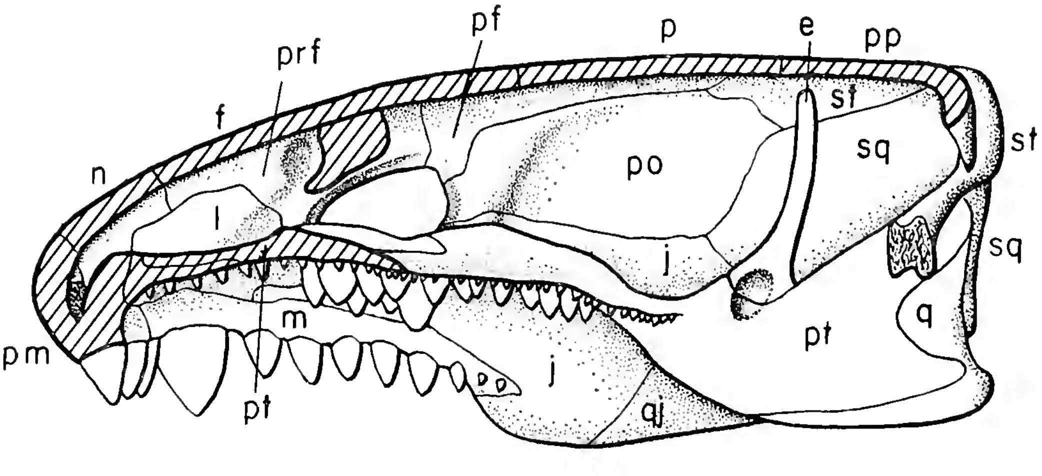

Fig. 11. As Fig. 10, but braincase removed, showing inner surface of right palatal complex. Anterodorsal to orbit is seen the area of contact of the prefrontal with the lateral flange at the front end of the sphenethmoid. A rugose area posteriorly is the sutural surface of the "supratemporal" articulating with the otic elements of the braincase.

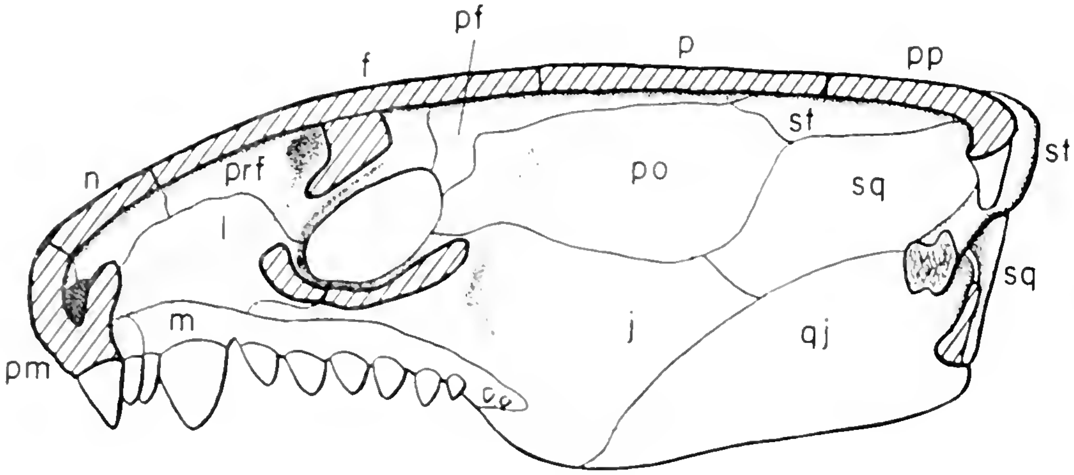

Fig. 12. As Fig. 11, but palatal elements removed, showing the inner surface of the dermal roofing elements of the right side. Posteroventrally is seen the area of contact of the quadratojugal with the quadrate.

Braincase (Figs. 4-6, 9, 10). The nasal capsule was unossified. As noted earlier, the external narial cavity is bounded posteriorly and medially by the septomaxilla. Behind this bone, the anterior part of the choanal opening was occupied by the large anterior lower teeth; it is hence obvious that the air passage ascended dorsally from the external naris and that the nasal capsules were dorsally placed, anterolateral to the front end of the sphenethmoid. Beginning anteriorly at about the level of the posterior margins of the choanae, and extending back to about the level of the posterior margins of the orbits, there is a well-developed sphenethmoid. The entire structure is a single ossification, essentially V-shaped in cross section. The ventral edge of the bone is keeled, and in life lay for most of its length in a groove on the upper surface of the parasphenoid rostrum; there is here a stout union between the two thin ascending flanges. These diverge from one another at a modest angle, and then approach each other to a slight degree dorsally. The cavity of the sphenethmoid is widely open both anteriorly and posteriorly. Laterally, opposite the orbit, there is on either side a foramen of considerable size through which the olfactory nerve presumably passed; a second large foramen, presumably for nerve II, lies toward the back end of the bone. Possibly the sphenethmoid may have been penetrated by small foramina for one or more of the eye-muscle nerves, but I have not been able to detect them in the sectioned specimen, and they may have emerged posterior to the sphenethmoid. The sphenethmoidal plates appear to have extended upward to the under side of the roofing elements, but I have not been able in the sections to determine the exact relations here (Williston, 1916a, fig. 25, shows sections in this region). On either side in front of the orbital rim the prefrontal sends in a powerful medial flange, broadening dorsally, which articulates strongly with the outer surface of the sphenethmoid near its anterior end.

The parasphenoid-sphenoid complex in the sectioned specimen was jolted out of position before burial; present between the lower jaws, it has undergone little damage except for the posterior margins of the parasphenoid (which, however, are preserved in other specimens). It can be replaced fairly accurately in its proper place in the figures because of the known position of the basal articulations and because it can be seen in place in lateral view in MCZ 2040. The anterior portion of the complex is a long parasphenoidal rostrum; a dorsal groove obviously received the ventral keel of the sphenethmoid in normal fashion. Posteriorly, the keel expands gradually and then abruptly produces ventrolaterally a pair of well-developed basipterygoid processes with stoutly rounded heads that fit into the sockets formed jointly by the epipterygoids and pterygoids.

In this region, the complex includes, inside the superficial parasphenoidal dermal component, spongy endochondral bone representing the basisphenoid; endochondral bone is included in the structure of the basipterygoid process. There is a distinct rounded medial pocket in the basisphenoid opposite the basipterygoid processes, obviously lodging the pituitary. A distinct crossridge behind the cavity represents the dorsum sellae; behind this point endochondral bone is absent. As in early tetrapods generally, it seems, there was a ventral gap in endochondral braincase ossification between the sphenoid and otico-occipital braincase elements. A pair of small foramina, presumably for internal carotid arteries, penetrates the bone from the under side opposite the posterior margin of the pituitary fossa. A remarkable feature is the presence of extensive wings extending far upward from the basisphenoid and continuous with it on either side; the type of ossification is such as to indicate their endochondral nature. They appear to represent the pila antotica of the embryonic braincase. Near the base of either flange is a good-sized foramen that presumably carried the transverse pituitary vein, as in the basisphenoid of various lower tetrapods. Although, as said above, the parasphenoid-basisphenoid can be replaced in a position close to that which it must have occupied in life, there is a degree of uncertainty as to the exact posture of these dorsal flanges. They certainly stopped short dorsally well below the level of the skull roof. In the sectioned specimen the sphenoid had broken loose from the sphenethmoid, but the two are seen in natural relationship in lateral view in MCZ 2040. Here there is seen a short area of connection between the ascending flanges and the sphenethmoid part way up the side, leaving a gap dorsally and a rounded foramen ventrally. Possibly small eye-muscle nerves emerged above; below is perhaps the point of exit of the profundus branch of nerve V, the more posterior rami of this nerve and nerve VII making their exits behind the dorsal flange of the sphenoid.

It was hoped that the sectioned specimen would show the otico-occipital elements in place. This was not the case. The supraoccipital remained essentially in position, but the other elements had been jarred loose before burial (suggesting, although we appear to be dealing with an adult, rather loose suturing of elements). Fortunately, much of the structure could be made out from MCZ 2040 and MCZ 3302. Dorsoposteriorly, the supraoccipital is firmly fused to the overlying postparietals; in addition, the latter bones, as noted earlier, partially sheath the supraoccipital posteriorly. A narrow process extends dorsolaterally toward the "supratemporal." On either side, the supraoccipital descends and expands to gain contact with the two otic elements and, posteriorly, with the exoccipital. The sections show that, as commonly, the supraoccipital encloses the upper part of both vertical canals of the internal ear, as well as the crus commune. Dorsally, the supraoccipital sends forward an anterior process. One would have expected this to run forward dorsally beneath the skull roof, as, for example, in many reptiles. This is not the case; it slants strongly downward, to terminate anteriorly at about the level of the pituitary rather below half the distance from the skull roof to the braincase floor and between the two ascending flanges of the sphenoid. Uniquely among known early tetrapods, this anterior extension is a dual structure, consisting of two closely apposed narrow rods. As is known from the developmental story in lower tetrapods, supraoccipital ossification takes place in a cartilaginous area formed by dorsal fusion of extensions upward of the two otic capsules; the situation here suggests that the fusion of the two was imperfect.

The exoccipitals are, as usual in early tetrapods, small elements, hung below the supraoccipital on either side. Between opisthotic and exoccipital is a typical jugular foramen. Ventrally, the exoccipitals form the lateral portion of the broad occipital condyle. The basioccipital is a wedge-shaped element, forming the central part of the condyle and tapering anteriorly on the braincase floor.

The pro- and opisthotics jointly form a pronounced lateral extension of the otic region (Fig. 5), tipped at its end by a broad area of articulation with the "supratemporal," somewhat after the fashion of the typical paroccipital process of many early tetrapods (which, however, articulates with the tabular). Below this articular area is the good-sized fenestra ovalis, bounded posteriorly by the opisthotic, anteriorly by the parasphenoid. This latter dermal element covers most of the surface of the prootic, except dorsally, and likewise sheathes the opisthotic ventrally. Parasphenoid and otic elements were apparently not bound closely together in life, since they have cleanly separated in the sectioned specimen. Dorsally the two otic structures are articulated with the supraoccipital. On the dorsal surface of the lateral otic process the suture between pro- and opisthotics lies in a deep groove; obviously the suture between the two was a comparatively loose one (as confirmed by their separation in the sectioned specimen).

In the sectioned skull, three isolated otic elements are clearly seen, but I must confess myself baffled in attempts to interpret them and orient them in a reconstruction. Two of the three, obviously a pair, have, crudely, the shape of a clam shell; the curved outer surface is smooth except for a ridge indicating the division between a free surface and that sheathed by the parasphenoid. The inner aspect, presumably housing part of the internal ear, shows some slight development of ossification. Attached to one of the two is a small area of ossified tissue which presumably represents an exoccipital; in consequence, I interpret the two as opisthotics. By elimination, the third element preserved is a prootic. Here again, the presumed external surface is featureless except for a ridge which may have separated a free dorsal surface from that sheathed by the parasphenoid. On the inner surface there is a considerable degree of ossification in a complex pattern which, however, I fail to interpret. As a result, I can give no description of the internal structure of the otic region except what can be seen rather imperfectly from the sectioned braincase of MCZ 3302. Apparently the internal ear region was widely open to the brain cavity opposite the two otic elements, although partial anterior and posterior ossified walls are formed by them.

Lower jaw (Figs. 13-15). Like the skull, this is a very stoutly built structure and is relatively broad, but shallow. As can be seen in the cross-sections figured by Williston (1916a), both external and internal walls of the jaw ramus are thick. In section, the jaw is somewhat triangular. The upper surface is broadened for the coronoid toothplate; the inner surface is essentially vertical. On the outer surface, a longitudinal, shallow shelf is present in the region opposite the adductor fossa; this corresponds to the lower boundary of the jugal flange of the skull. The lower part of the outer surface curves gradually medially, to compensate for the dorsal width, so that most of the splenial-angular area and the lower part of the dentary are seen in a ventral rather than a lateral view. Much of the outer surface of the jaw is sculptured in a fashion similar to the skull roof, but in the posterodorsal portion of the external surface,

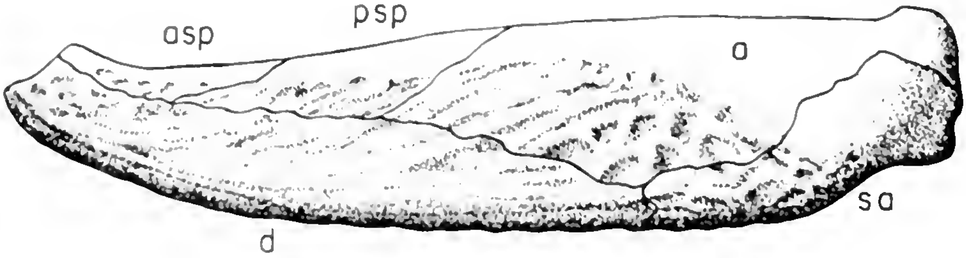

Fig. 13. Ventrolateral view of right jaw ramus, ventral margin at the top, × 1½.

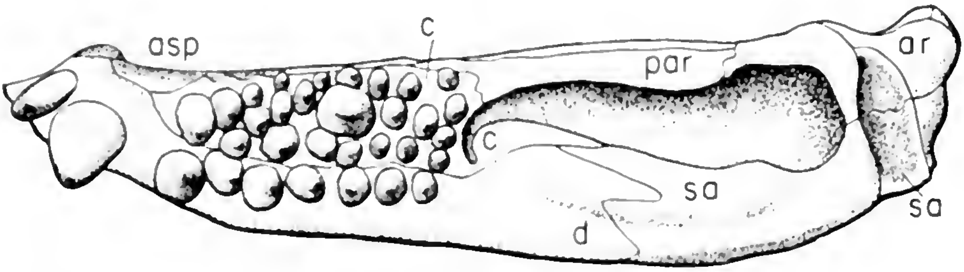

Fig. 14. Dorsal view of left jaw ramus, × 1½.

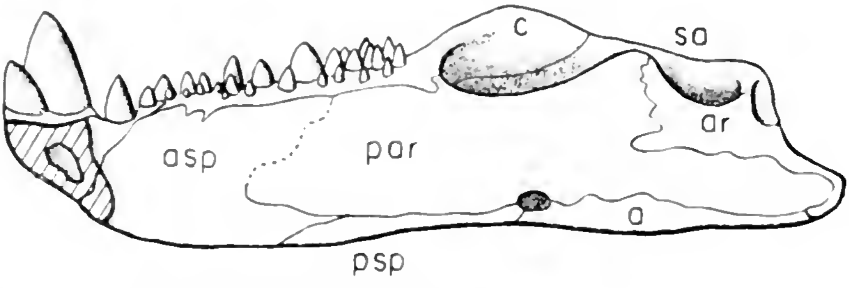

Fig. 15. Internal view of right jaw ramus, × 1½.

from the coronoid process down to the longitudinal shelf already mentioned, the jaw (here covered by the jugal flange) is smooth-surfaced. The ventromedial margin of the lateral surface also lacks sculpture, presumably due to the fact that here, between the jaw rami, the skin was lifted free from the bone. Rather unexpectedly in such a strongly built structure, the symphysis, although stoutly fused, is of modest extent — a triangular area with a vertical posterior border and a curved anteroventral external surface. The opening of the adductor fossa is large, extending about half the length of the jaw back from the curved posterior border of the coronoid plate to the articular area. A large cavity of subcircular shape, corresponding to the Meckelian canal of reptiles, extends forward without interruption from the adductor fossa nearly to the symphysial region. Presumably this carried in its floor the anterior part of the Meckelian cartilage.

Lateral to the opening of the adductor fossa there is an elongate coronoid process, which rises fairly rapidly from a point near the posteroexternal border of the coronoid toothplate and decreases gradually in height posteriorly. It slants gently toward the medial side above. Opposite the coronoid process there is a smaller, thin, process extending upward from the medial margin of the adductor fossa. As in the upper jaw, the articular surface is broad mediolaterally, narrow anteroposteriorly. It is gently concave in anteroposterior section. The broad posterior margin of the jaw slants nearly directly downward for a short distance below the articular surface, but then turns strongly backward to form a pronounced and broad retroarticular process, rather more developed medially than laterally. On the inner surface of the jaw there is a typical Meckelian foramen opening into the adductor fossa; this lies close to the ventral jaw margin, about a third of the jaw length forward from its posterior end. Williston (1916a) described a second, smaller, Meckelian foramen much further forward along the inner jaw surface; I have not been able to identify this small opening in the available material. Presumably a fossa for the chorda tympani was present, but I have not observed this opening.

As commonly, the dentary is the largest element of the jaw. Anteriorly, it forms most of the jaw symphysis, behind which it is exposed on the inner surface for a short distance only. Externally it occupies a large part of the surface of the ramus. Anteriorly, where it is bounded ventrally by the splenials, it occupies the greater part of this outer surface; more posteriorly, adjacent to the angular and surangular, its lower boundary retreats gradually upward. At the level of the longitudinal shelf mentioned above, the surangular extends forward in V-shaped fashion to overlap the dentary to some degree; above this, on the coronoid process, however, the dentary succeeds in extending well backward, and forms much of the outer surface of the process, although not reaching its summit. Anteriorly, the medial boundary of the dentary descends along the outer surface of the coronoid process to extend forward along the medial margin of the lateral tooth row, where the suture lies in a marked groove.

Of the infra-dentary series, the two splenials are found in their usual position externally, occupying a modest area near the ventromedial termination of the morphologically lateral surface. The posterior splenial extends around the lower jaw margin to be exposed along a narrow ventral strip on the medial surface. The anterior splenial is more extensive in medial exposure. I have some doubts as to its boundaries, but the anterior splenial appears, as Williston figures it, to extend upward as a thin sheet over the anterior end of the prearticular to border the anterior end of the coronoid plate and gain contact with the dentary behind the anterior tooth pair; it forms the ventral third of the symphysis. The angular has its normal exposure, of considerable extent, over the posteroventral region of the outer surface; posteriorly it forms the outer part of the retroarticular process. Internally it is exposed ventrally, running forward to partially bound the Meckelian foramen. The surangular is well developed externally, where it forms much of the region of the coronoid process, excepting its highest and most anterior portion. Posteriorly it participates in the formation of the retroarticular process. Paralleling its upper jaw analogue, the quadratojugal, the surangular turns medially at the posterior end of the ramus and forms the lateral third of the articular condyle.

It is possible that the presumably primitive series of three coronoids was present in *Pantylus*, but I have not been able to distinguish sutures in available material. The coronoid area forms a large plate bounded laterally by the dentary, superficially on the medial side by the prearticular, and anteriorly by the anterior splenial. Medially, beneath the last-named elements, a thick flange of the coronoid, at right angles to the exposed portion, extends far ventrally, giving stout support to the toothplate, as figured by Broom (1913, fig. 4) and Williston (1916a, fig. 27). Posteriorly, behind the termination of the toothplate, the coronoid complex takes part in the formation of the coronoid process; it forms the inner surface of the high anterior portion of the process and is also exposed externally at its summit.

The prearticular is extensively developed. For the most part, it covers the surface of the coronoid area along the inner aspect of the jaw as a thin plate of bone; anteriorly, it appears to be covered in turn by the anterior splenial. In the middle section of its extent, it is bounded ventrally by the splenials. It forms much of the boundary of the Meckelian foramen, posterior to which it is constricted in ventral extent by the angular. Back of the coronoid plate it forms by itself the whole of the medial wall of the adductor fossa to the summit of the medial dorsal process which was mentioned earlier. Behind this point it is constricted dorsally by the articular; it extends to the posteromedial corner of the jaw as a restricted strip of bone between the articular above and the angular below.

The articular forms the medial two-thirds of the jaw articulation. Below, it descends to bound the posterior end of the adductor fossa and form part of the substance of the retroarticular process; as far as I could determine, however, it does not appear on the surface of that process. Medially it turns forward above and internal to the prearticular to form a portion of the inner wall of the adductor fossa.

Lying within the floor of the Meckelian canal for much of its extent is a thin sheet of bone, shown in the sections of Mehl (1912, fig. 4). It is somewhat broken and discontinuous in my sections, but is obviously not part of any one of the dermal ossifications lying external to it. It seems surely to be a Meckelian ossification in the lower surface of the cartilage which probably filled much of the canal.

Dentition (Figs. 2, 5, 7-12, 14, 15). *Pantylus* was endowed with a powerful dentition of stout but blunt teeth, both on the jaw margins and internally on broad areas of the palate and the coronoid area of the lower jaw. In section there is no trace of labyrinthine infolding of the enamel; nor is there any trace of a division of teeth into basal and distal portions, as might be hoped for in a member of a group possibly related to the modern amphibian orders (cf. Parsons and Williams, 1963). Evidence of tooth replacement was looked for, but not found. It seems clear that *Pantylus* subsisted on some type of durophagous material. A molluscan diet has been suggested by various authors. This is not unreasonable; but it is to be noted that little trace of molluscs has been seen in the beds from which *Pantylus* specimens have been collected, and probably some hard plant material formed the food supply. The massive construction of skull and jaw is reasonably to be correlated with strong masticatory movements, and great strength of the jaw muscles is indicated by the great size of the subtemporal fossae, through which the temporal muscles descended — the breadth of these cavities being correlated with the unusual width of the temporal region of the skull.

The upper marginal teeth, particularly the more anterior ones, are somewhat tilted inward at their tips (a reverse outward slant is present in the lower anterior teeth). Three teeth are generally present on each premaxilla. The first is large and powerful and is, next to the "canine," the largest tooth in the upper jaw. Lateral to this are usually two further "incisors," somewhat smaller, but nevertheless rather longer than any of the maxillary teeth except the "canine"; the two are crowded close together and are somewhat compressed from side to side. One small and presumably young specimen shows but one tooth in this position. Immediately behind the lateral "incisor" is the powerful "canine," most anterior member of the maxillary row. Behind the "canine" is a series of cheek teeth. The first of these is little more than half the length of the "canine," and the first few following teeth are of about the same length. More posteriorly there is a gradual diminution in size. The specimen sectioned is somewhat imperfect posteriorly along the jaw margins, so that there is some question as to the exact number in the series; there are, in this specimen, certainly eight and possibly nine post-"canine" teeth. Some specimens show a larger number of cheek teeth. Williston (1916a), for example, states that there are 15 or 16 maxillary teeth (but figures only 16 for premaxilla and maxilla combined). Discrepancies in tooth counts may be due to individual variation or, quite possibly, to posterior additions to the tooth row during life.

In the marginal row of the lower jaw, there are two anteriorly-placed "incisors." The more medial of the two is the smaller, but this is, nevertheless, more powerful than any but the most anterior of the lower cheek teeth. This tooth is somewhat compressed from side to side at its base. The lateral "incisor" is of considerable size and strength, equalled only by the upper "canine." As noted earlier, this tooth is so highly developed that when the jaws were closed, it extended well up into the anterior part of the bony choanal opening (as did the median incisor to a lesser degree). Beyond the lateral "incisor" there is a slight dip in the height of the jaw rim and a gap, allowing for the passage of the upper "canine." Following this short diastema there is a series of marginal teeth, which mainly match in size the more anterior post-"canine" teeth in the maxilla. I have found but seven teeth in the post-"incisor" series in the lower jaw of the sectioned specimen, in contrast with the higher number above, and there is relatively little diminution in size toward the back of the series.

Teeth are highly developed on the palate. I have seen no evidence of parasphenoidal teeth (found occasionally in early tetrapods). Beginning a short distance anterior to the basal articulation, the anterior ridge of the pterygoid is studded with small teeth. These are rather irregularly placed, but for most of the length of this long ridge they are essentially arrayed in two irregular rows. The vomers, lateral to the anterior ends of the pterygoids, bear a series of teeth of somewhat larger size.

The major palatal tooth assemblage is found on the extensive palatine bones. There is some irregularity in the arrangement, even between the two sides of a single individual (as that sectioned and figured), but there is, in the few palates I have seen, a uniform basal plan. Somewhat to the lateral side of the center is a very large but quite blunt tooth with an oval base and a crown slanting anteromedially. Just behind and medial to this tooth is a bare area of the palate into which, in the closed jaw position, a similarly large lower tooth is lodged. A longitudinal row of rather large teeth runs along the lateral margin of the bone; the lower marginal teeth in closure lay between this row and the marginal upper teeth. Anteromedially, a row of teeth of modest size continue backward from the vomerine series. A few teeth of a size comparable to those of the marginal row are present in front of the large central tooth, and good-sized teeth are present medial to it. About a score of teeth are present in the posterior portion of the palatal plate. They are of variable size; many are moderately large, but there is a decrease toward the angular posteromedial boundary of the palatine.

The coronoid region of the broadened upper surface of the lower jaw bears a battery of teeth, somewhat over a score in number, which correspond roughly to the palatal assemblage above. There are, however, no lower teeth to oppose those on the pterygoids or (naturally) those on the vomers. Further, the lower tooth plate is much narrower than that of the palatine, and the teeth are more closely crowded. As in the case of the palatine, there is a large, broad-based tooth centrally situated on the coronoid plate. Despite the crowding of the lower plate teeth, there remains, in the sectioned specimen, a small bare area just anterior to this tooth, in which was received the summit of the crown of the major upper plate tooth. As in the palatine plate, there is a row of stout teeth along the lateral margin of the plate, and well-developed teeth are present anterior and posterior to the major tooth. Teeth forming a medial row are of smaller size.

Individual variations in the number and position of teeth in the palatine and coronoid toothplates are to be expected, and it was mentioned earlier that in some cases the large, centrally-placed teeth in these plates may be absent. In the sectioned specimen, upper and lower jaws were in occlusion at death, and it could be seen that there was a perfect coordination between upper and lower toothplate sets. There was never any direct opposition between an upper and lower tooth; each upper tooth fitted into a gap between lower teeth, and vice versa.

Visceral arch elements (Fig. 16). As attested by the presence of a pebbly sheet of dermal ossicles similar to those seen in *Tuditanus* and "*Ricnodon*" *limnophyes*, the skin between the jaw rami was still present when the sectioned specimen underwent burial, and various bones were preserved in this "pocket" for fossilization. We have already mentioned the presence here of detached vomers, epipterygoids, and otico-occipital elements. Further, the first three vertebrae had been pushed forward into this

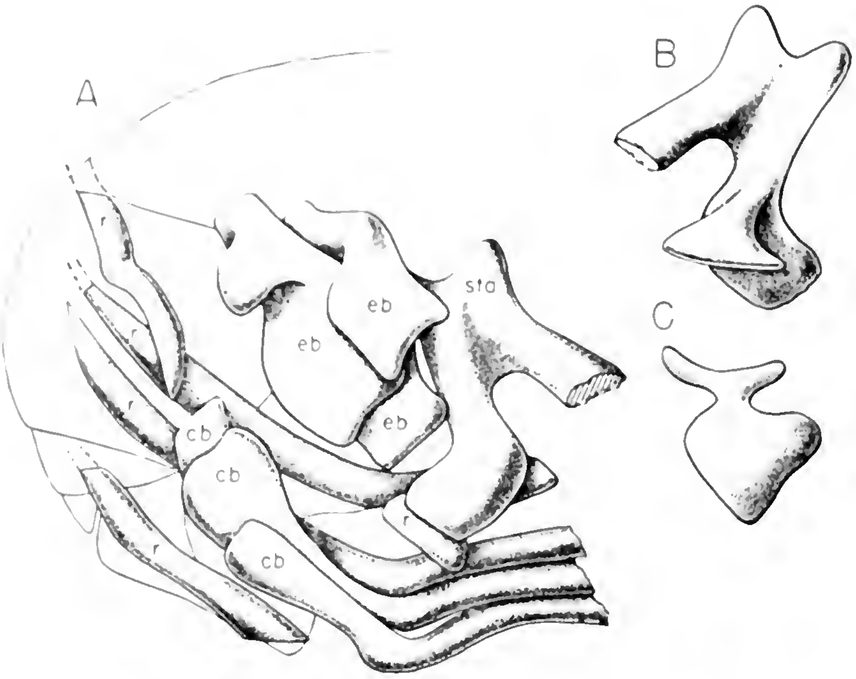

Fig. 16. *A*, Postcranial structures preserved behind left side of occiput, from reconstruction of the sectioned specimen. Outlines of the skull elements shown for orientation; *cb*, ceratobranchials, *eb*, epibranchials, *r*, rib fragments, *sta*, stapes. *B*, Stapes from anterior side, as oriented. *C*, Ventral view of main shaft of stapes. All × 3.

area, and ventrally a fraction of the dermal shoulder girdle is included also in the block. On the right, the sectioned block terminates directly back of the occiput and jaw articulation; on the left, however, the block extended a short distance farther back, so that there are present part of the cervical rib series and — much more interesting — part of the visceral arch series of the left side.

Fairly high up in the block, centered about behind the left otic region, are three elements which appear rather certainly to be epibranchials. These are thin-walled, incompletely ossified internally, with a spongy structure. They are essentially leaf-shaped, each with a broad distal expansion, thin anteroposteriorly; the three are closely appressed. Dorsally, each narrows somewhat to a "stem"; however, the one seen farthest to the left in the figure has a rather broad expansion at its "head."

Separate from the presumed epibranchials and running transversely lower down in the block are three further structures, which appear to be ceratobranchials. Each consists of two contrasting segments. At the left, and slanting ventromedially, are "head" portions which resemble the epibranchials in being thin-walled, spongy internally, broad in the transverse plane, but thin and rather closely appressed, one to the other, anteroposteriorly. At their lower ends, each turns directly medially and assumes the form of a tube, thick-walled but hollow centrally. These extend for a (relatively) considerable distance to the right. They terminate somewhat irregularly; this may be due either to post-mortem damage or to the presence of cartilaginous terminations. At their distal ends each of the three narrows dorsoventrally but broadens anteroposteriorly, like flattened cornucopias.

A further visceral structure is present in the sectioned specimen, to the right of the presumed epibranchials. This is a stout element which, as preserved, begins dorsally high up just behind the lower inner portion of the occipital plate of the left supratemporal. For a short distance there are two semi-distinct "heads," but these shortly unite to form a single, rather large structure, of rhomboidal shape in section, relatively thin-walled, and with a spongy interior. A short distance down there is a bifurcation. One branch slants sharply to the right and somewhat posteriorly; distally this ramus becomes shattered, so that nothing can be said of its extent or distal terminus in life. The other branch runs nearly directly ventrally. For a short distance it contracts, to have a relatively small diameter and good walls; beyond, it expands to a large diameter, with a spongy interior and with thin walls except toward the right and anteriorly. Anteriorly there develops a well-formed projection, thin at its base but then expanding toward each side, giving a T-shaped section.

It seems certain that this element is a stapes, and rather surely that of the left side. In its disarticulated state there is no certainty as to its interpretation and position in life. At first thought, one would tend to interpret it in terms of the pattern common in early tetrapods and crossopterygians (cf., for example, Romer, 1956, fig. 197). On this assumption, the upper end as figured would be that associated with an ear drum (if present), the shorter branch to the right a dorsal process, the vertical processes the main shaft, with the footplate at the bottom. But various considerations suggest an alternative hypothesis — that the upper terminus is a broad footplate, that the complex lower end of the main shaft was associated with an eardrum or other auditory structure, and that the branch to the right braced the structure laterally in some fashion on the occipital aspect of the cheek (somewhat analogous to the crossopterygian opercular process). On this assumption, the posterior surface of the stapes is that seen in Figure 16B. The somewhat bifurcate nature of the presumed footplate may be due to close apposition of shaft and dorsal process, but is also slightly suggestive of initiation of the lissamphibian division of the apparatus into stapes plus operculum.

PANTYLUS AS A MICROSAUR

Two facts seem immediately clear: (1) *Pantylus* is closely related to microsaurs of the gymnarthrid group, and (2) neither *Pantylus* nor its microsaur relatives are reptiles or ancestral to reptiles.

The description above has, I think, made it obvious that *Pantylus* is a microsaur. It is specialized for a durophagous diet in its massive skull build, accommodation for powerful temporal muscles, and powerful dentition. Otherwise it compares readily in many regards with the contemporaneous gymnarthrid microsaurs; dentitions of intermediate type are known among Carboniferous microsaurs in Canada and Bohemia. *Pantylus* exhibits the diagnostic cranial patterns of the group, such as those which I specified in 1950 and the additional features noted by Carroll (1966) and by Carroll and Baird (1968). The most obvious feature is, of course, the presence between parietal and squamosal of a large roofing element generally termed "supratemporal." In all labyrinthodonts we find here a row of elements, including a tabular posteriorly and more anteriorly a distinct supratemporal and, in many primitive forms, an intertemporal as well. Supratemporal and tabular are present as distinct elements in primitive captorhinomorph reptiles. Never, however, is there any growth of a large element such as the microsaur "supratemporal." In specialized captorhinomorphs tabular and supratemporal are reduced, so that — in strong contrast to microsaurs — squamosal and parietal come in direct contact for most of their length.

In all early tetrapods there is a trend for the development from the posterior elements of the dermal roof of flanges sheathing the occipital surface. Such flanges are highly developed in *Pantylus,* particularly that from the "supratemporal." The occiput is poorly known in most microsaurs; however, a similar occipital sheathing is known in a few other cases, and *"Ostodolepis,"* as figured by Case (1929), shows an even greater development of such dermal structures than that in *Pantylus.* It is highly probable that the presence of extensive dermal flanges in the occiput is a diagnostic microsaur feature.

Typical of microsaurs (and early amphibians in general) is the rounded posterior contour of the palatal plate, in contrast with the development of the stout pterygoid flange seen in early reptiles. In various primitive amphibians we find narrow interpterygoid vacuities and a movable basal articulation of braincase and palate, in contrast to the "open" palate and fused basal articulations seen in most temnospondyls and modern anurans and urodeles. The primitive condition persists here in microsaurs in which the palate is known; *Pantylus* is in agreement with this condition.

The braincase is poorly known in most microsaurs. It is possible, although of course not certain, that the structures described above in *Pantylus* are typical of microsaurs in general. We have seen in *Pantylus* a well-developed sphenethmoid of a type widespread among primitive tetrapods and presumably typical of microsaurs in general. The basisphenoid region, again, in the presence of well-developed basipterygoid processes and a good pituitary fossa, with adjacent openings for the internal carotids and a transverse pituitary vein, is of a primitive and generalized nature. Quite different, however, from other known primitive types is the structure of the more posterior and posterodorsal regions of the braincase. The sharp downward inclination of the anterior process of the supraoccipital is a feature not seen or expected in any other early tetrapod group. Case (1929), in *"Ostodolepis,"* described such a structure. Until I discovered it in *Pantylus,* I was inclined to consider its position in Case's specimen as due to post-mortem injury. Its presence in both these forms strongly suggests that it was characteristic and definitive of microsaurs. Again, the broad sheet of bone extending independently upward from the basisphenoid in *Pantylus* finds no homologue in other ancient groups. It is difficult to imagine a brain configuration fitting this braincase structure. The downward tilt of the supraoccipital eliminates the possibility of the midbrain having extended forward into the area between these dorsal extensions of the sphenoid. If brain tissues were shielded by them, the only possibility is that the cerebral hemispheres were tilted strongly upward and backward here above the diencephalon.

The strong lateral projection of the otic bones and the near-terminal ventral position of the fenestra ovalis are unusual features, somewhat reminiscent of the Seymouriamorpha. The occipital condyles are known in several other microsaurs; where seen, they appear to be essentially similar to the tripartite, *Eryops*-like condyle of *Pantylus*.

Since visceral arches are seldom reported in the older Amphibia, the epi- and ceratobranchials described above in *Pantylus* are at present of little significance in problems of early amphibian relationships. My identification of a V-shaped element as the stapes is supported by information given me by Dr. Carroll that an identical structure, likewise a presumed stapes, is present in *Ostodolepis*, and by Dr. Olson that such a structure is also present in an as yet undescribed gymnarthrid from the Permian of Oklahoma. The whole question of stapedial elements in microsaurs is still an unsettled one. Since many modern amphibians have two auditory ossicles, operculum as well as stapes, there has been a tendency to look for a pair of ossicles in microsaurs, as possible ancestors of the modern Lissamphibia (cf., for example, Gregory, Peabody, and Price, 1956). Shell-shaped structures seen in the ear region of gymnarthrids have been interpreted as stapedial elements, and in some cases other fragmentary materials seen in this region have been thought to be accessory auditory ossicles. I rather doubt both interpretations. As described above, the otic bones in *Pantylus* are essentially shell-shaped and separate readily from the parasphenoid and other braincase elements. The shell-shaped presumed ossicles are probably disarticulated otic bones; the fragmentary materials mentioned are not improbably remains of the adjacent hyoid apparatus.

MICROSAUR RELATIONSHIPS WITH OTHER AMPHIBIANS

In 1933 I provisionally united the various amphibian types possessing "holospondylous" vertebrae in a single group of Lepospondyli, using this Zittel term in an expanded sense and including as Paleozoic components the three groups established by the Miall committee in 1875 — Nectridea, Aistopoda, and Microsauria. Study of the *Pantylus* skull neither adds to nor subtracts from the rather tenuous bonds which may possibly unite these three very diverse groups.

In addition to the more typical microsaurs, such as the gymnarthrids, *Tuditanus,* and *Microbrachis,* a number of other Paleozoic lepospondyls, such as *Lysorophus, Molgophis,* and the "adelogyrinids," are often united, although with some doubt, with the microsaurs. Recent and current studies have done nothing to strengthen this supposed association. It is, in fact, weakened by the results of "modern" studies which show, despite my fond hopes to the contrary, that extreme reduction of the cheek elements, beyond that of the microsaurs, had already taken place in the "adelogyrinids" of fairly early Mississippian times. These forms had departed at the dawn, so to speak, of amphibian evolution very far from the skull pattern of the Labyrinthodontia, while more typical microsaurs, as suggested below, could have been readily derived, as regards most cranial structures, from labyrinthodonts during Carboniferous times.

If we compare the skull of such a microsaur as *Pantylus* with that of early labyrinthodonts, we find that the two agree in many features. Apart from the diagnostic change in the temporal region and greater overlap of roof elements onto the occiput, the dermal roof pattern and that of the jaw are very close to the early labyrinthodont plan. The palate, too, is similar to that of the more primitive labyrinthodonts, and even the broadening of the concave occipital condyle parallels the trend in temnospondyls. The only really distinctive skull features, apart from the "supratemporal" region, are in the dorsal development of the sphenoid, the down-turned anterior process of the supraoccipital, and the lateral extension of the otic region. As far as skull structure is concerned, there is no difficulty in deriving typical microsaurs from labyrinthodonts; and, disregarding vertebral structure, the changes necessary need not, one would think, necessitate more than a fraction of Carboniferous time for their accomplishment. Typical microsaurs, considering skull structure alone, could have evolved from Lower Carboniferous — Mississippian — labyrinthodonts.

I have previously (1950, etc.) suggested that microsaurs may have given rise to part, at least, of the modern amphibian groups. Parsons and Williams (1963) are inclined to doubt this, citing such features as the long and slender body and feeble limbs of many microsaurs as tending to throw them out of consideration as ancestors of the Lissamphibia. But as Carroll and Baird (1968) point out, such forms as *Pantylus* and *Tuditanus* show more sturdy body proportions and stouter limbs than most earlier described types. There is no positive proof, but I continue to believe that microsaurs are still worthy of consideration as possible ancestors of the modern orders. From time to time, most recently by Estes (1965), the rhachitomes, particularly the Dissorophidae, have been suggested as possible ancestors of part or all of the lissamphibian groups. But although Estes is inclined to consider the balance slightly tipped in favor of the rhachitomes, there seems to be little in the way of conclusive evidence.

MICROSAURS AND REPTILES

Certainly typical microsaurs resemble early reptiles in various ways, implying a considerable degree of parallelism if not true relationship, notably in such characters as the tarsus and the attainment of a "holospondylous" construction of the vertebral column. But I am quite unable to understand how anyone who looks even superficially at the skull can believe that any reptiles, such as captorhinomorphs, can be of microsaur descent. The pattern of the temporal region has evolved in a fashion very different from that leading to reptiles; the "supratemporal" (or tabular), reduced and soon lost in reptiles, has enlarged in spectacular fashion in microsaurs. And even in such features as the tripartite condyle, the microsaurs have gone in a direction quite at variance with that proper to reptile ancestors, which have retained and emphasized the primitive single condyle of the ancestral amphibians. It seems to me high time that this impossible theory of reptile descent from microsaurs should be given permanent burial.

I suggested at one time that possibly microsaurs, although not ancestral to reptiles, might, on the contrary, be an offshoot of primitive captorhinomorphs. I have never considered this as too probable, and now believe this to be no more worthy of belief than the opposite relationship. Sudden great expansion of a "supratemporal," already much reduced in even the most primitive captorhinomorphs, a radical shift in structure in the posterior part of the braincase away from the reptilian pattern seen in captorhinomorphs, a paralleling of temnospondyls and modern amphibians in a "last-minute" expansion of the occipital condyle — such shifts seem highly improbable indeed.

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BREVIORA

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STELLICOLA DENTIFER N. SP. (COPEPODA, CYCLOPOIDA) ASSOCIATED WITH A STARFISH IN JAMAICA

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ABSTRACT. *Stellicola dentifer* n. sp., a lichomolgid copepod, is described from Jamaica, where it is associated with the asteroid *Luidia clathrata* (Gray).

INTRODUCTION

The genus *Stellicola,* containing twenty species, has been reported from Europe, West Africa, the Indian Ocean, and the western Pacific Ocean. The new species described here extends the range to Jamaica, and brings to fifteen the number of species in the genus known to occur on asteroids.

The host of the new copepod, *Luidia clathrata* (Gray), is a common starfish in shallow water from North Carolina through the West Indies.

The figures have been prepared with the aid of a camera lucida. The letter after the explanation of each figure refers to the scale at which it was drawn. The abbreviations used are: A_1 = first antenna, A_2 = second antenna, MXPD = maxilliped, and P_1 = leg 1.

ACKNOWLEDGEMENTS

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I wish to thank Dr. Elisabeth Deichmann, Museum of Comparative Zoology, for the identification of the host starfish.

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Family LICHOMOLGIDAE Kossmann, 1877

Genus STELLICOLA Kossmann, 1877

STELLICOLA DENTIFER[1] n. sp.

Figures 1-30

Type material. — 27 ♀♀, 17 ♂♂, and 4 copepodids from 13 *Luidia clathrata* (Gray) in a depth of 2 m, near mangroves, east of the small boat channel leading from the hurricane anchorage, Port Royal, Jamaica. Collected September 10, 1959. Holotype ♀, allotype, and 32 paratypes (21 ♀♀, 11 ♂♂) deposited in the United States National Museum, Washington, and the remaining paratypes in the author's collection.

Female. — The body (Fig. 1) has a moderately wide and only slightly depressed prosome. The length (not including the setae on the caudal ramus) is 1.39 mm (1.31-1.47 mm) and the greatest width is 0.48 mm (0.43-0.51 mm), based on 10 specimens in lactic acid. The ratio of the length to the width of the prosome is 1.47:1. The segment of leg 1 is incompletely separated from the head by laterodorsal furrows and bears a transverse band of fine striae on its dorsal surface. The epimeral areas of the metasomal segments are more or less rounded, except for that of the segment of leg 4, which is truncated.

The segment of leg 5 (Fig. 2) is 104 × 161 μ. Between this segment and the genital segment there is a distinct ventral intersegmental sclerite (Fig. 3). The genital segment is 180 μ long, in dorsal view divided by lateral constrictions into a broad anterior half (width 187 μ) with convex lateral margins and a much narrower and unexpanded posterior half (width 120 μ) with almost straight margins. In lateral view (Fig. 3) the thicker anterior half is separated from the posterior half by an abrupt transverse dorsal constriction (indicated also in Fig. 2). The areas of attachment of the egg sacs are located laterally (Fig. 3), each area (Figs. 4 and 5) bearing two naked setae 20 μ and 11 μ in length and a spiniform process about 8 μ long. The three postgenital segments are 81 × 97 μ, 55 × 83 μ, and 83 × 78 μ from anterior to posterior. The posteroventral margin of the anal segment is smooth.

The caudal ramus (Fig. 6) is elongated, 148 μ in length, its greatest width proximally 31 μ, and its least width distally 19 μ. The

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[1] The specific name *dentifer*, from Latin *dens* = a tooth, and *fero* = to bear, refers to the toothlike process on leg 5 in the female.

ratio of length to width (greatest dimensions) is 4.77:1. The outer lateral seta is 78 μ and the dorsal pedicellate seta 29 μ, both of them naked. The outermost terminal seta is 81 μ, finely barbed in its distal half. The innermost terminal seta is 86 μ, with a few minute barbules near its tip. The two median terminal setae are 176 μ (outer) and 330 μ (inner), both naked and inserted a little ventrally. There is a minute setule 6 μ long on the outer proximal area of the ramus. The ornamentation consists of a few small hairs.

The dorsal surface of the prosome and both dorsal and ventral surfaces of the urosome bear numerous hairs (sensilla) and refractile points. The ratio of the length of the prosome to that of the urosome is 1.1:1.

The egg sac (Figs. 1 and 7) is an elongated oval, about 420 × 200 μ, extends as far as the anal segment, and contains 7-13 eggs, each approximately 100 μ in diameter, but somewhat variable in shape.

The rostrum (Fig. 8) has a broad and rather truncated posteroventral margin.

The first antenna (Fig. 9) is 7-segmented, but a sclerotization on the ventral surface of the third segment (Fig. 10) suggests an intercalary segment. The lengths of the segments (measured along their posterior non-setiferous margins) are: 32 (48 μ along its anterior margin), 75, 31, 33, 32, 20, and 18 μ respectively. The formula for the armature is 4, 13, 6, 3, 4 + 1 aesthete, 2 + 1 aesthete, and 7 + 1 aesthete, as usual in the genus. All the setae are naked.

The second antenna (Fig. 11) is 3-segmented, without a trace of division of the third segment. The first two segments are short, and each bears one seta. The longer third segment bears the usual inner group of three setae, is ornamented with a diagonal row of small spinules on its proximal posterior surface, and has distally three recurved claws and four setae. One claw (50 μ along its axis and inserted terminally) is much larger than the other two claws (both about 19 μ, one inserted on the subterminal anterior surface of the segment, the other subterminally near the large claw). One of the setae has a swollen base, the others are slender. All the elements are naked.

The labrum (Fig. 12) has two divergent lobes, each with a small inner pointed process and a distal hyaline lamella. The mandible (Fig. 13) has on its concave margin a row of long slender spinules; its convex margin bears proximally a group of minute spinules followed by a large hyaline dentiform process and a row of smaller teeth. The long terminal flagellum has a row of spinules along the proximal half of its inner margin. The paragnath (Fig. 14) is a small hairy lobe. The first maxilla (Fig. 15) bears four setae, three terminal and one subterminal. The second maxilla (Fig. 16) has an unarmed first segment. The second segment bears a surficial posterior seta and an inner setiform spine. The terminal lash has on its convex side a large, weakly-sclerotized tooth followed by a row of long slender spinules, and on its concave side a few barbules; across the base of the lash there is a diagonal row of small spinules. The maxilliped (Fig. 17) is 3-segmented. The slender first segment bears two minute distal inner spinules. The second segment is expanded medially and bears two naked setae and numerous spinules. The small third segment bears a barbed spine, a hyaline seta, and a minute spinule; the segment terminates in a large spiniform prolongation with an attenuated tip.

The ventral surface between the maxillipeds and leg 1 is slightly protuberant. A sclerotized line connects the bases of the maxillipeds (Fig. 18).

Legs 1-4 (Figs. 19, 20, 21, and 22) have the following armature (the Roman numerals indicating spines, the Arabic numerals representing setae):

P_1	coxa	0-1	basis	1-0	exp	I-0	I-1	III, I, 4
					enp	0-1	0-1	I, 5
P_2	coxa	0-1	basis	1-0	exp	I-0	I-1	III, I, 5
					enp	0-1	0-2	I, II, 3
P_3	coxa	0-1	basis	1-0	exp	I-0	I-1	III, I, 5
					enp	0-1	0-2	I, II, 2
P_4	coxa	0-1	basis	1-0	exp	I-0	I-1	II, I, 5
					enp	0-1	2, 1	

The inner seta on the coxa of legs 1-3 is long and plumose, but in leg 4 this seta is short (15 μ) and naked. The inner side of the basis in leg 1 is smooth, but in legs 2-4 bears a row of hairs. The endopod of leg 4 (Fig. 22) is much shorter than the exopod, the ratio being about 1:2.3. The first segment is 34 × 29 μ, with its inner seta 105 μ. The second segment is asymmetrical, 43 × 29 μ, and armed with an inner seta 110 μ and two terminal setae 61 μ (outer) and 75 μ (inner). All four endopodal setae have very fine distal barbules. The outer margins of both segments bear a row of hairs, and the second segment has a row of very small spinules on its distal margin.

Leg 5 (Fig. 23) has a prominent, toothlike, distally-directed process on the inner margin of the free segment. This segment is 39 μ long, 34 μ in greatest width at the level of the tooth, and 46 μ in greatest diagonal dimension. The two terminal setae are 91 μ and 39 μ, and the seta on the body near the insertion of the free segment is 31 μ. All three setae are naked. Near the outer side of the free segment there is a slight oblique dorsal ridge with a series of extremely small points (spinules ?).

Leg 6 is probably represented by the two setae near the attachment of each egg sac (Fig. 5).

The color in life in transmitted light is opaque, the eye red.

Male. — The body (Fig. 24) has a prosome more pointed anteriorly than in the female. The length (without the ramal setae) is 1.18 mm (1.11-1.21 mm) and the greatest width is 0.35 mm (0.31-0.41 mm), based on 10 specimens in lactic acid. The ratio of the length to the width of the prosome is 1.74:1.

The segment of leg 5 (Fig. 25) is 55 × 112 μ. Between this segment and the genital segment there is no ventral intersegmental sclerite. The genital segment is 156 × 160 μ, with rather flattened lateral margins in dorsal view. The four postgenital segments are 78 × 99 μ, 73 × 81 μ, 62 × 68 μ, and 62 × 62 μ from anterior to posterior.

The caudal ramus resembles that of the female, but is smaller, 110 × 25 μ.

The rostrum, first antenna (with no aesthetes added), second antenna, labrum, mandible, paragnath, first maxilla, and second maxilla are like those of the female. The maxilliped (Fig. 26) is slender and 4-segmented, assuming that the proximal part of the claw represents the fourth segment. The second segment bears two setae and two rows of spinules. The strongly recurved claw, 159 μ along its axis, bears two very unequal proximal setae and is divided about midway.

The area between the maxillipeds and leg 1 resembles that in the female.

Legs 1-4 are similar to those in the female, with the same segmentation and armature, but the second segment of the endopod of leg 4 (Fig. 27) is more symmetrical.

Leg 5 (Fig. 28) has a free segment 26 × 13 μ, without an inner toothlike process. The two terminal setae are 72 μ and 32 μ, and the adjacent seta on the body is 32 μ.

Leg 6 (Fig. 29) consists of the usual posteroventral flap on the genital segment, bearing two naked setae 32 μ and 44 μ.

The spermatophores (Fig. 30), attached to the female in pairs, are each about 120 × 48 μ, not including the neck.

The color in life resembles that of the female.

COMPARISON WITH RELATED SPECIES

S. dentifer may easily be distinguished from all other species in the genus by the presence of the toothlike process on leg 5 in the female. The genital segment of the female also has a configuration unlike that of any other species.

In most species of *Stellicola* the caudal ramus is not more than twice as long as wide. Two species, however, have a relatively long caudal ramus. In *S. gracilis* (Thompson and A. Scott, 1903), the ratio of length to width of the ramus is 4:1, and in *S. affinis* Humes and Ho, 1967, it is 6.3-7:1 (in the female) and 7.5:1 (in the male). The new species is readily separated from these two species, both of which have a single claw on the second antenna and, in addition, differ in the two points mentioned in the previous paragraph.

S. dentifer seems to be most closely related to the four West African species described by Humes and Cressey (1958), *S. frequens*, *S. astropectinis*, *S. luidiae*, and *S. lautus*, all of which similarly have three claws on the second antenna. Unlike most other species of *Stellicola*, the inner edge of the free segment of leg 5 in these four species is somewhat swollen or irregular; a toothlike process is absent, however.

The twenty-one species of *Stellicola* may be grouped geographically on the basis of the number of claws on the second antenna. Those from the Indian and western Pacific oceans (15 species) have one such claw. The only known species from Europe and the Mediterranean Sea, *S. clausi* (Rosoll, 1889), has two claws (see Bocquet and Stock, 1962). The five species from the tropical Atlantic Ocean (four from West Africa and one from Jamaica) have three claws.

SUMMARY

The new species *Stellicola dentifer* is associated with the asteroid *Luidia* clathrata (Gray) in Jamaica. The copepod may be recognized within the genus by the prominent toothlike process on leg 5 in the female. Four West African species of *Stellicola* appear to be related to the new Jamaican form.

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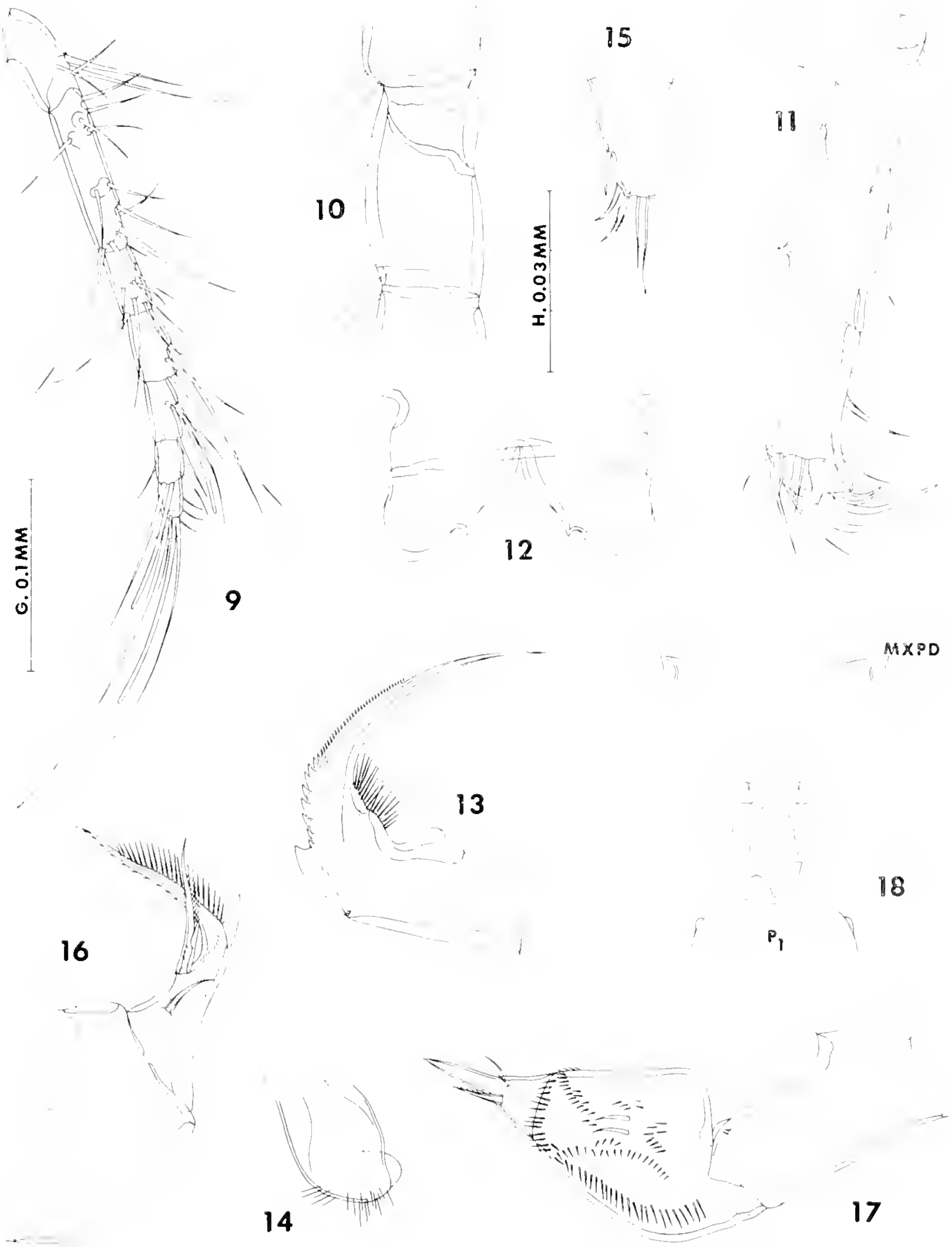
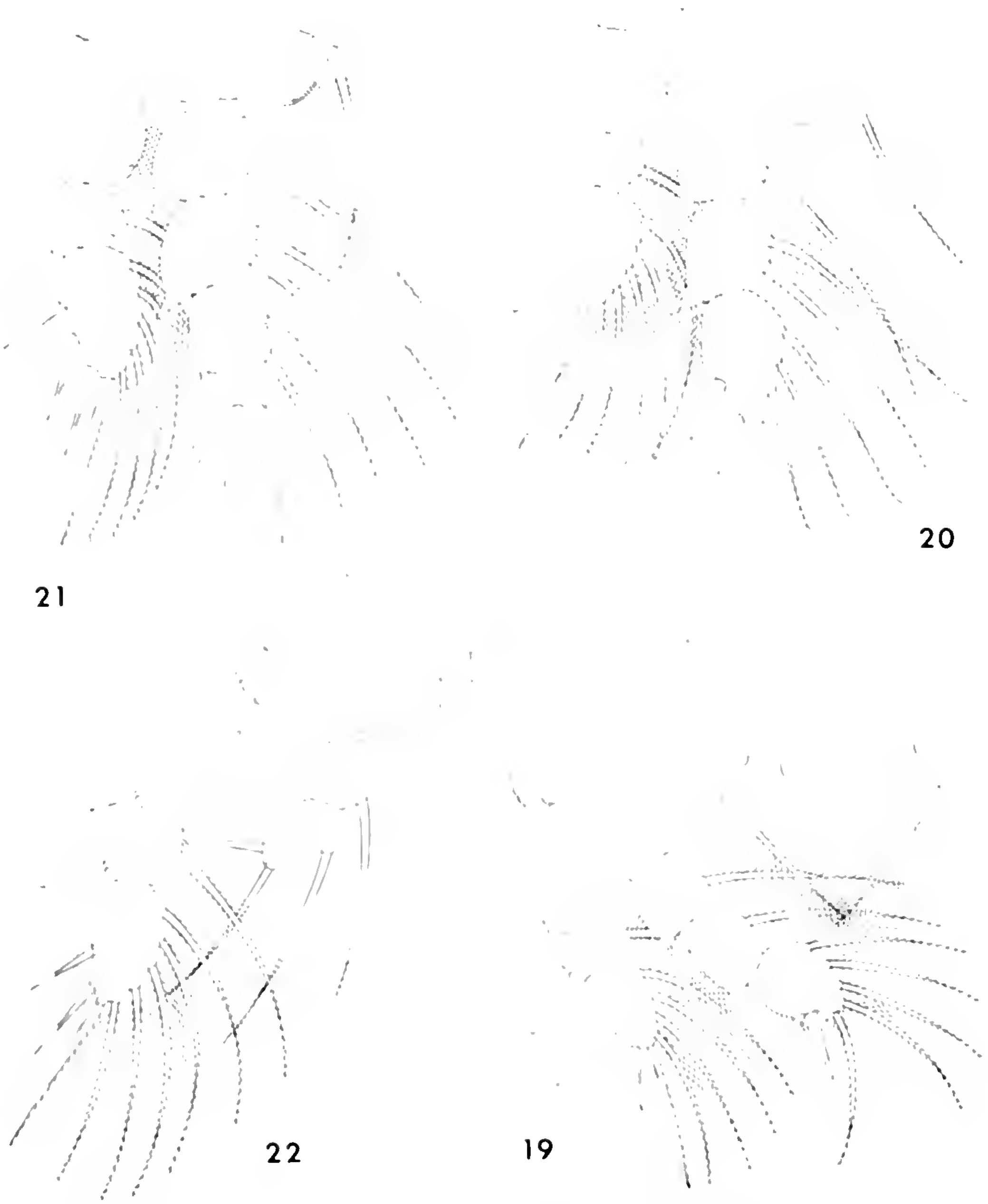
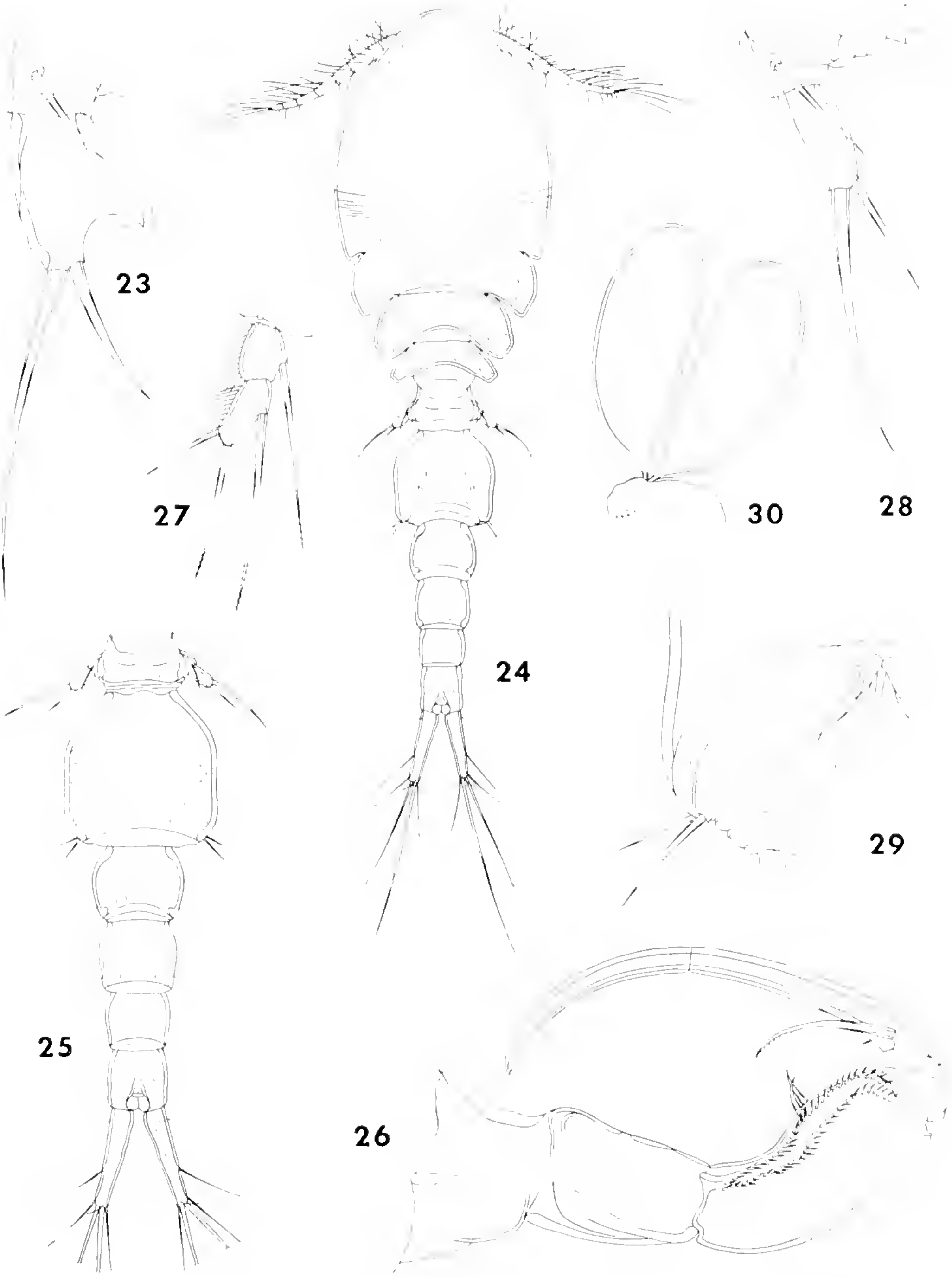
Figures 1-8. *Stellicola dentifer* n. sp., female: 1, dorsal (A); 2, urosome, dorsal (B); 3, segment of leg 5 and genital segment, lateral (B); 4, area of attachment of egg sac, dorsal (C); 5, area of attachment of egg sac, lateral (C); 6, caudal ramus, dorsal (D); 7, egg sac, dorsal (E); 8, rostrum, ventral (F).



Figures 9-18. *Stellicola dentifer* n. sp., female: 9, first antenna, anterodorsal (G); 10, third segment of first antenna, posteroventral (H); 11, second antenna, posterior (D); 12, labrum, ventral (D); 13, mandible, posterior (C); 14, paragnath, posterior (C); 15, first maxilla, posterior (C); 16, second maxilla, posterior (C); 17, maxilliped, antero-inner (C); 18, area between maxillipeds and leg 1, ventral (G).



Figures 19-22. *Stellicola dentifer* n. sp., female: 19, leg 1 and intercoxal plate, anterior (G); 20, leg 2, anterior (G); 21, leg 3, anterior (G); 22, leg 4 and intercoxal plate, anterior (G).



Figures 23-30. *Stellicola dentifer* n. sp. Female: 23, leg 5, dorsal (C). Male: 24, dorsal (E); 25, urosome, dorsal (B); 26, maxilliped, anterior (D); 27, endopod of leg 4, anterior (G); 28, leg 5, dorsal (C); 29, leg 6, ventral (D); 30, spermatophores, attached to female, lateral (G).

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CYTOTAXONOMIC STUDIES ON SOME UNUSUAL IGUANID LIZARDS ASSIGNED TO THE GENERA *CHAMAELEOLIS, POLYCHRUS, POLYCHROIDES,* AND *PHENACOSAURUS,* WITH BEHAVIORAL NOTES

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INTRODUCTION

ABSTRACT. Chromosome data are presented for four species of iguanid lizards. *Phenacosaurus heterodermus* has a diploid number of 36, with 12 metacentric macrochromosomes and 24 microchromosomes. *Chamaeleolis porcus* also has 12 metacentric macrochromosomes. The exact number of microchromosomes was not ascertained, but it is quite similar to that in *Phenacosaurus.* The karyotypes found in these two species resemble the primitive iguanid condition and that most frequently found in alpha *Anolis. Polychrus femoralis* has an apparent diploid number of 26, with 10 pairs of acrocentric and one pair of submetacentric macrochromosomes, and two pairs of microchromosomes. *Polychrus peruvianus* has 20 acrocentric macrochromosomes and 8 microchromosomes ($2n = 28$). A karyotype with low diploid number ($2n = 30$ or less) and few metacentric macrochromosomes is very unusual in iguanid lizards — previously reported only for *Polychrus marmoratus.* Its presence in the two presently studied *Polychrus* confirms their very close relationship *inter se,* but gives no clue to their relationship to other members of the family Iguanidae. *P. peruvianus* has previously been assigned to the monotypic genus *Polychroides.* However, osteological and cytological data show its very close relationship to *Polychrus,* and we formally propose the synonymy of *Polychroides* with *Polychrus.* Notes on behavior and ecology are appended for the four species. Although there may be a nomenclatural problem surrounding the use of the name *P. femoralis,* our Peruvian animal resembles *P. femoralis* from Loja,

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Ecuador. This is the first record of an apparent *Polychrus femoralis* from Peru.

We have recently obtained several poorly known iguanid lizards on field trips to Peru (RBH), and Cuba and Colombia (GCG). Although our observations and chromosome data are meagre, they provide insight into the relationships of these lizards. Field and behavioral notes are appended because of the paucity of information on these species and because we have the first record of an apparent *Polychrus femoralis*[3] from Peru.

The genus *Chamaeleolis* is endemic to Cuba and the adjacent Isle of Pines. Long considered monotypic, Garrido and Schwartz (1968) have demonstrated that there are two distinct species. Both are arboreal, moderate-sized lizards (snout-vent of adult males 155 mm), quite closely related to *Anolis*. They share with anoles extensible dewlaps and adhesive lamellae on the toes but differ in a number of osteological features, the most conspicuous of which is a parietal crest that extends far back over the neck (Etheridge, 1960), giving the animals a marked resemblance to true old-world chamaeleons.

Phenacosaurus is an iguanid genus with very close affinities to *Anolis*. Dunn (1944) listed a series of characters by which the genus was supposed to differ from *Anolis* (e.g. a prehensile tail, a heterogeneous scutellation with large and small scales intermixed, a dorsal crest of enlarged scales), but Etheridge (1960) pointed out that all of these characters occur individually in a number of species of *Anolis*. However, because of a number of osteological peculiarities (low number of sternal ribs, high number of parasternal chevrons), Etheridge retained the genus.

Phenacosaurus is known predominantly from high altitudes (1800-3500 m) in the Eastern Andes of Colombia. There are currently four recognized species, but *richteri* and *paramoensis* are undoubtedly synonyms of *P. heterodermus*, and there is at least

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[3] The single specimen reported here runs down to *P. femoralis* in the key provided by H. W. Parker (1935: 516). Examination of comparative material (all of it *femoralis* by Parker's key) indicates that there may be as many as three distinguishable populations. A specimen in the United States National Museum from Guayaquil, the type locality of *femoralis*, has markedly larger scales than Parker's Loja specimens, which closely resemble the Peruvian animal. Pending revisionary studies, we believe it to be preferable to use the name *femoralis* for all this material, including our Peruvian animal.

one undescribed species from Ecuador (J. D. Lazell, Jr., personal communication).

Polychrus is a genus of arboreal lizards from Central and South America (including Trinidad) comprising about five distinct species (Parker, 1935). Etheridge (1960) compared 22 characters in *Anolis* and *Polychrus* (excluding characters unique to *Anolis* or common to the family Iguanidae) and found that 20 were shared by *Anolis* and *Polychrus*. He wrote, "Although there appears to be a close correspondence between *Polychrus* and the anoles, there are striking differences. Most of these differences, however, are features which are either unique to the anoles or unique to *Polychrus* and therefore tell us little more than that the anoles are separated from other members of the family, including *Polychrus*, by a wide morphological gap" (Etheridge, 1960: 111). He also pointed out that *Polychrus* and *Chamaeleolis* are highly arboreal, "and unusual in their habit of slow, deliberate movement. The similarities of these genera may well be parallel adaptations to a similar way of life, yet the occurrence of multiple parallel developments may, in itself, be an indication of relationship between the groups in which it occurs" (Etheridge, 1960: 113).

The monotypic genus *Polychroides* was erected by Noble (1924) when describing a new species of iguanid lizard (*P. peruvianus*) from the provinces of Cajamarca and Piura, northern Peru. Noble's comments on the affinities of the new genus were quite confused and are here quoted verbatim. On p. 109 in "Remarks" following the generic diagnosis he wrote: "The generic status of many of the slow-moving arboreal iguanids is very uncertain. The species described below cannot be referred to either *Enyalius*, *Enyalioides* or *Polychrus* as at present defined. It seems most closely related to *Polychrus* with which it agrees in its femoral pores, large head scales, subequal third and fourth toe and its sacculated lung. I have seen both *Polychrus* and *Polychroides* alive and have been struck by their great similarity in behavior. The pronounced nuchal crest of the latter readily distinguishes it from the former."

On p. 110, however, in the "Remarks" which follow description of the species he stated: "This species is closely allied to *Enyalioides festae* Peracca from which it differs in its larger head scales and gular sac, also in certain differences in the scutation of the digits and head. I would not hesitate to refer it to the genus *Enyalioides* were it not that this procedure would require a considerable modification of our present conceptions of that genus."

Etheridge (1960) was unable to find any skeletal differences between *Polychrus* and *Polychroides* in X-ray studies of iguanid genera, and he therefore cited *peruvianus* in his list of material examined as another species of *Polychrus*. Only the external character of a dorso-nuchal crest distinguished *peruvianus* from other *Polychrus*.

Chromosomes have been useful in elucidating relationships of iguanid lizards. The majority of species studied have a karyotype consisting of six pairs of metacentric macrochromosomes and eleven or twelve pairs of microchromosomes (Gorman, Atkins and Holzinger, 1967; Gorman and Atkins, 1967, 1968). One species, *Plica plica*, showed apparent centric fissioning with four pairs of acrocentric macrochromosomes. The chromosomes of the single species of *Polychrus* examined, *P. marmoratus*, were so different from all other species of iguanids of which karyotypes are known that it was difficult to relate this genus to any of the others (Gorman, Atkins, and Holzinger, 1967). Female *P. marmoratus* have a diploid number of 30, consisting of 20 acrocentric macrochromosomes and 10 acrocentric microchromosomes. Males have a diploid number of 29, with 1 metacentric and 19 acrocentric macrochromosomes, and 9 acrocentric microchromosomes. In both *Anolis* (Gorman, 1967) and *Sceloporus* (Lowe, Cole, and Patton, 1967), species have now been found with high numbers of acrocentric macrochromosomes. These species, however, are characterized by high diploid numbers, greater than $2n = 30$, the formula which appears primitive for the family Iguanidae (Gorman, et al., 1967). The probable explanation for these high numbers is centric fission of the metacentric macrochromosomes (Gorman, Baptista, and Bury, 1969).

MATERIALS AND METHODS

Chromosome preparations were made by tissue culture of whole blood following methods already outlined; by culture of marrow obtained from the femur and treated in the same fashion as blood; and by direct testis preparations (see Gorman, et al., 1967). The specimens used were one female *Polychrus peruvianus* (Museum of Vertebrate Zoology, no. 82834), one female *Polychrus femoralis* (M.V.Z. 82835), one male *Chamaeleolis porcus* (Museum of Comparative Zoology, 100472), and one male *Phenacosaurus heterodermus* (M.C.Z. 104409).

Chromosome spreads were photographed and karyotypes analyzed as best we could. Unfortunately, for *Chamaeleolis*, *Polychrus peruvianus*, and *P. femoralis*, we obtained few mitotic divisions, and we are unable to present fully definitive karyotypes or diploid numbers, though the material permits interesting comparisons. Numerous divisions from the testis of *Phenacosaurus* were studied.

RESULTS AND DISCUSSION

Only four clearly resolved metaphase plates were found in *P. peruvianus*, all with 28 chromosomes, all acrocentric. There is not a sharp break in size between macro- and microchromosomes; however, 20 might be termed macrochromosomes and 8 microchromosomes (Fig. 1a). This is very similar to the karyotype of female *Polychrus marmoratus*, and this is only the second species of iguanid reported to date that has a karyotype of all acrocentric chromosomes. So few cells were seen that we cannot safely assume that the diploid number is 28 — but it is quite clear that the karyotype of *P. peruvianus* resembles that of *P. marmoratus* to such a great extent that considering these forms as members of separate genera obfuscates their close relationship. We formally propose the synonymy of *Polychroides* with *Polychrus*.

Few divisions were obtained in our specimen of *P. femoralis* — but, again, there are enough data to establish both its close relationship to the other *Polychrus* in the similarity of the specialized karyotype and its uniqueness among the species thus far examined. The diploid number appears to be 26. (This is based upon only four metaphase plates; additional spreads were seen, but, because of overlaps, precise counts could not be made.) In all cells, there is one pair of submetacentric chromosomes (Fig. 1b). Within the genus *Polychrus*, a submetacentric chromosome had previously been seen only in the male of *P. marmoratus*, where it is quite clearly the Y chromosome (Gorman, et al., 1967). In *P. femoralis* also, the largest chromosome pair is clearly subacrocentric with minute short arms present. There is a total of 11 pairs of macrochromosomes and 2 pairs of microchromosomes in the cells that were carefully analyzed. The karyotype of *P. femoralis* is most likely derived from a *marmoratus*-like karyotype of 2n=30. Centric fusions of microchromosomes to macrochromosomes would account for the reduction in diploid number and the appearance of submetacentric and subacrocentric chromosomes.

Numerous metaphase plates were observed in *Chamaeleolis porcus,* but we lack definitive information on the number of microchromosomes. It is quite clear that the karyotype resembles the "typical" iguanid in having six pairs of metacentric macrochromosomes and a series of more than 20 microchromosomes (Fig. 2).

Fig. 1. Karyotypes of *Polychrus*. a., *P. peruvianus* female. There are 28 acrocentric chromosomes. Bone marrow preparation, Giemsa Stain. b., *P. femoralis* female. There are 26 chromosomes; one pair (top row, far right) is submetacentric. Leukocyte culture, Giemsa stain.

Only testis preparations were made for *Phenacosaurus heterodermus*. There were numerous meiotic and mitotic divisions. In meiosis we can clearly see six large macrobivalents and 12 considerably smaller microbivalents (Fig. 3). In mitosis, it was quite clear that the macrochromosomes were metacentric. Thus, the diploid number is 36, with 24 microchromosomes.

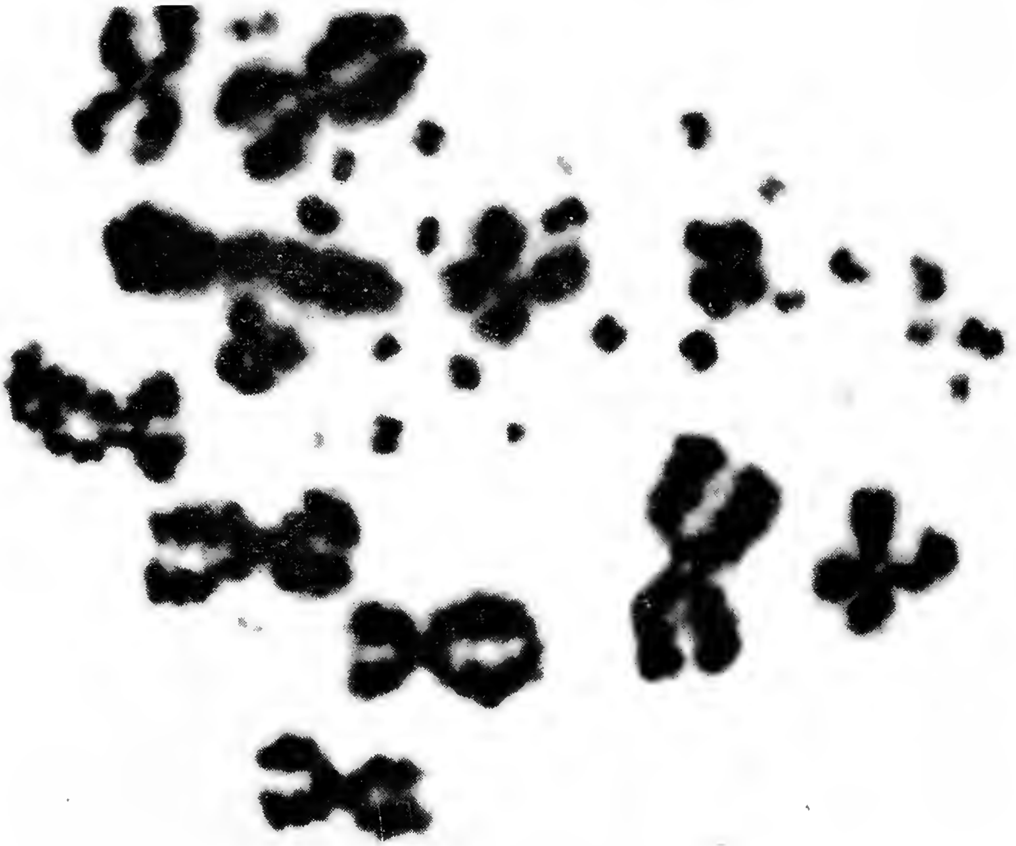

Fig. 2. Mitotic metaphase of *Chamaeleolis porcus* male showing the "typical iguanid" condition of 12 metacentric macrochromosomes, and a sharp break in size between the macro- and microchromosomes.

Among *Anolis*, Etheridge (1960) defined two major groups termed *alpha* and *beta*. Chromosome studies (Gorman, et al., 1967) have shown that the primitive *alpha* karyotype is identical with that of the primitive iguanid condition (12 metacentric macrochromosomes, 24 microchromosomes). In a recently proposed classification of iguanids on the basis of structure of the caudal vertebrae (Etheridge, 1967), *Chamaeleolis* and *Phenacosaurus* were placed in a group with the *alpha* anoles; chromosomes support this classification.

Polychrus remains a puzzle within the iguanids. Now that three species have been studied it is quite clear that they are close to each other *inter se,* but distinctly different from anoles and anoline genera such as *Chamaeleolis, Phenacosaurus,* and *Anisolepis* (Gorman, et al., 1967).

Since this paper was originally written, we have received the following new data.

On November 26, 1968, Dr. John Wright of the Los Angeles County Museum collected a male *Polychrus peruvianus* at 3.5 km east of the junction between Bagua Grande and Bagua Chica, 15.5 km west of Bagua Grande, Amazonas Dept., Peru, at an altitude of 2,000 feet. (Field catalog number P-927; to be deposited in L.A.C.M.)

Testes were minced and allowed to settle in a hypotonic citrate solution (as no centrifuge was available), the citrate was removed with an eye-dropper, and fixative was added. This field preparation was then brought back to the United States, where slides were made some two months later.

Dr. Wright has kindly consented to our examination of the slides and utilization of the data. At diakinesis there are 13 bodies.

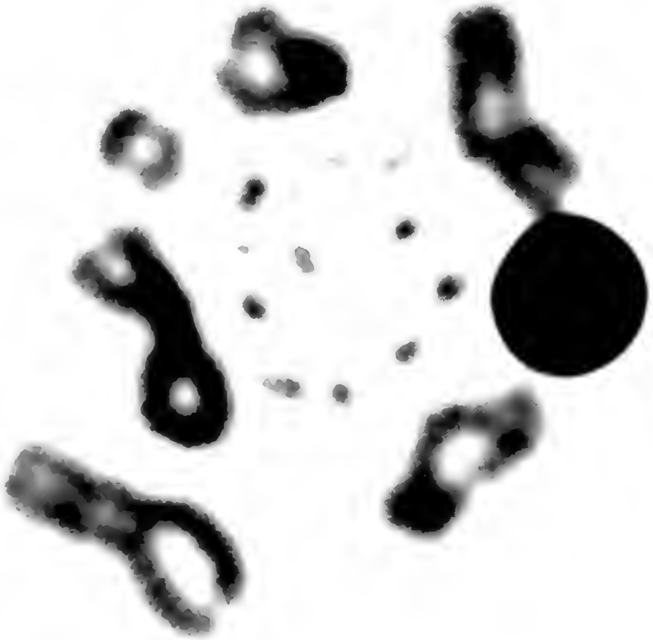

Fig. 3. Diakinesis in *Phenacosaurus heterodermus*. There are six large bivalents, and 12 microbivalents. n = 18. Large round black area is a sperm head, not part of the meiotic figure.

12 bivalents, and a trivalent. The male diploid number is thus expected to be 27. One mitotic metaphase was seen, and 27 chromosomes were counted. Position of the centromere could not be ascertained. One clear metaphase II cell had 14 chromosomes, all acrocentric.

These data are consistent with the sex chromosome situation known in *Polychrus marmoratus*, in which the males have a diploid

Fig. 4. Diakinesis of *Polychrus peruvianus* male. There are 13 bodies, 12 bivalents, and a sex trivalent (arrow).

number one lower than the females, the Y chromosome is metacentric (not demonstrated for *P. peruvianus*), and a sex trivalent is clearly evident at meiosis (Gorman, Atkins, and Holzinger, 1967).

The finding of 12 bivalents and a trivalent in *P. peruvianus*, with an expected male 2n of 27, gives further strength to our assumption that female 2n = 28 (the latter figure having been arrived at with the examination of relatively few cells). Figure 4 illustrates diakinesis in *P. peruvianus*.

NOTES ON *POLYCHRUS*

POLYCHRUS PERUVIANUS

Five specimens of *Polychrus peruvianus* were collected:

MVZ 82834 El Arenal, Rio Huancabamba, elevation 3000
82388 ft., 7 km N, 50 km E of Olmos, Dept. Caja-
83678 marca, Peru.
83679
MVZ 82413 (skin and skeleton). Tingo, Rio Utcubamba, elevation 3000 ft., 30 km S, 41 km E of Bagua, Dept. Amazonas, Peru.

El Arenal is on a terrace above the Rio Huancabamba. The hillsides are dry and rocky, and the terrace has a predominance of mesquite (*Prosopis*) interspersed with cultivated areas. All specimens were collected on mesquite branches.

The Tingo individual was captured by Dr. Carl Koford at night on a horizontal branch of an unidentified tree. Stomach contents included several Hymenoptera and a leaf fragment. The largest ovarian follicles were less that 2 mm in diameter.

This locality is much wetter than El Arenal. Bromeliad-laden trees up to 40 feet are found on the steep hillsides, and dense second-growth vegetation covers the valley floor.

Body coloration in life (MVZ 82834) was medium yellow-green with a narrow, pale yellow band running from the eye to the groin and olive-drab saddles on the dorsum and tail. Small irregular yellow marks were spaced between the saddles. Some capacity to darken the body colors was observed in captivity.

The tail of this specimen was slightly prehensile. *P. femoralis* gave no evidence of this ability. Both species emitted a nasal salt solution in captivity (see Templeton, 1967).

P. peruvianus has a more protrusive gular flap than *P. femoralis*. In addition, only *P. peruvianus* possesses a row of raised scales forming a mid-gular crest.

POLYCHRUS FEMORALIS

On 31 August 1967, one gravid female of this species was captured near Molino, elevation 2300 ft., 21 km E, 7 km N of Olmos, Dept. Lambayeque, Peru (5.9° S/79.6° W). This specimen (MVZ 82835) represents a considerable range extension from the record in Loja (Parker, 1932) and an apparent Peruvian record.

She was oriented head down on a vertical branch of a plant about 5 ft. tall and remained motionless until capture. The locality is in a narrow river valley. Deciduous woodland alternates with open areas cleared for farming.

She was kept alive and placed in a runway with a temperature gradient beginning 18 September. Water was sprinkled daily at the cool end. On 27 September she laid 12 eggs at the cool, moist end of the runway. The eggs were removed and placed in an incubator. Egg size eight hours later averaged 19.6 mm in length and 11.3 mm in width. The shell texture was soft and leathery. Mold developed on the eggs by 4 October and they subsequently decayed.

In captivity movement was rare. When prodded, she exhibited a leaping form of locomotion described by Boker (1935) as "bipedal leaping" for *Polychrus marmoratus*. Davis (1953) observed a similar method of locomotion in *Corythophanes cristatus*.

In life she was light yellow-green with pronounced brown saddles on the dorsum. The capacity for color change in this specimen was less marked than in *P. peruvianus*.

BEHAVIOR IN CAPTIVITY

Davis (1953) outlined a sequence of four defensive responses used by *Corythophanes cristatus* against apparent predators. These can be grouped into two general categories:

I. Passive defense
    A. Behavioral and morphological camouflage
    B. Catalepsy to eliminate all movement not associated with a positional change and thus decrease the probability of detection
II. Active defense
    A. Active postural movements to increase the apparent size of the animal
    B. Aggressive biting as a last resort

Davis stated that the defensive response given was geared to the relative immediacy of the threat to the animal's safety. The more immediate the threat, the more active the response.

Both *Polychrus peruvianus* and *P. femoralis* exhibited this sequence of defensive traits in captivity but did differ in degree of response. Since only one specimen of each species was observed, these notes should be considered tentative.

Behavioral and morphological camouflage is well marked in both species. The colors and patterns render detection of these animals difficult in their arboreal habitats. Their relative immobility and capacity for color change accentuate this concealment. In both the field and captivity, *P. femoralis* relied more on immobility than on other defensive responses.

Behavior similar to the catalepsy of walking sticks (Phasmidae) has been reported for several arboreal lizards (reviewed in Davis) and was present in these two species as well. *P. peruvianus* could be easily induced into this behavior by forcibly altering its position, but both used it when coming to rest after voluntary movement. When matched with other types of camouflage, Davis felt that this behavior aided in concealment.

In response to a threat, many animals are recorded to increase the apparent size of the body or parts of the body by behavioral posturing. This behavior is manifest in social encounters, as well. Postural movements common to both *Polychrus* species involve lateral compression of the body, expansion of the throat fan, and head bobbing. The plane of expansion is sagittal and presented broadside for both, as is the case in *Corythophanes*. The expanded area is thus displayed to maximum advantage.

P. peruvianus would often gape when posturing. If approached closely, she would lunge forward, maintaining balance by the two hind legs and tail. She would bite vigorously if given the opportunity. In contrast, *P. femoralis* could rarely be induced to bite. But it would often attempt to escape by leaping.

Of the two species of *Polychrus* under discussion, the behavior of *P. peruvianus* was more similar to that of *Corythophanes* than was that of *P. femoralis*. It is perhaps of significance that *P. femoralis*, having a much less pronounced gular flap than the other two species, relied less on active postural movements and more on passive camouflage.

NOTES ON *CHAMAELEOLIS*

Although rare in collections, *Chamaeleolis* is widely distributed throughout Cuba. Through the help of Orlando Garrido, we obtained a juvenile male *C. porcus* from La Florida, Sabanilla, Oriente Province, and a larger (but subadult) male from La Casimba, eight kilometers west of Maisi, Oriente Province.

Wilson (1957) published a note on the behavior of a captive *Chamaeleolis*. Although he called this *C. chamaeleontides* (sic.), the specimen has been subsequently re-identified by Schwartz as *porcus*. Wilson reported, "its behavior was strikingly chamaeleon-like and quite different from that of several species of *Anolis* (including the giant *A. equestris* Merrem) which the author has observed in captivity." He stated that it was very sluggish even when freshly captured, and that it could be left on a laboratory table without much danger of its wandering. Often, it would remain in the same spot for hours or even days without changing its position. When confronted with food in the form of living insects, it would move deliberately and without hurrying. Experiments using a live male *Anolis equestris* and a cardboard model resembling a male *Chamaeleolis* failed to elicit any aggressive response. Only once, in the year that he had the specimen, did it extend its dewlap — and this was without any apparent external stimulus.

Our observations are not at all in accord with this description. Our specimens would actively jump toward prey (crickets, grasshoppers, and mealworms). They would often scamper away when left out in the open. Garrido and Schwartz (*op. cit.*) point out that *C. porcus* is "at least capable of quick and decisive action." They give a detailed account of the escape behavior of one specimen encountered in the field. Our *Chamaeleolis* were not so quick as *Anolis*, but certainly did not show the incredibly slow movements of true chamaeleons. Furthermore, they were quite aggressive. They would display to each other by extending the dewlap fully, opening the mouth and protruding the tongue. They also displayed in similar manner to *A. equestris*. When handled, they would extend the dewlap and often would bite. Unfortunately, no films were taken of the displays

It appears, then, that the social behavior of *Chamaeleolis* has been misunderstood. Its reported sluggishness and immobility appear to be facultative rather than obligatory and may well be associated with its cryptic coloration. The ability to move quite quickly, and the fact that anole-like territorial responses were easily elicited implies that the behavior and social structure of *Chamaeleolis* may be quite similar to that of most anoles.

NOTES ON *PHENACOSAURUS*

Previous notes on *Phenacosaurus* have dealt with specimens in captivity (Osorno-Mesa and Osorno-Mesa [1946], on shedding of skin, incubation of eggs, feeding habits, etc., and Kästle [1965], a detailed ethological study with particular emphasis on social behavior).

On July 10, 1968, Dr. Jorge Hernandez, of the Universidad Nacional, Bogota, led Gorman and J. F. Lynch on a one-day trip specifically to collect *Phenacosaurus* in Chia (Cundinamarca), a semi-rural suburb of Bogata (at about 35 km distance, alt. ca. 2700 m.) and collected between 11 am and 2:30 pm. The day was overcast, with intermittent showers, and cold. A thermometer was not available, but the temperature for most of the time was probably not in excess of 14° C., the mean temperature of that immediate area.

The roads were lined with shrubbery, often blackberries, which separated either pasture-land or homes.

Three *Phenacosaurus* were in the first blackberry bush examined. Two, a male and a female, were collected. In the course of the afternoon, 14 of these supposedly rare lizards were collected. Most often, more than one was taken at a time, usually in groups of two, sometimes of three. One pair was actually in bodily contact — the male's chin was touching the tail of the female.

All but two of the lizards were on blackberry bushes, generally 1-3 feet above the ground, and usually on a bare branch. It is likely that as many were missed as were caught — especially those in leafy parts of the bushes. The escape response is to drop down, often clinging to a branch with the prehensile tail, and then to slink slowly away. The most usual perch position was almost horizontal; only one individual was perched vertically, head down.

In review of body temperatures in reptiles, Brattstrom (1965) listed 18.0° C. as the minimum voluntary temperature for an iguanid lizard. This was *Uma notata*, which, in fact, has a mean body temperature of 38.6° when active, and the 18° probably represents an unusual reading. Normally, iguanids living in cold temperatures bask in sunlight until warmed to a preferred body temperature of 33 ± 3°. An extreme example was reported by Pearson (1954) for *Liolaemus multiformis* at high altitudes in Peru. He found that the intense isolation enables these species to warm to body temperatures of 35°, with shade temperatures as low as 11°.

Phenacosaurus was remarkable for an iguanid lizard because it was normally active at low temperatures with no opportunity to warm up. We consider it quite possible that its preferred body temperature is well below that of any other iguanid reported to date.

ACKNOWLEDGMENTS

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RELATIONSHIPS OF TWO CRETACEOUS LIZARDS (SAURIA, TEIIDAE)[1]

Richard Estes

ABSTRACT. *Peneteius aquilonius,* n. gen., n. sp., from the late Cretaceous of Montana, is a small teiid lizard with complex cheek teeth. It most closely resembles the modern South American teiids *Dicrodon* and *Teius* and also shows resemblance to the large Cretaceous teiid *Polyglyphanodon* from Utah. *Chamops segnis* Marsh, from the late Cretaceous of Wyoming, resembles the modern teiid *Callopistes maculatus. Meniscognathus altmani* Estes, from the same locality as *Chamops,* may be related to the modern teiids *Cnemidophorus* and *Kentropyx.*

These resemblances indicate that three distinct groups of primitive teiids living today in South America were in existence in North America during late Cretaceous time.

INTRODUCTION

In 1964 I described teiid lizards of modern type from the late Cretaceous Lance Formation of Wyoming. These included: (1) *Chamops segnis,* a species suggested to resemble the Recent *Crocodilurus-Tupinambis* line in dental adaptations (see below), although it differed from all other so-called "macroteiids" (Vanzolini and Valencia, 1965) by having a parietal foramen; and (2) *Meniscognathus altmani,* which bore resemblances to the *Kentropyx-Ameiva* line in both dental apparatus and externally-concave mandibles. Two other forms, (3) *Leptochamops denticulatus* and (4) *Haptosphenus placodon,* were less clearly related to modern forms.

Polyglyphanodon sternbergi, a large late Cretaceous lizard from Utah, was originally described by Gilmore (1940). In 1942 he placed it in a separate family Polyglyphanodontidae, but stated

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[1] Fossil vertebrates from the late Cretaceous Hell Creek Formation, Montana: Contribution No. 2 (Contrib. No. 1 is Estes, 1965, Copeia, No. 1, pp. 90-95.)

that only tooth characters separated it from the Iguanidae. Hoffstetter (1955) was the first to note the resemblance of *Polyglyphanodon* to the teiids and in 1962 suggested that it be referred to the Teiidae. A smaller, related genus *Paraglyphanodon* was also named by Gilmore (1940, 1943). These animals are currently being restudied by Mr. William MacLean, 3rd.

A vertebrate fauna recently recovered from the late Cretaceous Hell Creek Formation, Montana, resembles that from the Lance Formation (Sloan and Van Valen, 1965; Estes, Berberian, and Meszoely, ms.). A single dentary from the Hell Creek Formation sample belongs to a teiid lizard of unusual type and is described here. I interpret this fossil as in some ways intermediate between *Polyglyphanodon* and the modern genera *Teius* and *Dicrodon*. It is probably closer to the latter genera and provides an indication that a third major living "macroteiid" line was already in existence in late Cretaceous time in North America.

ORDER SAURIA

SUBORDER SCINCOMORPHA

Family Teiidae

Peneteius aquilonius, n. gen., n. sp.

Holotype. MCZ (Museum of Comparative Zoology, Harvard University) 3612, fragmentary right dentary with four complete teeth and the bases of four others (Fig. 1).

Horizon and locality. West half section 9, T 22 N, R 43 E, McCone County, Montana; Hell Creek Formation. Collected by MCZ party in 1964.

Etymology. Latin, *pene*, almost; *aquilonius*, northern.

Diagnosis. Differs from Recent *Teius* and *Dicrodon* in having tooth crests nearly transverse, but the lateral cusp anterior to medial cusp rather than posterior. Differs from fossil genera *Paraglyphanodon* and *Polyglyphanodon* in lacking transverse expansion of tooth and in having external crests of principal cusp less well developed.

Description. Jaw fragment relatively delicate; Meckelian groove wide, indicating a large splenial; bony separation between Meckelian canal and more lateral canal (for vascular and nervous structures) set far medially, reducing depth of Meckelian groove. Teeth subacrodont, becoming molariform posteriorly; most posterior (broken) tooth evidently the largest; tooth bases subcircular, relatively thin-walled; *sulcus dentalis* absent. Tooth crowns anteroposteriorly compressed into crests; crests essentially transverse and formed by two main cusps, the labial one relatively the higher; both cusps connected by a transverse crest. Main cusps closer together and difference in height less pronounced in more anterior teeth, but cusp axis remains transverse; crests extending anteriorly and posteriorly from main cusps, forming slight basins on each side of crown; faint depressions present lingually on each side of main lingual cusp.

Discussion. The widely-open Meckelian groove in combination with the unusual tooth crowns and heterodonty indicate relationship of *Peneteius* to the Teiidae. Closest resemblances within that family are to Recent *Dicrodon* and *Teius* from South America

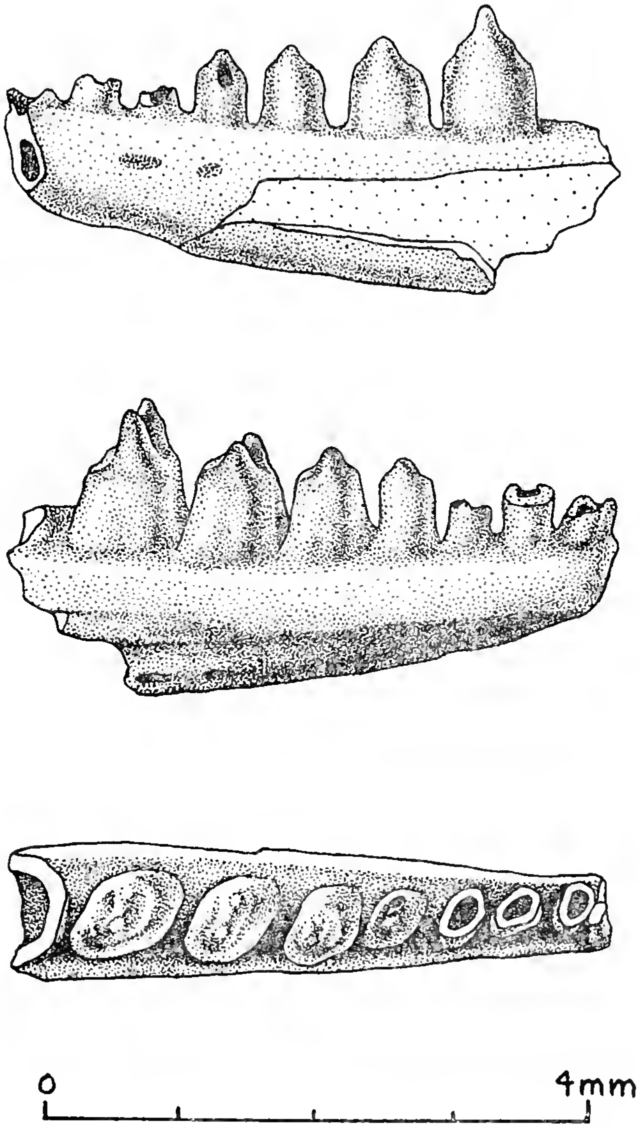

Fig. 1. *Peneteius aquilonius,* n. gen., n. sp., MCZ 3612; *a,* labial, *b,* lingual, *c,* occlusal view of fragmentary left dentary.

and the fossil *Paraglyphanodon* and *Polyglyphanodon* from the Cretaceous of Utah. *Paraglyphanodon* is the smaller of the two fossil genera. Teeth of the two described species *P. utahensis* and *P. gazini* show a morphological series that could lead to the strongly transverse, crested tooth condition seen in *Polyglyphanodon*, and it is possible that *Paraglyphanodon* is only a small individual or the young of the former. The most complex and cuspate teeth in any Recent teiid occur in *Teius teyou;* Figure 2 shows occlusal views of teeth of pertinent living and fossil species. The two species of *Dicrodon* are quite distinct in tooth patterns and in many other characteristics as well (Schmidt, 1957); Schmidt's species *D. holmbergi* has been synonymized with *D. guttulatum* by Fugler (1967). The Recent species figured here all differ from *Peneteius aquilonius* in orientation of the two major cusps and in lacking a faint depression on the lingual side of the crown. The tooth pattern of *Peneteius* is distinct from the Utah Cretaceous genera in lacking strongly-curved, prominent labial crests that may (*Polyglyphanodon*) or may not (*Paraglyphanodon*) connect with the secondary cusp. Resemblances are shown to the modern genera

Fig. 2. Crown patterns of teiid teeth. All are posterior teeth of left dentaries. *a*, *Dicrodon guttulatum*, MCZ 111415; *b*, *D. heterolepis*, MCZ 12329; *c*, *Teius teyou cyanogaster*, MCZ 39982; *d*, *T. teyou*, MCZ 43351b; *e*, *Peneteius aquilonius*, n. gen., n. sp., MCZ 3612; *f*, *Paraglyphanodon utahensis*, United States National Museum 15668; *g*, *P. gazini*, USNM 16580; *h*, *Polyglyphanodon sternberghi*, USNM 15477. *a*-*g* × about 16, *h* × about 9.

in the latter character, especially to *Teius teyou* and *Dicrodon heterolepis.* Additional similarities with the former are the apparently small number and relatively large size of the teeth. The basin-crest structure on tooth crowns of Recent species and *Peneteius* recalls anterior teeth of *Paraglyphanodon* (Gilmore, 1942, fig. 22), but the similarity is not great. However, resemblance to the Utah Cretaceous forms is shown in the more transverse rather than oblique orientation of the tooth cusps. Restudy of the Utah fossil forms must precede further speculation on the affinities of *Peneteius.*

THE RELATIONSHIPS OF *CHAMOPS*

Chamops segnis Marsh (1892) is relatively common for a late Cretaceous lizard and is known from the Lance Formation (Wyoming), Hell Creek Formation (Montana), and Wapiti Formation (Alberta). Estes (1964) noted that *Chamops* was "quite probably ancestral to both *Crocodilurus* and *Tupinambis.*" Comparison of *Chamops* and *Callopistes* (a genus not available to me in 1964) requires some modification of that statement. *Callopistes maculatus* (MCZ 2751) is close to *Chamops* in several ways, principally in the relatively deep shape of the maxilla (Fig. 3c,d), the more normal (less conch-like, or curved) quadrate shape, and relatively elongate parietal (Estes, 1964, fig. 49). The parietals and quadrates are referred to *Chamops* on the basis of both size and frequency, as well as on their generally teiid appearance; *Chamops* is the largest and most common teiid in the Lance Formation.

The tooth row of *Callopistes maculatus* is more heterodont than that of *Chamops* and fewer teeth are tricuspid; I interpret both heterodonty and bicuspid teeth as specialized features. However, the nasal in *Callopistes maculatus* extends further forward on the maxilla than in *Tupinambis* and is thus more like the condition in *Chamops* (Estes, 1964: 107). The latter, *Tupinambis,* and *C. maculatus* share a pointed lateral premaxillary process of the maxilla (Fig. 3). The dentary of *Chamops* is relatively deeper than that of *Tupinambis* of equal size and resembles the proportions seen in *C. maculatus.* Tooth number is essentially the same in all these genera, contrary to my statement in 1964 (p. 107), which was based on only a few individuals.

Facial elongation is characteristic of many "macroteiids" and is most extreme in *Cnemidophorus.* The latter does not differ from *Ameiva* in facial elongation, although I so stated in 1964 (p. 108); examination of a large series shows considerable size variation in

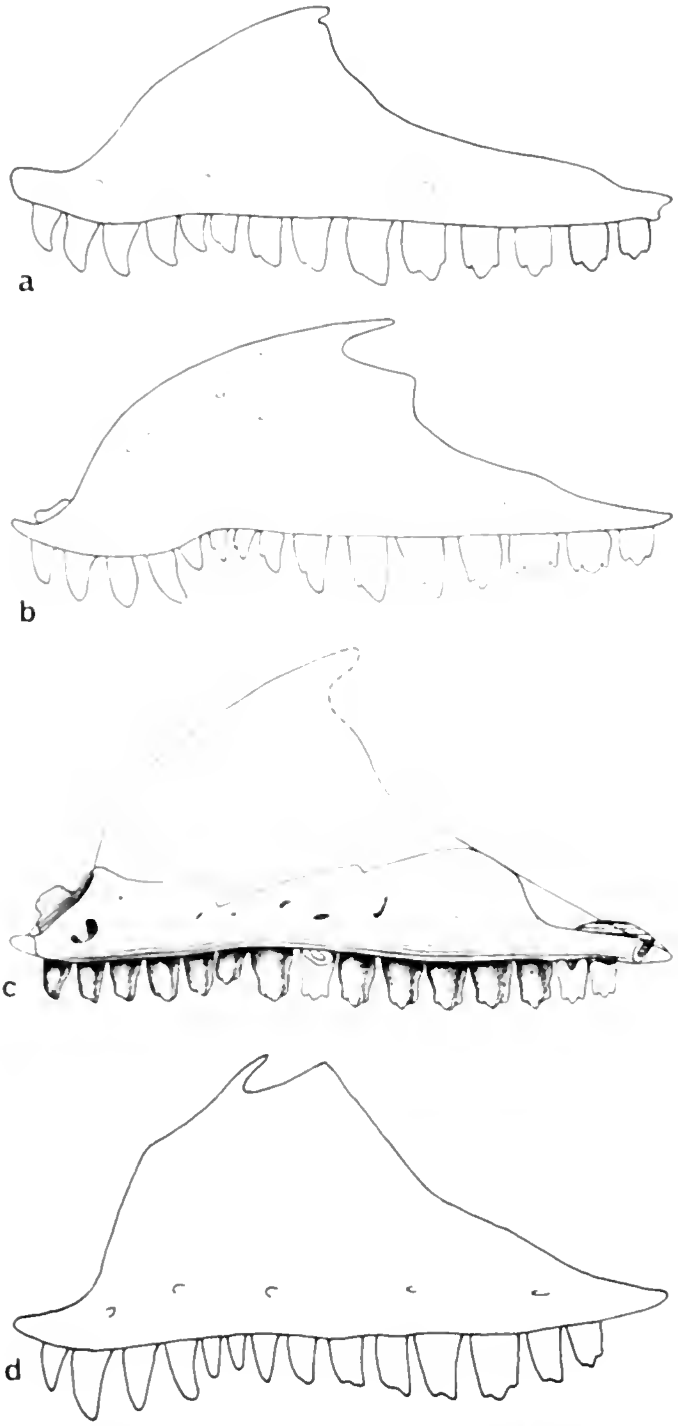

Fig. 3. *a, Crocodilurus lacertinus,* American Museum of Natural History 46290; *b, Tupinambis nigropunctatus,* Los Angeles County Museum R-74; *c, Chamops segnis,* University of California Museum of Paleontology 46033, restored dorsally from UCMP 46094 and other specimens; *d, Callopistes maculatus,* MCZ 2751; not to scale, all reduced to a common length.

this character and the two genera are probably synonymous, as indicated by recent studies (Gorman, pers. comm. and ms. 1968). *Tupinambis nigropunctatus* and *Callopistes maculatus* of equal size show the former slightly exceeding the latter in facial length; *Crocodilurus* resembles the latter. *Kentropyx calcaratus* resembles *Cnemidophorus* in this feature; my statement to the contrary in 1964 (p. 108) was based on a misidentified skeleton.

In summary, the Recent *Callopistes maculatus* appears to be the closest relative of *Chamops segnis*. *Tupinambis nigropunctatus* is the most primitive member of that genus and is close to *Chamops* but appears more advanced than the latter and *Callopistes* in a number of features. The maxilla of *Crocodilurus* is relatively less high than that of *Chamops* and the former seems to be less closely related to the latter than it is to *Tupinambis*.

CONCLUSIONS

Current study of "macroteiids" by Gorman, Presch, MacLean, and myself is in general agreement with Vanzolini and Valencia (1965) in separating two major subgroups: one including *Callopistes, Tupinambis, Crocodilurus,* and *Dracaena;* the other formed of *Ameiva, Cnemidophorus, Kentropyx, Teius,* and *Dicrodon*. The latter two genera possess distinctive, crested, cuspate cheek teeth. *Peneteius aquilonius,* n. gen., n. sp., from the late Cretaceous of Montana, has similar teeth and is probably related to the Recent *Teius-Dicrodon* line. *Chamops segnis,* from the late Cretaceous of Wyoming, Montana, and Alberta, appears to be related to the Recent species *Callopistes maculatus*. The latter two species are probably more primitive, on the basis of high maxilla and less well-developed heterodonty, than are *Tupinambis, Crocodilurus,* or *Dracaena*. With the possible relationship noted above of the fossil genus *Meniscognathus* to the *Ameiva-Kentropyx* group, it thus appears that three distinct groups of "macroteiids" living today in South America were in existence in North America during late Cretaceous time.

ACKNOWLEDGMENTS

I am grateful to Mr. William P. MacLean, 3rd., Mr. William Presch, and Drs. Arthur C. Echternacht and George Gorman for comments. Figures 1 and 2 are by Mr. Laszlo Meszoly. This research was supported in part by National Science Foundation Grant GB-7176.

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B R E V I O R A

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LEUCOLEPIDOPA SUNDA GEN. NOV., SP. NOV. (DECAPODA: ALBUNEIDAE), A NEW INDO-PACIFIC SAND CRAB

Ian E. Efford[1]

Abstract. *Leucolepidopa* gen. nov. is described along with the only known species in the genus, *Leucolepidopa sunda* sp. nov. The single specimen is from the Sunda Strait between Sumatra and Java. The position of this new genus is discussed and the relationships of all the genera within the family Albuneidae are reviewed. *Leucolepidopa* is most closely related to *Austrolepidopa* and *Lepidopa*.

The Danish Kei Island Expedition collected a single specimen of a new sand crab during dredging operations in the Sunda Strait between Sumatra and Java. This new crab is from an undescribed genus closely related to *Austrolepidopa,* recently described from Australia (Efford and Haig, 1968), and to an entirely American genus, *Lepidopa* (Efford, in ms.). In this paper I describe the new species and present a preliminary outline of the probable evolutionary relationships within the family so that the position of the new genus can be seen.

LEUCOLEPIDOPA GEN. NOV.

The type and only known species of this genus is *Leucolepidopa sunda.* This new genus is in the family Albuneidae and is closely related to *Austrolepidopa* and *Lepidopa.* It can be distinguished from other genera in the family by (1) the antennae having three articles in the flagellum and (2) the eyeplates possessing long setae on the dorsal surface. The following characters are not specific to the genus but can be used to separate it from others within the family: (3) a pleural expansion is present on the fifth abdominal segment; (4) the lateral spine is on the carapace and above the linea anomurica; (5) the scaphocerite is short, only just

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extending up to the base of the fourth antennal segment; (6) the rostrum is smoothly convex and lacks a subrostral spine; (7) there are no terminal spines on the anterolateral lobes; and (8) the anterolateral lobes carry six or seven teeth.

The generic name refers to the whiteness of the carapace and to the close relationship of this genus with the genera *Lepidopa* and *Austrolepidopa*.

LEUCOLEPIDOPA SUNDA SP. NOV.

Holotype. A male, 7mm carapace length and 8mm carapace width (Fig. 1, 1-8, and Fig. 2, 1-6). Collected on 29 July 1922 from 75 6′ 10″ S, 105 44′ E in the Sunda Strait between Sumatra and Java, by the Danish Kei Island Expedition. The specimen was collected by dredging from a sand-shell bottom in 40 m of water. Deposited in the Zoologisk Museum, Kobenhavn.

The specific name *sunda* is derived from the name of the geographical location.

Description. The carapace has a rostrum that is gently rounded and lacks spines or teeth. It is flanked on either side by a shallow, gently curved ocular sinus and by rounded anterolateral lobes, the edges of which carry six or seven teeth. From the anterolateral lobes the anterior edge of the carapace curves backwards and outwards in a smooth sigmoid curve to the large, distinct, lateral spines. There are no spines along the anterior edge of the carapace as there are in most other members of the family. The edge is lined with long, branched setae, which gradually become shorter toward the lateral spines. From the lateral spines the carapace widens slightly back to the midline, behind which the edges are straight and converge. The posterior end of the carapace is smoothly rounded, with a deeply rounded medial concavity.

The carapace has an extensive pattern of setae. The basic pattern is similar to that of both *Austrolepidopa* and *Lepidopa*; the main difference is that the M-shaped pattern across the anterior end of the carapace extends up to the anterior edge and some way back along the sides. There is a smooth area in the middle of this pattern on either side. The setae in this area are longer than those on the posterior part of the carapace. Those lining the lateral spine groove are very long and branched, and extend beyond the anterior edge of the carapace. The posterior half of the carapace is almost equally setose, but here the setae are in small groups rather than in one continuous expanse. In contrast, the posterior edge of the carapace, round the cavity, is free of setae and very smooth. The groove running down the side of the carapace stops before it reaches the posterior edge and does not follow the edge round as in *Lepidopa.*

The carapace is chalky white with some iridescence.

The first abdominal somite is shorter than wide, and the exposed posterior part forms a raised crescent-shaped area lined along its anterior edge by a dense row of setae. The second somite has broad pleural expansions with slightly concave anterior edges. The edges are lined with long setae that all face forward. Those along the lateral and posterior edges arise from a groove that runs round parallel with the edge. There are no setae along the edge of the central part of the plate. The third, fourth, and fifth segments are also winged, but unlike those of *Lepidopa,* all the pleural expansions are rather straight, narrowing towards the ends, and both the anterior and posterior edges of the expansions have grooves lined with forward-projecting setae. The setae near the outside tips of the pleural expansions of the fifth segment are particularly long and, in this case, project laterally, away from the abdomen. One noticeable character is the presence of distinct bumps along the posterior edge of the fourth pleural expansion. The sixth segment is shorter than wide and narrows towards the anterior edge. It has a distinct waist, and the posterior edge is lined with backward-projecting setae. The telson is broad and pear-shaped.

The eye-plate is quite distinct, as the dorsal surface is covered with long setae. In *Austrolepidopa* and *Lepidopa* the upper surface of the plate is smooth, although there may be setae around the edges. The plate is broadest about one third from the proximal end. The inner edge is fairly straight and the outer edge convex. From the broadest point the eyes narrow towards the rounded distal end. The edge of the plate is stepped, and long setae are attached at each step. No cornea or eye-spot is visible.

The antennules have a broad basal segment. The second segment is broad, partially compressed, and has a large, right-angled bulge on one side. The third segment is about as long as the second and widens towards the distal end. The two first antennule flagella of the holotype have been broken off so that their length is unknown; however, the lower part of the first flagellum suggests that in this species they are very long, as in *Lepidopa.* No second flagellum is present on the antennule.

The antennae are unusual because the setae are arranged terminally or along the inner side of the segments and they are not found scattered around on other parts as they are in other genera. This gives the antennae a rather bare appearance. The scaphocerite is very small and hardly overlaps the base of the fourth segment. It has a group of very long setae arising from the outer surface. The fifth segment is shorter than the fourth; it is cylindrical and terminates in a flagellum of three long cylindrical articles. The last article is longer than the other two. All three articles have areas of very long setae on their distal ends. In the holotype the setae are broken off the terminal article.

The mandible is strong, smoothly shaped, and carries a three-segmented palp. There is a very sharp cutting edge, two distinct teeth at the distal end, and three similar teeth at the proximal end. The maxillula was not examined. The maxilla is similar to those of others in the family, although I did not examine the scaphognathite. The first maxilliped is flattened and leaf-like; the endopod consists of two distinct segments. The second maxilliped is similar to others found in the family; the exopod is single and well developed. The third maxilliped has a very well-developed expansion of the anterodorsal end of the carpus, which extends over the propodus and reaches the junction of the propodus with the dactylus. The dactylus is over half as long as the propodus. The exopod is a single, long, cylindrical segment.

The pereiopods resemble those found in other members of the family. The first is subchelate with a sickle-shaped dactylus. The sides of the dactylus are smooth, and the upper surface is covered with long setae that point towards the proximal end of the segment. The propodus has a distinct cutting edge lined with very short, blunt setae and terminating in a large, hooked tooth. The side is covered with rows of long setae. The second and fourth pereiopods have broad, blunt, sickle-shaped dactyla. The third pereiopod has a long, smoothly-curved dactylus without any distinct basal projection; the carpus is very much expanded at the anterior end, with the anterior half of the upper surface covered with a dense mat of setae. The fifth pereiopod is long and chelate. The genital pore is round.

Relationships. To examine the relationships of *Leucolepidopa* with the other members of the family, I used characters that seem to vary little between species within a genus, although they do vary between genera. These were: (1) the number of articles in the flagellum of the antenna; (2) the presence or absence of pleural expansions on the fifth abdominal segment; (3) the presence of the lateral spine above or below the linea anomurica; (4) the length of the scaphocerite; and (5) the shape of the rostral region of the carapace. When the genera are examined using these characters, it becomes clear that some of the characters always occur together. The presence of a pleural expansion on the fifth abdominal somite is always associated with a short scaphocerite and with a rostrum that is quite clearly convex in shape. The opposite three characters are associated with the absence of a pleural expansion on the fifth abdominal somite. These two groups can be used as the basis for separating the family into its evolutionary groups. I should mention here that *Blepharipoda* and *Lophomastix* are so distinct from the other genera in the family Albuneidae that they form a side branch off the main stream, and were not included in the analysis.

The family can be divided into three groups (Fig. 3). The first, the *Lepidopa* group, contains *Lepidopa, Austrolepidopa,* and *Leucolepidopa. Leucolepidopa* is most clearly related to *Austrolepidopa,* as shown by the similar shape of the eye-plates and by the stiff, straight, pleural expansions on the fifth abdominal somite compared to the rather delicate curved ones in *Lepidopa.* They differ in the length of the antennal flagellum, the presence of setae on the dorsal side of the eye-plate, the absence of a second flagellum to the antenna, and the setal pattern on the carapace. It is assumed that *Leucolepidopa* is more specialized than *Austrolepidopa,* as it has only three articles in the flagellum, whereas both of the other genera have seven or eight. *Austrolepidopa* is closely related to *Lepidopa,* as is shown by the similar lamellated eye-plates, the antennal flagellum of seven or eight articles, as well as the elongated carpus of the third maxilliped, short scaphocerite, pleural expansion, and convex rostrum common to the three species.

A second group, the *Albunea* group, has only two species, *Albunea* and *Stemenopa.* The former genus occurs throughout the tropical regions and is rather generalized in form. *Stemenopa,* recorded from only one location in Western Australia, is a very specialized form with extremely long eye-stalks. It closely relates to *Albunea,* as is shown by the absence of a pleural expansion on the fifth segment, the concave rostrum, and the long scaphocerite.

Zygopa is specialized in having both fused eye-plates and a single article in the antennal flagellum; it occupies a place somewhere between the other two groups. According to Holthuis (1960), it is more closely related to the *Lepidopa* group because of the position of the lateral tooth. Possibly more weight should be put on its similarity to the *Albunea* group in its long scaphocerite, concave rostrum, and pleural expansion of the fifth abdominal segment, rather than its similarity to the *Lepidopa* group in having the lateral spine above the linea anomurica. Until we have more information, we must assume that a closer relationship is suggested by three characters held in common than by only one, which places *Zygopa* closer to the *Albunea* group than to the *Lepidopa* group.

The final group in the family is the rather separate off-shoot of *Blepharipoda* and *Lophomastix*.

Apart from the position of *Zygopa*, the genera fall rather easily into these separate groups. These relationships could be tested, and more information obtained to confirm or reject the tentative position of *Zygopa*, by comparing the larvae. At the present time, however, we know the larvae only of *Lepidopa* and *Blepharipoda*, so that we are still some way from understanding the evolution of the family Albuneidae.

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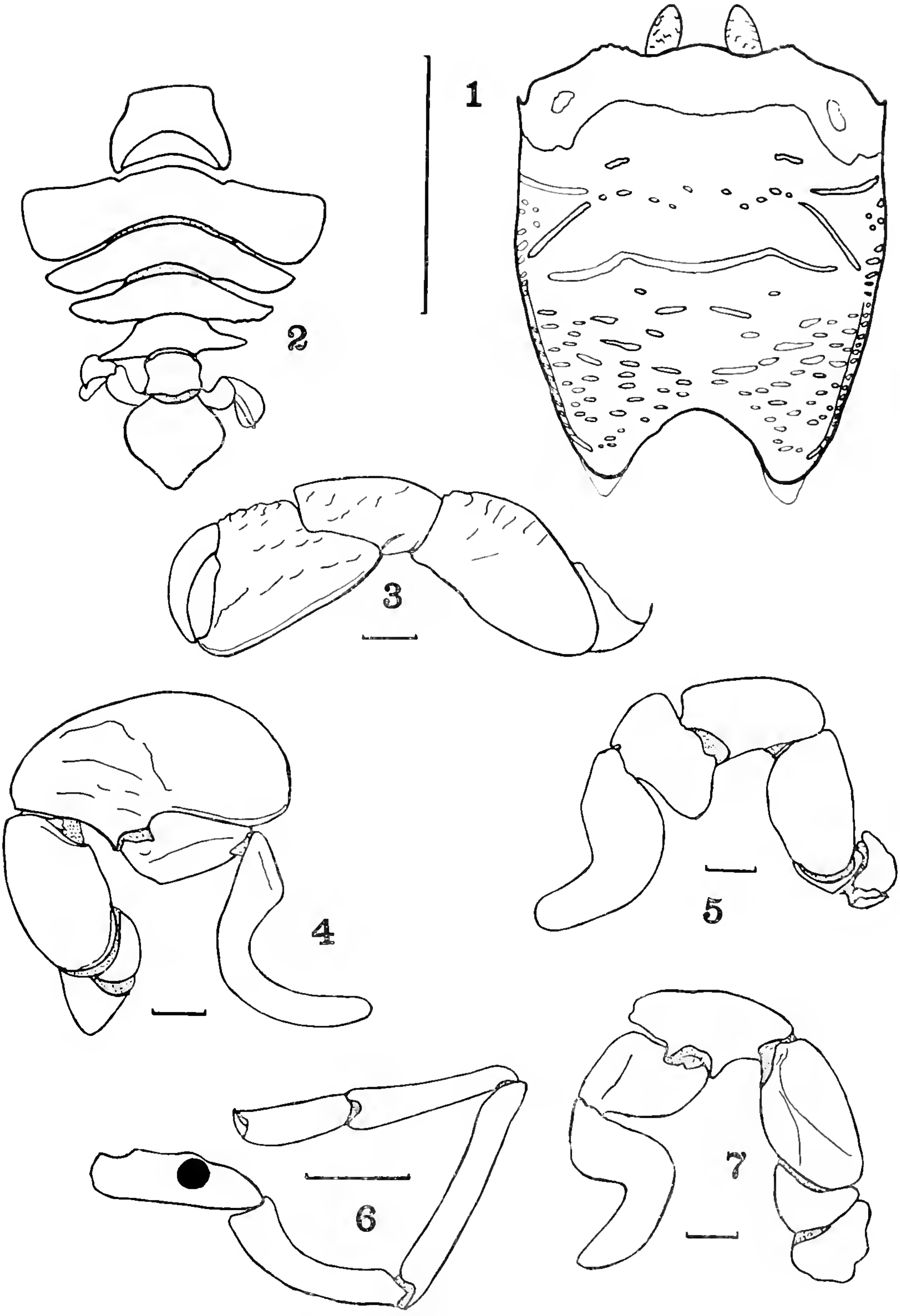

Fig. 1. Holotype of *Leucolepidopa sunda* gen. nov., sp. nov., male cl. 7 mm. 1. Dorsal view of the eye-plates and carapace with the setae pattern shown. 2. Dorsal view of the abdomen and telson. 3. Left first pereiopod. 4. Right third pereiopod. 5. Left fourth pereiopod. 6. Left fifth pereiopod showing round genital pore. 7. Left second pereiopod. Scale 1 mm, except in 1 and 2, where it is 0.5 cm.

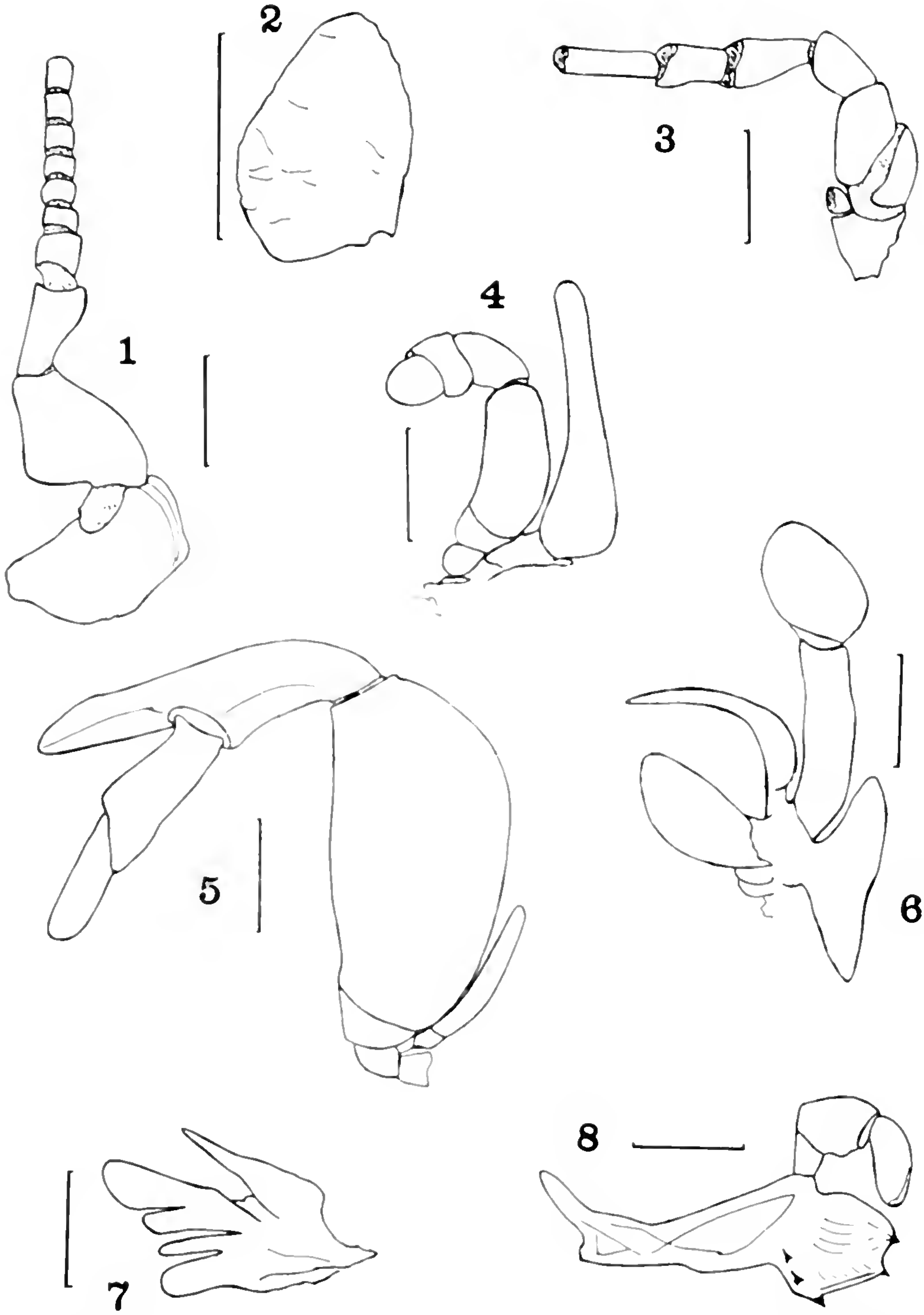

Fig. 2. Holotype of *Leucolepidopa sunda* gen. nov., sp. nov. 1. Base of antennule. 2. Dorsal view of left eye-plate. 3. Left antenna. 4. Left second maxilliped. 5. Left third maxilliped. 6. Left first maxilliped. 7. Left maxilla with the scaphognathite missing. 8. Left mandible. Scale 1 mm.

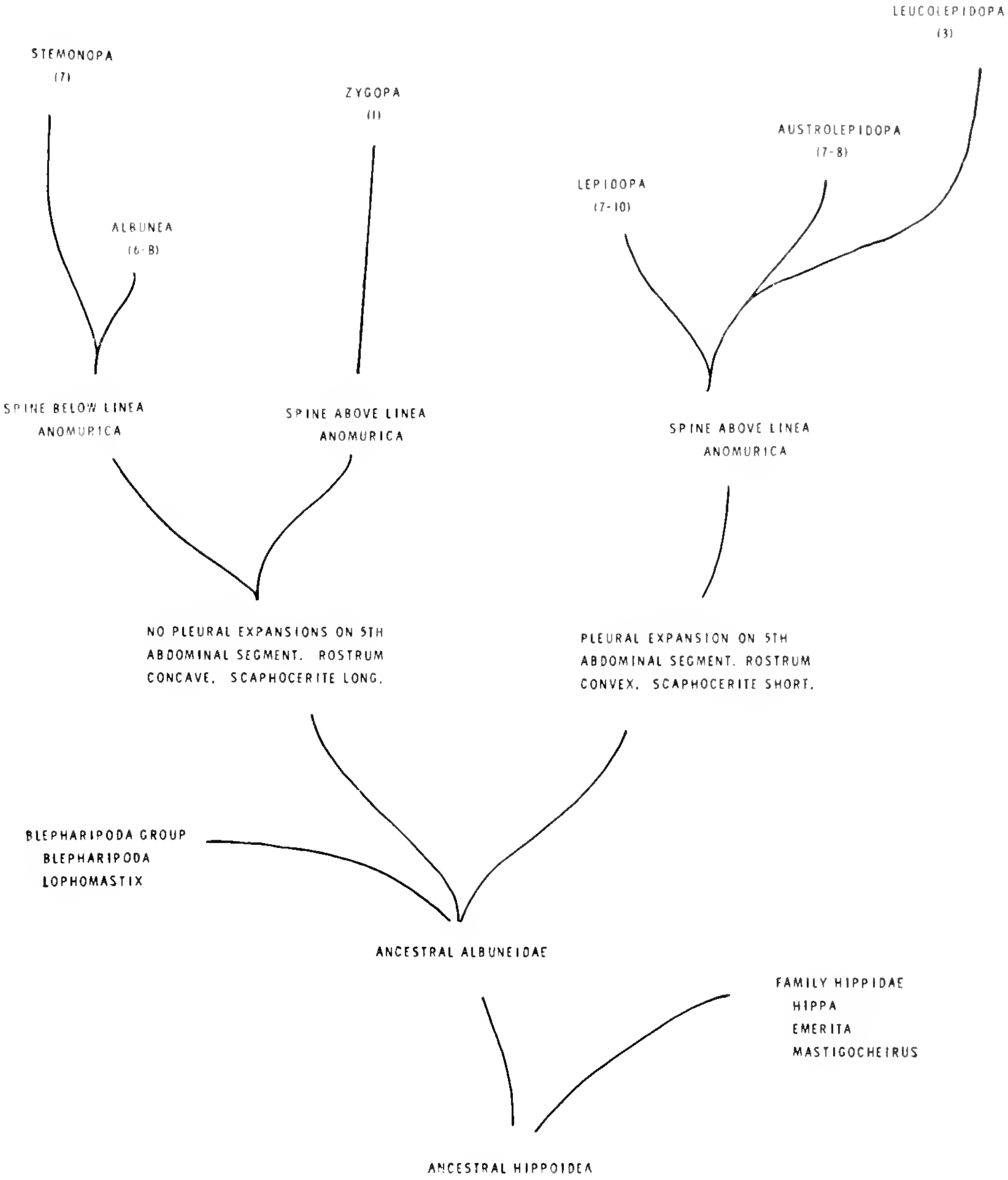

Fig. 3. Evolutionary relationships within the family Albuneidae. Number of articles on the antennal flagellum is given for each genus.

B R E V I O R A

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COMPETITIVE EXCLUSION AMONG ANOLES (SAURIA: IGUANIDAE ON SMALL ISLANDS IN THE WEST INDIES[1]

A. Stanley Rand[2]

ABSTRACT. Each of the Greater Antilles has been a largely independent center of anole radiation and there has been little exchange of species between them. Together they are the source areas from which the other islands of the Antilles have been colonized. The area and number of anole species known from 122 of these smaller islands on 44 banks are tabulated.

There are two kinds of small islands in the West Indies. The islands of one class show a correlation between area and number of anole species, and the larger islands may have up to 4 or 5 species. Islands of the other class do not show an area effect and never have more than 1 or 2 species. The first class includes the islands of the Great Bahama Bank and the islands fringing the Greater Antilles and lying on the same bank as one or another of them. The second class includes the Lesser Antilles and the small isolated islands of the Caribbean.

The difference between the two classes seems to be a result of their Pleistocene history and the way in which they received their anole faunas. The islands of the first class were all connected or very close to a source area during the Pleistocene sea level minima and so probably received their anoles overland and more or less at the same time. The area effect now seen was probably produced by differential extinction subsequent to a sea level rise and separation of the various islands. The islands of the second class must all have been colonized over an appreciable water gap.

The absence of islands with more than 1 or 2 species in this second class cannot be due to ecology, size, distance, or species of anoles involved, since some of the islands are large, diverse, and no further from a suitable source than some fringing islands are today. The data suggest that a first species finds it relatively easy to colonize an island. A second species finds it difficult, and a third may find it impossible, even though three species may coexist on a very small and ecologically impoverished island if they have colonized it overland. The exclusion effect occurs not because of the difficulties in reaching the island, but because of the difficulties in establishment. The latter are the result of inter-specific competition in which an

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already established species can exclude an invader even though if both were established together they might coexist. It is suggested that competitive exclusion may also explain the small number of exchanges of species among the Greater Antilles.

This paper deals with the factors influencing the number of species of *Anolis* per small island in the West Indies. Darlington (1957) relates faunal size and complexity in the West Indies to island area and to distance from the postulated source area of Central America. However true these generalizations are for the fauna as a whole, they must be modified for the genus *Anolis*: first, because the West Indies have been a center of speciation and have not received their modern fauna directly from Central America and, second, because there is a class of small West Indian islands that have only one or two species of *Anolis* regardless of area or distance from source islands. The following discussion of the distribution of a single genus in one area is an approach to the theoretical problems of the zoogeography of archipelagos that I hope is complementary to the more mathematical treatments of Hamilton, Barth, and Rubinoff (1964), MacArthur and Wilson (1967), and others.

There are approximately 3,000 islands in the West Indies. Many of the islands stand on more or less extensive banks and are separated from one another or from one of the Greater Antilles by only shallow water. When the sea level was lowered during the last Pleistocene glaciation, the banks must have largely been exposed. At that time the islands on each bank must have been connected to one another by dry land, so that an exchange of land faunas was possible. The anole faunas of the islands on each bank are very similar to one another. The water between the banks is very deep, and there is no possibility that islands on different banks were connected during the Pleistocene.

During the interglacial period that preceded the last glaciation, the sea level was higher than it is at present, and the maximum probably was high enough to submerge completely many of the low-lying West Indian islands and exterminate any anoles living there.

Anolis is represented in the West Indies by about 100 species, more species than are known for any other genus of land vertebrates in the area. These species may be the results of as few as two overwater invasions, one from Central America into Jamaica or Cuba and the other from South America into Puerto Rico or perhaps Hispaniola. Here and below the conclusions of Etheridge (1960) and Williams (personal communication) on the relationships within the genus *Anolis* have been followed.

Each of the four Greater Antilles has been a largely independent center of evolution for anoles. Cuba has 23 species of *Anolis,* Hispaniola 21 species, Jamaica 7 species, and Puerto Rico 10 species. Despite the fact that several of these species have crossed large water gaps to live on distant small islands, only one species is shared by two of the large islands. Even in the more distant past, the number of colonizations between the Greater Antilles was small. Only eight such events are necessary to explain the relationships between living forms: four between Puerto Rico and Hispaniola; two between Hispaniola and Cuba; two between Cuba and Jamaica. On the four large islands, speciation has been largely within and not between islands.

The Greater Antilles, with their older and richer anole faunas, are probably the source areas from which the smaller (some only recently habitable) West Indian islands have been colonized. An anole invading one of the Greater Antilles from a small island is probably even rarer than the invasion of one of the Greater Antilles by an anole from another.

Anoles have repeatedly crossed water gaps. They have not only reached and spread throughout the West Indies, but one West Indian species has reached the coast of Central America and another the Bay Islands of Honduras. It has been suggested that anoles may be blown from island to island in hurricanes or float across in rafts of vegetation carried by ocean currents. Perhaps they travel in the masses of debris and vegetation that are torn loose from a hurricane-lashed shore and blown out to sea. The heavy rains that accompany hurricanes would reduce the danger from salt water during the journey.

On the assumption that the large islands have been the source areas, most but not all colonizations have been from east to west, which is the general direction of both ocean currents and prevailing winds, as well as the storm track of many hurricanes (see Fig. 1).

Data on area and number of *Anolis* present have been collected for 126 small islands on 44 banks. Anole distributions from Barbour (1937), Cochran (1934, 1941), Grant (1932a, 1932b, 1936, 1937), Grant and Roosevelt (1932), Oliver (1948), Ruibal (1964), Underwood and Williams (1959) have been supplemented by the collections in the Museum of Comparative Zoology and unpublished information from the files of their curator, Dr. Ernest E. Williams. Mr. J. D. Lazell, Jr., and Dr. Albert Schwartz generously shared the results of their extensive field experience. Thanks are due to all three. Information on island areas was taken from the Columbia Lippincott Gazetteer of the World and

Fig. 1. The major overseas colonizations by *Anolis* of the West Indian isolated islands, the Bahamas, and the Lesser Antilles from the Greater Antilles. The most probable directions are indicated by arrows.

U. S. Hydrographic Office charts. The data are given in Table 1. Almost all the major islands are included; the number of smaller ones could be increased greatly, but there is no suggestion that this would change the picture.

The smaller islands of the West Indies fall into four geographical categories: (1) the islands fringing the Greater Antilles; (2) the Lesser Antilles; (3) the isolated islands of the Antilles; and (4) the islands of the Bahamas. Each of these groups shows a somewhat different pattern of anole distribution.

(1) The fringing islands of the Greater Antilles stand on a bank with one or another of the four Greater Antilles and are separated from it by only shallow water. Most are close to the associated large island, but some of the Virgin Islands are almost 100 miles from Puerto Rico. These islands vary ecologically from very simple to moderately complex. I have data on 44 islands in this group, all inhabited by anoles.

The fringing islands show a definite area effect, i.e., size of island and number of species are directly correlated (Fig. 2). Many are low, and most must have been submerged during the last Pleistocene sea level maximum. During the last Pleistocene sea level minimum, these islands must have become hills on the coastal plains of the Greater Antilles and been inhabited by the common lowland species of *Anolis*. After the sea level rose, the larger islands (more than 25 square miles) kept their original three to five species, but on the smaller islands there appears to have been a tendency for species to become extinct. The number that remains is related in part to island area, and the very smallest islands (less than 1 square mile) frequently now have only a single species left. On none of these islands has there been any appreciable differentiation except for the endemic, *A. roosevelti*, on Culebra.

(2) The Lesser Antilles extend in a 500 mile arc from just east of the Virgin Islands south almost to Trinidad and Tobago. Many reach altitudes of several thousand feet and show a variety of climatically different habitats with rich floras. I have data on 33 islands on 16 different banks, all inhabited by anoles.

Comparing these islands among themselves there is no apparent area effect. Five of the banks have islands with two species, the islands on the remaining 11 banks have only a single species (excluding certain introductions by man). The Lesser Antilles have been colonized by two different stocks. One, the *bimaculatus* species group, including *wattsi*, has spread throughout the Northern Lesser Antilles, crossing at least nine water gaps. It probably came from the Greater Antilles, though the ancestral species has either disappeared or changed so much that it is unrecognizable. The stock has differentiated on every island, and taxonomists differ on how many populations have reached the species level. On several islands these anoles show marked geographical variation within the island (Lazell, 1962, 1964). Though the *bimaculatus* group has been in the Lesser Antilles a long time, there seem to have been very few cases of double invasions. On only the three northernmost banks do two species (one of them *wattsi*) occur together.

The second stock, the *roquet* group, has invaded the Lesser Antilles from the south, crossing at least seven water gaps, but it is not known to be closely related to any living South American species. There are two banks on which two species of this group coexist. The degree of differentiation between islands is less in this group than in the *bimaculatus* group.

(3) The isolated islands are those islands or small groups of islands scattered throughout the West Indies and separated from all other islands by very deep water. Most are low and quite simple ecologically. Some are very far from any source area, others are quite close. I have data on 11 islands, on 9 banks, all inhabited by anoles. (There are also a very few, very small, isolated cays [e.g. Pedro Cays, Aves Island] that are uninhabited; they are the only islands in the West Indies known to lack anoles.)

These islands show no area effect. One island has two species of anoles, the others a single species. Most of these islands were probably submerged during the Pleistocene sea level maximum and colonized overwater since their emergence. All of these islands are occupied by species that are conspecific with or clearly derived from a species now living on one of the Greater Antilles. The one exception is *acutus* on St. Croix, probably derived from a Puerto Rican stock but not from one of the living species.

(4) The Bahamas are a large group of islands stretching for some six hundred miles in an elongate cluster from Florida, along the northeast coast of Cuba, almost to Hispaniola. They are all low islands with little ecological diversity and were probably all submerged during the last Pleistocene sea level maximum. The islands lie on a number of banks of various sizes. I have data on 53 islands on 15 banks, all inhabited by anoles.

The largest bank is the Great Bahama Bank. During the Pleistocene sea level minimum, its many islands must all have been part of a single very large island lying next to Cuba. The present islands show an area effect very like that of the fringing islands. The larger islands on this bank are inhabited by four species of anoles, three from Cuba (*sagrei, carolinensis,* and *angusticeps*) and one from Hispaniola (*distichus*). These species must have reached the bank overwater and then probably spread through it overland.

The remaining Bahamas lie on a number of smaller banks. Of the 14 banks for which I have data, the islands on 10 are occupied by a single species and on 4 by two species. Many of these islands are much larger and at least as varied ecologically as some of those on the Great Bahama Bank that are occupied by four species of anoles.

The Bahamas on other banks that lie close to the Great Bahama Bank are occupied by one or two of the anoles that occur on the Great Bahama Bank. The Bahamas farther southeast are occupied by a single endemic species, *scriptus.* The ancestors of *scriptus* may have reached the Bahamas in a single long overseas crossing from Puerto Rico, where its very close relative, *cristatellus,* occurs, though it may have come from a now extinct form on Hispaniola. *A. scriptus* does not occur with any other anole, though it lives on West Plana Cay only ten miles from East Plana Cay, which is occupied by *A. carolinensis.*

From this survey it appears that, on the basis of the size of their anole faunas, there are two kinds of small islands in the West Indies. The first class of island includes the fringing islands of the Greater Antilles and the islands of the Great Bahama Bank. These clearly show an area effect and only the smallest have a single-species fauna (Fig. 2, *upper*). The second class of island includes all of the Bahamas off the Great Bahama Bank, the Lesser Antilles, and the isolated islands (Fig. 2, *lower*). These show little if any area effect, and even the largest islands have only one or two species.

The difference in numbers of anoles between these two types of islands cannot be explained on the basis of differences in their ecological diversity or carrying capacity. The Lesser Antilles, with only one anole species, are larger, much richer, and more varied ecologically than are many fringing islands with three or four species of anoles. Within the Bahamas there seems to be no difference in the ecology between the islands on the Great Bahama Bank, where four species coexist, and those on other banks, where only one or two species occur together. The difference cannot be in behavioral or ecological peculiarities of the species involved, for the species that replace one another in some of the Bahamas occur

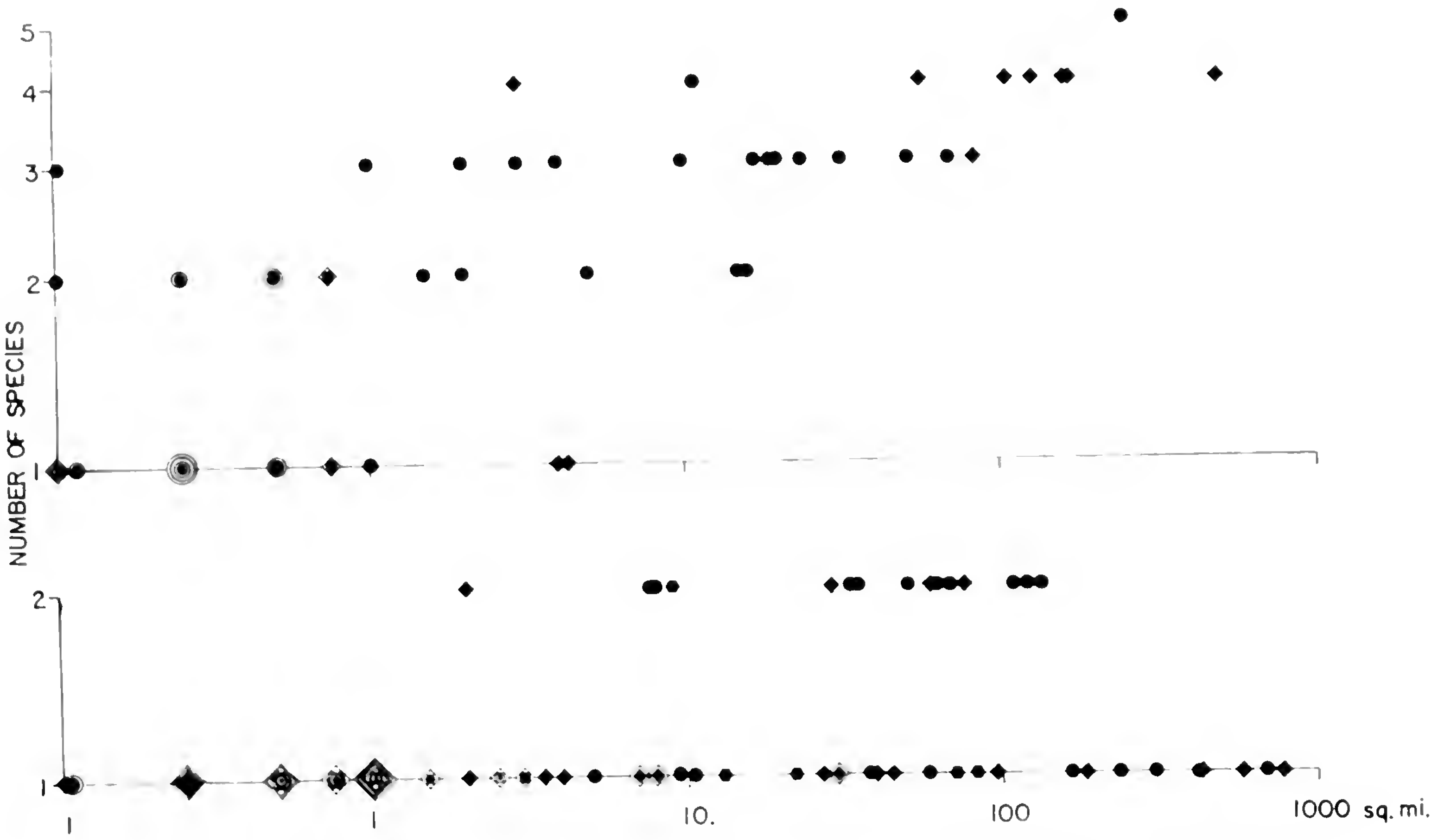

Fig. 2. Island area and number of species of *Anolis* on the small West Indian islands. Each symbol represents an island. *Upper.* The islands of the Great Bahama Bank (diamonds) and those fringing the four Greater Antilles (circles). These show a clear area effect. *Lower.* The Lesser Antilles (circles), the West Indian isolated islands (hexagons), and the Bahamas off the Great Bahama Bank (diamonds). These show little area effect.

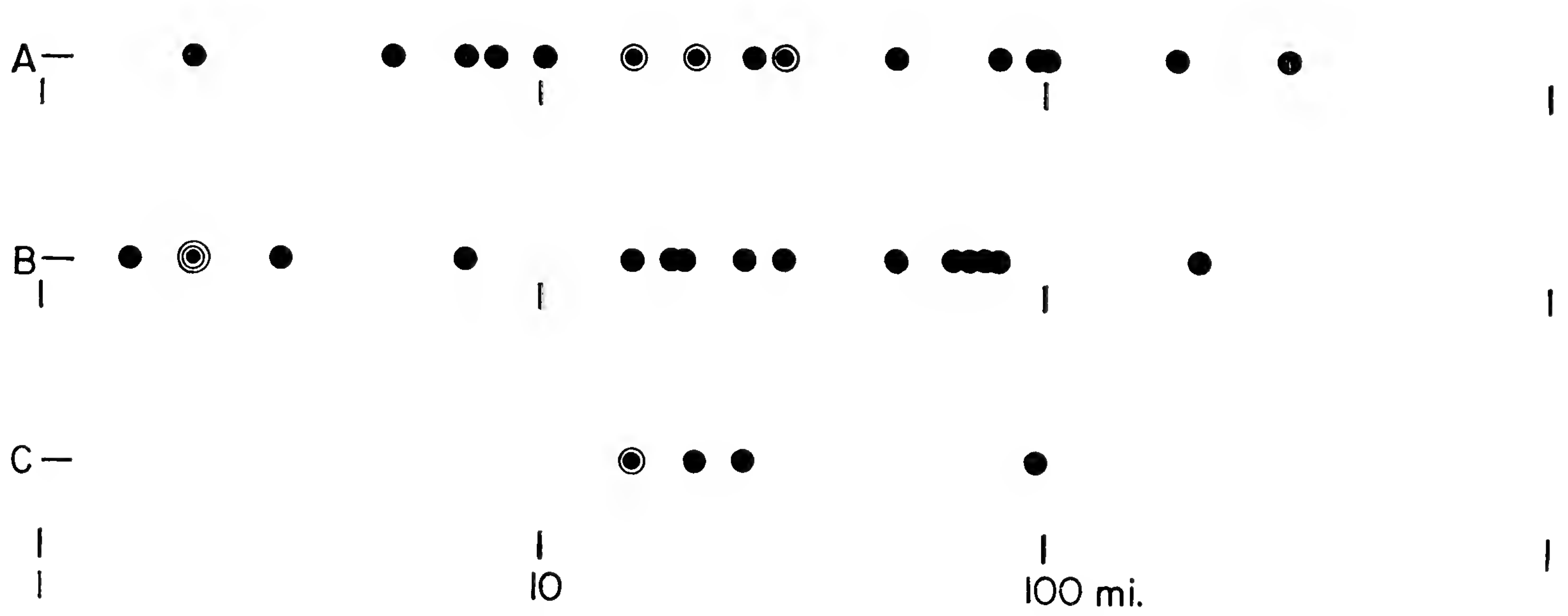

Fig. 3. Distance from source and number of species of *Anolis* on the West Indian isolated islands and the Bahamas off the Great Bahama Bank. Each symbol represents a bank of islands. Distances are measured between one hundred fathom lines and are approximate. *A*. One-species islands — the distance from the nearest point from which their species could have come. *B*. One-species islands — the distance from the nearest point from which an additional species could come. *C*. Two-species islands — the distance from the nearest point (or points) from which their species could have come. The similarity of these three sets of distances demonstrates that it is not distance from the source areas that distinguishes the one-species from the two-species islands.

together on the Great Bahama Bank. The width of present-day water gaps is another factor that will not explain the differences in number of species (Fig. 3).

The factors that do seem important in causing the difference are related to the Pleistocene history of the islands and the manner in which they were colonized, either over land or over water. The fringing islands could, and probably did, receive their several species of anoles over land, all more or less at the same time, during the period of lower sea level. Each species was represented by many individuals. The present islands of the Great Bahama Bank probably received their faunas in the same way, though the bank itself must have been colonized over water. The isolated islands, the Lesser Antilles, and the Bahamas off the Great Bahama Bank probably received their anoles over water. The species probably arrived separately and only one or a very few individuals reached an island at one time.

One species or another of *Anolis* has succeeded in colonizing every West Indian island of more than a square mile in area, and almost all of the even smaller ones have been colonized, as well. It can be suggested that the reason so few of these islands have two species and none three is that the additional species have never reached them. But if the difficulty of reaching the islands were the explanation, then one would find that the islands that were easier to reach, because they were down wind, down current, or close to the source, would have more species than the islands that were harder to reach. This is not the case. The position of an island relative to the source area has more effect on *what* species will reach it than on how many. Figure 3 shows there is no simple correlation between number of species and distance from source area.

The limited anole faunas must result from interactions between species. Apparently a species established on an island makes it more difficult for the second species that reaches the island to establish itself. If the second species is successful, it is even more difficult for additional species to establish. I would suggest that, because of the low probability of overwater colonization of an island, the first species reaching it has time to occupy it completely before any other species lands. The only island large enough and close enough to the source areas for several species to colonize it before any one of them occupied it completely was the Pleistocene island that is now the Great Bahama Bank. Once the four species were established, they were able to coexist, so that the modern islands show an area effect like fringing islands rather than like the other Bahamas. The phenomenon of an established species of *Anolis* preventing a newly arrived species from colonizing can be called competitive exclusion, because it must be the result of interspecific competition.

The four species that exclude one another on the Bahamas off the Great Bahama Bank were studied by Oliver (1948) on an island on the Great Bahama Bank where they occur together. He reports that they occupy different microhabitats. Similar differences in microhabitats probably serve to reduce competition between sympatric anoles on Puerto Rico (Rand, 1964) and Jamaica (Rand, 1967a). In both Puerto Rico and Jamaica, differences in microhabitat between some species are reinforced by interspecific territorial defense (Rand, 1964, 1967b). Where one of these species is abundant and another rare, all of the available territories in the preferred microhabitat of the abundant species may be occupied by large adults, so that young individuals are forced to establish their territories in the microhabitat characteristic of the second species. These observations suggest that interspecific competition can occur even between species with different microhabitat preferences, particularly whenever one of the species is very abundant. We do know that on small islands the species present may be there in large numbers. One species of *Anolis* that occurs without congeners, *lineatus* on Curaçao, occupies a more varied microhabitat than do many populations of Greater Antillean species which occur sympatrically (Rand and Rand, 1967).

It is possible that successful colonizations of already inhabited islands were successful because the colonist landed at a time and in a place where the population density of established species was temporarily low. The larger and older the island and the more frequent the colonization attempts, the more likely it is that a colonist will land at a favorable time and place. This may explain the minor age, area, and position effects seen.

The difficulty of colonizing an inhabited island accounts for the very small number of species occurring on many of the small West Indian islands. This phenomenon of competitive exclusion may also help to account for the relatively small amount of anole interchange among the Greater Antilles themselves and to explain why their anole radiations have been largely independent of one another.

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TABLE 1

NUMBERS OF SPECIES OF ANOLIS ON VARIOUS ISLANDS IN THE WEST INDIES

Island (those indented under another lie on the same bank)	Number of *Anolis* species	Island area in sq. mi.
Islands fringing the Greater Antilles; 44 islands on 4 banks.		
Cuba	23	43,036.0
Isla de Piños	8	1,159.0
Hispaniola	21	28,242.0
Gonave	5	254.0
Ile Tortue	3	70.0
Ile Vache	3	20.0
Grand Cayemite	3	17.0
Beata	2	16.0
Saona	3	4.0
Pte. Cayemite	1	0.5
Jamaica	7	4,450.0
Bogue	1	0.25
Pigeon	1	0.125
Salt	1	0.125

Island (those indented under another lie on the same bank)	Number of *Anolis* species	Island area in sq. mi.
Booby	1	0.062
Cabaritta	2	0.062
Emerald	1	0.062
Lime	1	0.062
Puerto Rico	10	3,421.0
Vieques	3	51.0
St. Thomas	3	32.0
Tortola	3	24.0
St. John	3	19.0
Anegada	2	15.0
Culebra	4	11.0
Virgin Gorda	3	10.0
Jost Van Dyke	2	5.0
Peter	3	3.0
Beef	2	2.0
Guana	3	2.0
Caja de Muertos	2	1.5
Water	3	1.0
Cooper	1	1.0
Savana	2	0.75
Salt	1	0.75
Hassel	1	0.5
Culebrita	1	0.5
Lovango	2	0.5
Little St. James	2	0.5
Fallen Jerusalem	2	0.5
Little Saba	2	0.25
Congo	2	0.25
Cockroach	1	0.25
Dutchman's Cap	1	0.25
Dead Man's Chest	1	0.25
Salt Key	1	0.25
Cayo Santiago	3	0.125
Dog	1	0.125
Lesser Antilles: 33 islands on 16 banks.		
Anguilla	2	35.0
St. Martin	2	35.0
St. Barthelmey	1	9.5
Antigua	2	108.0
Barbuda	2	62.0
Saba	1	5.0
St. Eustatius	2	7.7
St. Kitts	2	68.0
Nevis	2	50.0
Redonda	1	0.5
Montserrat	1	38.0

Island (those indented under another lie on the same bank)	Number of *Anolis* species	Island area in sq. mi.
Désirade	1	10.5
Guadeloupe	1	687.0
Les Saintes, Terre de Bas	1	3.0
Terre de Haut	1	2.5
Marie-Galante	1	58.0
Dominica	1	305.0
Martinique	1	427.0
St. Lucia	1 (2 introduced)	233.0
Barbados	1	166.0
St. Vincent	2	133.0
Grenada	2	120.0
Quatres	1	0.5
Carriacou	2	8.0
Mustique	1	2.5
Petit Mustique	1	0.125
Petit Nevis	1	0.125
Baliceaux	1	0.75
Petit Martinique	1	1.0
Frigate	1	0.25
Ronde	1	1.0
Caille	1	0.25
Diamond	1	0.125
Isolated islands; 11 islands on 9 banks.		
St. Croix	1	82.0
Buck	1	0.75
Grand Cayman	1	71.0
Mona	1	21.0
Cayman Brac	1	13.0
Little Cayman	2	9.0
Navassa	1	1.5
Swan (Larger)	1	1.0
Swan (Smaller)	1	0.5
Desecheo	1	0.75
Alta Vela	1	0.5
Bahamas; 53 islands on 15 banks.		
Great Bahama Bank (15 islands)		
Andros	4	500.0
Eleuthera	4	164.0
Cat Island	4	160.0
Long Id	4	130.0
Great Exuma	4	108.0
Mangrove Cay	3	85.0
New Providence	4	58.0
Little San Salvador	1	4.25
Stocking Id	1	4.0

Island (those indented under another lie on the same bank)	Number of *Anolis* species	Island area in sq. mi.
South Bimini	4	3.0
North Cat Cay	2	0.75
Margaret Island, Ragged Island Group	1	0.75
Flamingo Cay	1	0.5
Knife Cay	1	0.062
Goat Cay	1	0.062
Acklins	1	185.0
Crooked Id	2	76.0
Long Cay	1	7.0
Castle Island	1	1.5
Cotton Cay	1	0.5
Atwood Cay	1	10.0
Grand Caicos	1	40.0
North Caicos	1	40.0
Providenciales	1	30.0
East Caicos	1	30.0
South Caicos	1	8.0
West Caicos	1	7.0
Pine Cay	1	1.0
Cotton Cay	2	2.0
Elbow Cay	1	1.0
Conception	1	4.0
East Plana Cay	1	3.0
Great Inagua	1	560.0
Sheep Cay	1	0.25
Little Bahama Bank		
Gr. Abaco Id	1	776.0
Grand Bahama	1	430.0
Little Abaco	1	27.0
Elbow Cay	1	2.0
Pensacola Cay	1	1.0
Water Cay, Grand Bahama	1	1.0
Strangers Cay	1	0.75
Moraine Cay	1	0.062
Little Inagua	1	45.0
Mayaguana Id	1	96.0
Booby Cay	1	0.25
Rum Cay	2	29.0
Grand Turk	1	8.0
Salt Cay	1	2.5
Cotton Cay	1	0.5
Long Cay	1	0.25
Great Sand Cay	1	0.25
Watlings Id	2	60.0
West Plana Cay	1	3.5

BREVIORA

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TAIMANAWA, A NEW GENUS OF BRISSID ECHINOIDS FROM THE TERTIARY AND RECENT INDO-WEST-PACIFIC WITH A REVIEW OF THE RELATED GENERA *BRISSOPATAGUS* AND *GILLECHINUS*

Robert A. Henderson and H. Barraclough Fell

ABSTRACT. *Taimanawa* gen. nov. is erected to include two New Zealand fossil species, *T. pulchella* sp. nov. (taken as the type species) of early Miocene age and *T. greyi* (Hutton) of Oligocene age, as well as a poorly known extant species from the Kei Islands, Indonesia, *T. mortenseni* sp. nov., which had hitherto been tentatively referred to *Plagiobrissus* Pomel. In spite of possessing an internal fasciole, *Taimanawa* is referred to the Brissidae, with which it agrees in other morphological features. The closely related genera *Gillechinus* Fell and *Brissopatagus* Cotteau are re-evaluated using type material of the type species; they are maintained as distinct, but most of the species previously referred to *Brissopatagus* are here transferred to *Gillechinus*.

INTRODUCTION

In the course of a preliminary survey of the New Zealand Tertiary Spatangoida by one of us (H. B. F., 1947-55), the genus herein named *Taimanawa* was recognized as new. However, the two fossil species referable to the genus seemed to be congeneric with an unnamed and poorly known form from the Kei Islands, west of New Guinea, which had tentatively been referred to *Plagiobrissus* by Mortensen (1951). Therefore, it was deemed advisable to defer publication of the material until the fossils could be compared with the suspected living species. In the interim, the responsibility for describing the entire New Zealand collection of Tertiary spatangoids has been assumed by the second author. In consequence, this report has been prepared as a joint project.

Through the kindness of Dr. F. Jensenius Madsen (University Zoological Museum, Copenhagen) it has been possible to study fragments of two specimens from the Kei Islands and to confirm that they represent a living species of *Taimanawa.* This species, together with *T. pulchella* (the type of the genus) and *T. greyi* (Hutton), which was described from New Zealand a century ago, are all treated here. Two additional species occur in the New Zealand Tertiary, but as they add little to the definition of the genus, they will be described in a monograph of New Zealand Tertiary Spatangoida now in preparation.

The closest relatives of *Taimanawa* are the genus *Gillechinus* Fell, 1964, based on *G. cudmorei* Fell, and a number of species which previously have been referred to *Brissopatagus* Cotteau, 1863. *Brissopatagus* is based on *B. caumonti* Cotteau, which is known from a single, poorly-preserved specimen. Recently Phillip (1966) has synonymized *Gillechinus* with *Brissopatagus.* In order to evaluate this contention and to determine the relationship of *Brissopatagus* and *Gillechinus* to *Taimanawa,* type material of *B. caumonti* and *G. cudmorei* have been compared. Paratypes of the former were supplied by Mr. T. A. Darragh (National Museum of Victoria), and the holotype of the latter was kindly lent to us by Professor J. Roger (Laboratory of Paleontology, University of Paris). As a result of this study, *Brissopatagus* and *Gillechinus* are here maintained as distinct, and most of the species previously referred to *Brissopatagus* have been regrouped in *Gillechinus. Taimanawa* is perhaps the direct descendant of *Gillechinus;* it is less closely related to *Brissopatagus.*

The authors wish to thank Dr. C. A. Fleming and Mr. I. W. Keyes (New Zealand Geological Survey), Mr. J. D. Campbell (Otago University), Mr. J. A. Grant-Mackie (Auckland University), Mr. D. R. Gregg (Canterbury Museum), and Dr. P. Kier (Smithsonian Institution) for the loan of specimens under their charge, and Mr. R. J. Foster (Hughesdale, Victoria, Australia) for a gift of specimens of *Gillechinus cudmorei.* The project was undertaken during tenure at Harvard University of a Frank Knox Memorial Fellowship and a Taranaki Post-Doctoral Fellowship by one of us (R. A. H.). The research was sponsored by a National Science Foundation grant, GB-3532.

Repositories. The repositories of type and other specimens are indicated by the following abbreviations: New Zealand Geological Survey (EC.); Geology Department, Otago University (OU.); Geology Department, Auckland University (E.); and Canterbury Museum (zfe.).

Localities. Localities of the New Zealand fossil specimens have been arranged in order of the sheet districts of the one mile to the inch topographic map series (New Zealand Department of Lands and Survey, series N.Z.M.S. 1) on which they appear. The sheet districts are designated "N" and "S" for the North and South Islands and are arranged numerically from north to south on each island. Sheet Fossil Numbers of the New Zealand Fossil Record Form System (e.g. S164/496) are recorded for those localities to which they have been allocated.

Stratigraphy. The sequence of New Zealand Tertiary stage divisions relevant to the stratigraphic ranges of *T. pulchella* and *T. greyi*, listed in order from youngest to oldest, are as follows: Whaingaroan, Duntroonian (Oligocene); Waitakian, Otaian, Awamoan (Lower Miocene).

Order Spatangoida Claus, 1876

Family Brissidae Gray, 1855

Genus *TAIMANAWA* nov.

Type species. T. pulchella sp. nov. Other included species: *T. mortenseni* sp. nov.; *T. greyi* (Hutton).

Diagnosis. Large, flattened forms with peripetalous, subanal, and internal fascioles. Frontal ambulacrum deeply depressed, crossing the ambitus in a deep, narrow frontal notch. Paired petals long, narrow, shallowly depressed, and with subparallel pore series. Anterior pair widely splayed, posterior pair less so. Primary tubercles crenulate, restricted to the posterior plate series of the paired interambs within the peripetalous fasciole. Labrum very short, extending only halfway along the first plate of the adjacent ambulacra.

Etymology. The name *Taimanawa* is derived from the Maori words *tai* (= sea) and *manawa* (= heart); it is here treated as a Latin feminine first declension noun.

Description. Test large, flattened, cordiform in outline, and almost as wide as long. Aboral surface gently convex, oral surface flattened, ambitus sharp. Apical system at or near the axis of maximum height, usually slightly pre-central and ethmolytic, with four gonopores. Peristome crescentic, labiate, and anterior; periproct situated on the truncated posterior test surface. Well-developed peripetalous and subanal fascioles and a clear but less well-developed internal fasciole. Neither the peripetalous nor the internal fasciole continuous across the frontal ambulacrum. Both primary and secondary tubercles perforate and crenulate.

Aboral surface: Frontal ambulacrum apetaloid, deeply depressed, crossing the ambitus in a narrow, deep frontal notch; ornamented with fine, dense miliary tubercles and perforated by minute, conjugate pore pairs. Paired petals long, narrow, and weakly depressed, with subparallel pore series. Anterior petals widely splayed, at an angle of approximately 120°; posterior petals less so, forming an angle of approximately 60°. Each pore pair weakly conjugate and separated from the next by a single row of miliary tubercles. Interambs with a broad, low ridge extending along or near the median suture of the plate series; ridges of the paired interambulacra subtend gently sloping, flattened surfaces posteriorly to the depression of each petal. Posterior plate series of the paired interambulacra bear prominent fields of primary tubercles located within the peripetalous fasciole. Tubercles surrounded by large, shallow scrobicules; those of each field generally arranged in a reticulate pattern with discernible rows both parallel and perpendicular to the axis of the adjacent petal. Median suture of the posterior interamb bordered on each side by a single or double row of well-spaced, coarse secondary tubercles. Each interambulacral plate of the two series bordering the frontal ambulacrum bears a small triangular field of coarse secondary tubercles. The remaining interambulacral areas of the aboral surface bear fine, dense secondary and miliary tubercles.

Oral surface: Plastron amphisternous, weakly keeled, and extending anteriorly almost to the peristome; it bears coarse, dense secondary tubercles arranged in lines radiating from the posterior of the keel. Subanal fasciole broad and reniform, enclosing a densely tuberculate area with an arcuate row of conjugate pore pairs on each side. Labrum very short, extending only halfway along the first plate of the adjacent ambulacra, twice as wide as long, and with a few secondary tubercles. Remaining interambulacral areas bear well-spaced secondary tubercles. Ambulacral areas not depressed, naked except for scattered miliary tubercles; those margining the plastron are conspicuous, being half as wide as the plastron itself. Secondary spines bear prominent longitudinal ribs and are akin to those of most other spatangoids.

Remarks. Judging from the fascioles alone, *Taimanawa* would be placed in the Loveniidae alongside *Breynia*, which is the only other spatangoid genus with peripetalous, subanal, and internal fascioles. However, its other characters show that it is unrelated to *Breynia* and that it cannot be referred to the Loveniidae in spite of possessing an internal fasciole. In general morphology it is very similar to the undisputed brissid genera *Gillechinus*, *Plagiobrissus*, *Brissopatagus*, *Macropneustes*, and *Eupatagus*. Its long, narrow petals with subparallel pore series, short labrum, crenulate primary and secondary tubercles, and the absence of ampullae set it apart from the loveniids and necessitate its inclusion in the Brissidae.

Taimanawa, by virtue of its internal fasciole, is unique among the Brissidae. Its nearest relative is *Gillechinus,* which also has primary tubercles restricted to the posterior plate series of the paired interambulacra within the peripetalous fasciole and which has similar petals. Most members of *Gillechinus* possess flattened interambulacral surfaces subtended posteriorly from ridges of the paired interambs into confluence with the depressions of the paired petals, as in *Taimanawa.* However, *Taimanawa,* in addition to possessing an internal fasciole, is distinguished by its shorter labrum (Fig. 1), its much more deeply depressed frontal ambulacrum, and its much stronger frontal notch. It is interesting to note that the earliest species of *Taimanawa,* from the late Eocene of New Zealand (as yet undescribed), resembles contemporaneous *Gillechinus* in possessing a slightly depressed frontal ambulacrum and a relatively weak frontal notch. Such a relationship strongly suggests that *Taimanawa* was derived directly from *Gillechinus.* The genera *Eupatagus, Gymnopatagus, Macropneustes, Plagiobrissus,* and *Brissopatagus* all bear some resemblance to *Taimanawa.* Besides lacking an internal fasciole, they are distinguished by possessing primary tubercles on both plate series of at least the posterior paired interambs (with the exception of *E. ibericus* Lambert). *Eupatagus, Plagiobrissus,* and *Brissopatagus* possess a weak frontal groove and frontal notch, and even in *Macropneustes* and *Gymnopatagus,* where these structures are better developed, they are not as strong as in *Taimanawa. Eupatagus* and *Gymnopatagus* are further distinguished by possessing spatangiform petals with curved pore series, *Plagiobrissus* by possessing lateral branches of the subanal fasciole, and *Brissopatagus* by the concave depressions of its anterior paired interambulacra.

The presence of an internal fasciole in *Taimanawa* was initially a perplexing feature, since this structure has not previously been reported from any member of the Brissidae and, indeed, Mortensen's (1951) diagnosis of the family excludes forms with an internal fasciole. However, it will be recalled that a similar perplexity arose in reviewing New Zealand species of the spatangid genus *Paramaretia* (Fell, 1963), though in this case the fasciole proves to be a transitory feature that disappears in the adult. The relationship of fascioles to environmental features and the loss or acquisition of fascioles during the life-span of certain spatangoid echinoids have recently been studied by R. H. Chesher (private communication), and the whole subject has now been considerably clarified by his recent publication (1968).

Most of the New Zealand Tertiary specimens of *Taimanawa* are from detrital limestones and from sandstones that were deposited in comparatively shallow water during the early and mid-Tertiary transgression of the New Zealand region. In contrast, the extant species is recorded by Mortensen (1951) from two deep-water stations (260 and 268 meters); the sediment type is known for only one of the stations and is recorded by Mortensen (1923) as mud and shells. The bottom temperature of the two stations is not known but is probably near 20° C and therefore some 8°-10° C higher than the mean annual temperature of surface water off the southeast coast of the South Island, New Zealand, where *Taimanawa* was abundant in Oligocene and earliest Miocene time. Such a relationship is consistent with the higher temperatures inferred for the mid-Tertiary marine environment of the New Zealand region on the basis of fossil echinoids (Fell, 1956), and by Beu (1966) and others on the basis of other fossil groups.

KEY TO SPECIES OF *TAIMANAWA*

1 (2) Crenulation of the primary tubercles strongly developed, contiguous with the mamelon, the platform therefore aborted 3

2 (1) Crenulation of the primary tubercles restricted to the periphery of the platform, widely separated from the mamelon . . . . . .*mortenseni*

3 (4) 23-40 primary tubercles in each interambulacral field, 22-25 well developed pore pairs in the anterior petals . ...*greyi*

4 (3) 12-16 primary tubercles in each interambulacral field, 18-19 well developed pore pairs in the anterior petals . ...*pulchella*

TAIMANAWA PULCHELLA sp. nov.

Plate 2, fig. 2; Plate 3; Plate 4. Figures 1, 2a, 2c.

Holotype. OU. 8590, Karitane, Otago; S155/538.

Paratypes. S75: E. 310, Burnt Hill, Trelissick Basin, mid-Canterbury; S75/517. *S127:* EC. 405, Ngapara, south Canterbury; S127/561. *S155:* OU. 8540, Puketeraki, Dunedin district, Otago. E. 302, 304, Waikouaiti North Head, Matanaka Beach, Otago; S155/540. *S163:* EC. 426, Blackhead, Dunedin district, Otago; S163/495. OU. 4736, 8566a, b, 8567b-d, 8568a-d, Blackhead, Dunedin district, Otago. *S164:* EC. 437, Green Island district, Otago; S164/496. OU. 8585, New Zealand Cement Co. pit, Burnside, Otago. *Locality unknown:* EC. 671.

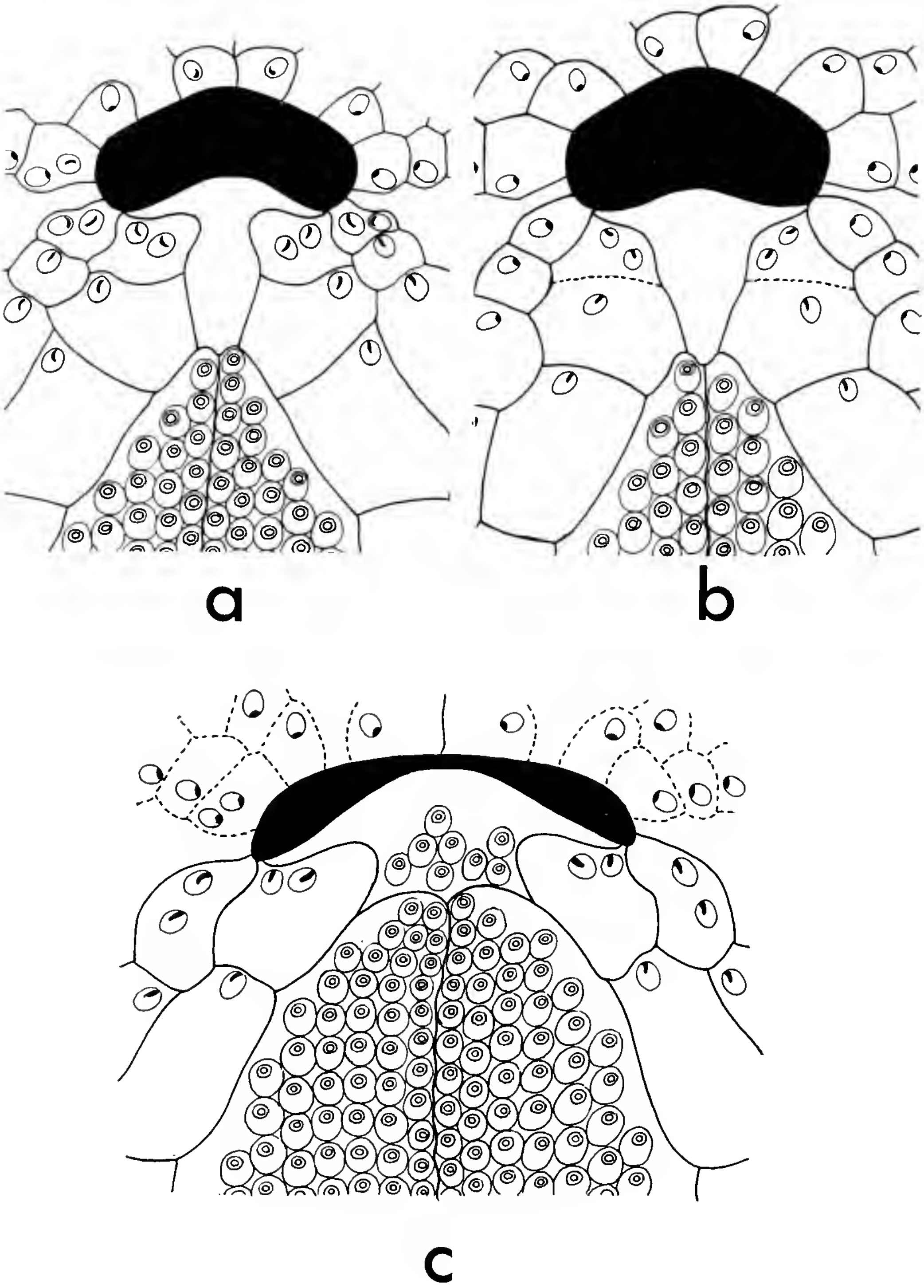

Figure 1. Comparison of the peristomial regions of *Gillechinus* and *Taimanawa*. a) *Gillechinus alabamensis* (Cooke), U.S. National Museum 562467; ×3.5. b) *Gillechinus cudmorei* Fell, Museum of Comparative Zoology 4147; ×3.5. c) *Taimanawa pulchella* sp. nov., holotype, OU. 8590; ×2.5.

Diagnosis. Adult tests compressed, with a moderately depressed frontal ambulacrum and a strong frontal notch; 18-19 well-developed pore pairs in the anterior paired petals, 12-16 primary tubercles in each lateral interambulacrum.

Description. Test up to 120 mm in length, cordiform in outline, almost as wide as long, with a sharp ambitus. Aboral surface shallowly arched, oral surface flattened; height breadth ratio approximately 0.27. Apical system central to slightly anterior in position, lying on the axis of maximum height of the test and morphologically typical of the genus. Peristome crescentic, anterior, and margined by a prominent lip. Periproct lies on the truncated posterior surface of the test; no specimen is sufficiently well preserved to show its shape. Peripetalous fasciole thin, not indented between petals. Internal fasciole thin, of variable width, located near the median suture of the anterior interambs and forming a tight loop posteriorly around the apical system. Neither the peripetalous nor internal fasciole is continuous across the frontal ambulacrum. Subanal fasciole well developed and reniform.

Aboral surface: Frontal ambulacrum of moderate depression; frontal notch prominent, as wide as deep in adult tests. Paired petals straight, lightly depressed; anterior pair generally slightly longer than those posterior. Pore pairs weakly conjugate and ovate. Adult tests have 18-19 pore pairs in the anterior petals and 15-16 in those posterior. Primary tubercles restricted to the posterior plate series of lateral interambs within the peripetalous fasciole. Adult tests with 12-16 tubercles in each such interambulacral field. Other features of the aboral surface typical of the genus.

Oral surface: Labrum very short, reaching only halfway along the first plate of the adjacent ambulacra. There are eight pores inside the subanal fasciole, arranged in two lines of four parallel to the lateral portions of the fasciole. In other characters the oral surface is characteristic of the genus.

Remarks. The most distal row of primary tubercles in the interambulacral fields, as in the other species of *Taimanawa*, is generally flush with the distal end of the adjacent petal. The anterior interambs of OU. 8540, however, have two additional rows of tubercles nearer the ambitus than the distal tip of the adjacent petal, giving an unusually high number of tubercles (22) compared to that of more normal specimens (12-16). One specimen (EC. 671) has a conspicuous boring perforating the test at its anterior margin, evidently the result of an attack by a large, predatory gastropod.

Age. Lower Miocene; Waitakian — Otaian. OU. 8585 is known to be of Waitakian age and EC. 405 has the age limits of Duntroonian — Waitakian. The remaining specimens, with the exception of E. 310, are from the Caversham Sandstone, which is largely of Otaian Age although Awamoan microfaunas are known from its uppermost horizons. The holotype is known to be of Otaian Age, and the other specimens from the Caversham Sandstone are most likely of Otaian Age also.

TAIMANAWA GREYI (Hutton)

Plate 1; Plate 2, fig. 1. Figure 2d.

Brissus greyi Hector, 1870: 192 (*nomen nudum*).
Eupatagus greyi: Hutton, 1873: 41.

Holotype. EC. 682, Cobden, north Westland; S44.

Additional material. N51: E. 296, near Waikawau Stream mouth, west Auckland; N51/677. *S37:* EC. 480, 481, Woodpecker Bay, north Westland; S37/528. *S44:* EC. 458, Cobden Limestone, Greymouth, north Westland; S44/465. EC. 543, Cobden Limestone Quarries, Greymouth, north Westland; S44/476. zfe. 286, 287, 290, Cobden Limestone, Greymouth, north Westland. *S102:* EC. 407, Kakahu River, south Canterbury; S102/1. OU. 8548b, Hanging Rock, Opihi River, south Canterbury. *S111:* E. 250, Lower Pareora Gorge, south Canterbury; S111/683. OU. 8606, Gordon Valley, south Canterbury. zfe. 284, Pareora Gorge, south Canterbury. *S127:* EC. 615, Pigeon Rock, Waitaki Valley, south Canterbury; S127/371. EC. 473, 474, Waihao River, south Canterbury; S127/376. EC. 472, Waitaki Valley, south Canterbury; S127/447. EC. 471, Awamoko Creek, Oamaru, south Canterbury; S127/450. E. 246, 248, Taylor's Road, Oamaru, south Canterbury; S127/639. OU. 8546, 8547, Waitaki Limestone, Duntroon, south Canterbury. OU. 8542, Ngapara, south Canterbury. OU. 8598, 8601, 8602, Earthquakes, Duntroon, south Canterbury. *S136:* OU. 8545, Weston, south Canterbury. *Locality unknown:* zfe. 278, Canterbury, unlocalised.

Diagnosis. Adult tests compressed, with a deeply depressed frontal ambulacrum, 22-25 well-developed pore pairs in the anterior petals, and 23-40 primary tubercles in each interambulacral field.

Description. Test up to 134 mm in length, cordiform in outline, almost as wide as long, with a sharp ambitus. Aboral surface shallowly arched, oral surface flattened; height/breadth ratio approximately 0.25. Apical system varies in position from slightly anterior to slightly posterior of center; it lies on the axis of maximum test height, and its morphology is typical of the genus. Peristome crescentic, anterior, and margined by a prominent lip. Anal region not preserved on any available specimens. Peripetalous fasciole thin, not strongly indented between the petals. Internal fasciole extending for a short distance near the sutures of the two plate series of interambs 2 and 3 and forming a tight loop posteriorly around the apical system. Neither the internal nor the peripetalous fasciole closed across the frontal ambulacrum.

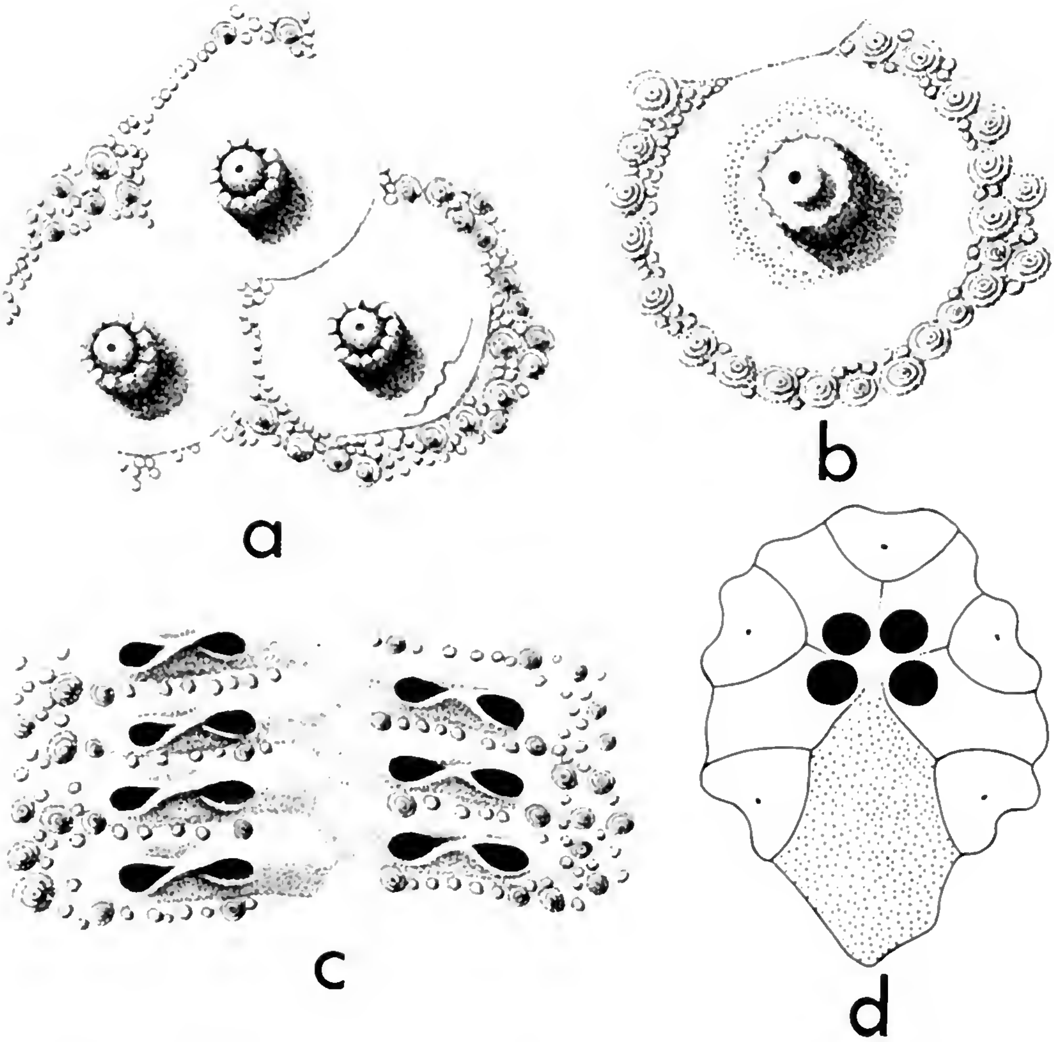

Figure 2. a) Primary tubercles of *Taimanawa pulchella* sp. nov., holotype, OU. 8590; ×7. b) Primary tubercles of *Taimanawa mortenseni*, holotype; ×7. c) Plates of ambulacrum V of *Taimanawa pulchella* sp. nov., holotype, OU. 8590; ×7. d) Apical system of *Taimanawa greyi* (Hutton), OU. 8598; ×7.

Aboral surface: Frontal ambulacrum deeply depressed, terminating in a conspicuous frontal notch that is as wide as deep on adult tests. Paired petals lightly depressed; anterior pair straight or gently curved towards the frontal ambulacrum and generally slightly longer than the posterior pair, which are straight or gently curved away from the posterior interamb. Pore pairs ovate and weakly conjugate; adult tests have 23-25 well-developed pore pairs in each anterior petal and 20-24 in each posterior petal. Fields of primary tubercles restricted to posterior plate series of the lateral interambs inside the peripetalous fasciole; 23-40 tubercles in each field on adult tests. Other features of the aboral surface as described for the genus.

Oral surface: As described for the genus. The anal region is poorly preserved on all the available specimens; the presence of a subanal fasciole cannot be confirmed, and the nature of the tuberculation within the anal fasciole is not known.

Remarks. The material, although abundant, offers but a single, indifferently preserved oral surface. The petals of different specimens are somewhat variable in length, breadth, and the degree to which they are depressed; the anterior petals of several specimens of about the same test width (114-119 mm) vary in length from 37 to 42 mm and vary in width from 5.0 to 6.5 mm. The number of primary tubercles in the interambulacral fields is also variable. Three specimens from the Cobden Limestone, Greymouth (zfe. 286, 287, 290), and a single specimen registered as from Ngapara, Oamaru (OU. 8542), differ from the remainder of the material in possessing more numerous primary tubercles (35-40 in each interambulacral field) and in bearing up to four rows of well-spaced, coarse secondary tubercles situated adjacent to and running parallel with the ambitus of the anterior interambs. The matrix of OU. 8542, a hard, fine-grained, muddy limestone, contrasts with the softer, coarse-grained, almost pure limestone that forms the matrix of other echinoids from Ngapara; it closely resembles the matrix of the Greymouth specimens. It may be that the locality of OU. 8542 has been incorrectly recorded.

Although the holotype has never been figured, it is known to be the specimen used by Hutton in the erection of the species. It is badly crushed and shows few of the characters of the species, but as it has at least 25 pore pairs in ambulacrum IV and approximately 36 primary tubercles in interambulacrum 4, it is undoubtedly conspecific with the other specimens herein referred to *T. greyi.*

Taimanawa greyi closely resembles *T. pulchella*, to which it was probably ancestral. It is distinguished by its petals, especially the anterior pair, having more numerous pore pairs (Fig. 3). Further differences include the deeper frontal goove and more numerous primary tubercles of *T. greyi.*

Age. Oligocene — lowermost Miocene; Whiangaroan — Waitakian. The exact age of the holotype is not known. From its locality and matrix, it can confidently be assigned to the Cobden Limestone, which ranges in age from Whiangaroan to Waitakian.

TAIMANAWA MORTENSENI sp. nov.

Plate 5, fig. 1. Figure 2b.

Plagiobrissus sp. ? Mortensen, 1951, p. 503, pl. 39, fig. 3.

Holotype. Fragments of a specimen from Station 32 of the Danish Expedition to the Kei Islands (1922), between Little Kei and Tajando Islands at a depth of 260 meters. Curated by the University Zoological Museum, Copenhagen.

Paratype. Fragments of a second specimen are represented in the collection from the same station.

Description. Known from fragments only, the largest of which comprises the anterior half of an aboral surface. Test large, and appears to be approximately as wide as long. Aboral surface inflated and ambitus more broadly rounded than in other members of the genus. Peripetalous fasciole well developed, not indented between the petals and not continuous across the frontal ambulacrum. Internal fasciole thin, of variable width, bordering the frontal ambulacrum for half the distance from the broken margin of the test, slightly anterior of the apical system, to the peripetalous fasciole. Subanal fasciole well developed and, as far as can be judged, reniform.

Aboral surface: Frontal ambulacrum deeply depressed, apetaloid, terminating in a pronounced frontal notch that is approximately as wide as deep. Amb plates bear a fine, dense, secondary and miliary tuberculation and are perforated by minute, conjugate pore pairs. Anterior petals slightly depressed, splayed at an angle of some 120°, and weakly flexuous, being concave away from the frontal ambulacrum proximally and concave towards the frontal ambulacrum distally. Each bears 25 ovate, weakly conjugate pore pairs; adjacent pairs are separated by a single row of secondary and miliary tubercles, and the interporiferous zone bears scattered miliary tubercles. Anterior plate series of the frontal interambulacra tumid, subtending a weakly concave surface posteriorly into confluence with the depressions of the frontal petals. Primary tubercles restricted to the posterior plate series of the anterior interambs lying within the peripetalous fasciole, surrounded by prominent scrobicules, and very weakly crenulate. The partially preserved anterior plate series of interamb 4 devoid of primary tubercles, suggesting that tuberculation of the posterior lateral interambs is akin to those anterior. Frontal ambulacrum margined by a zone of coarse secondary tubercles. The remaining aboral interambulacral surfaces bear a dense miliary and secondary tuberculation.

Oral surface: Nature of the plastron and labrum unknown. Interambs bear well-spaced secondary tubercles; ambulacra naked except for scattered miliary tubercles. The area enclosed by the subanal fasciole bears dense secondary tubercles and is perforated on each side by seven conjugate pore pairs.

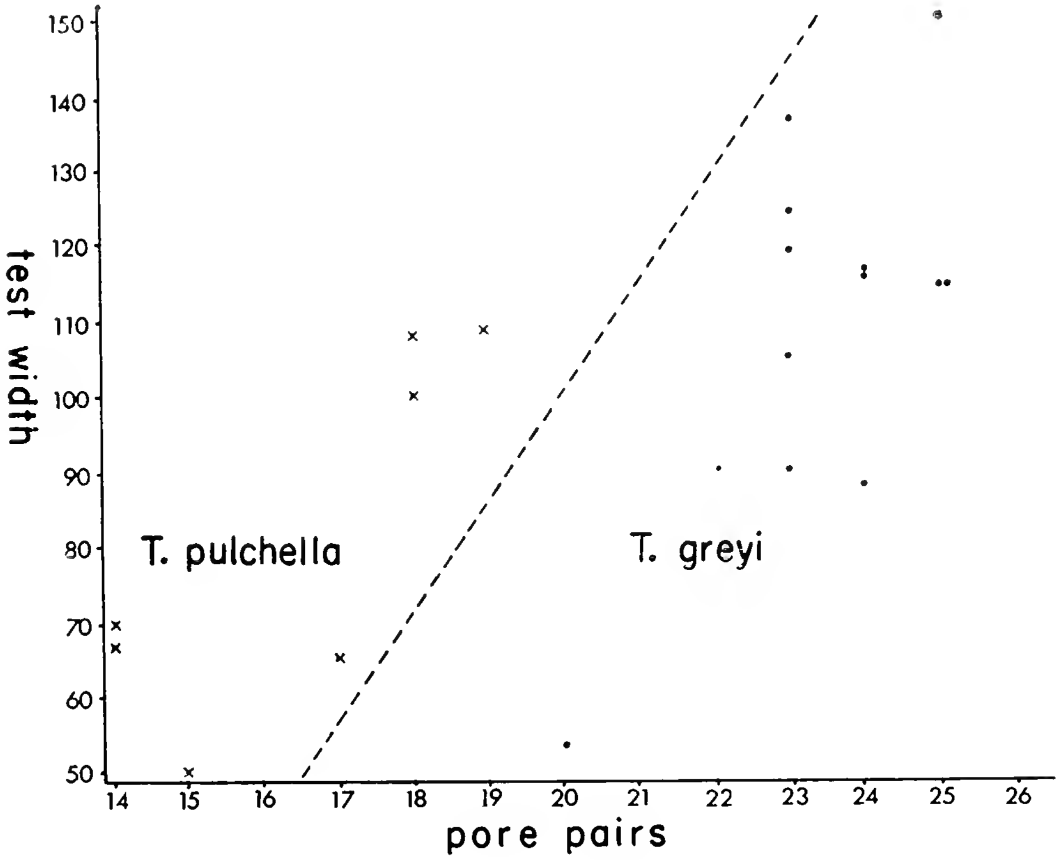

Figure 3. Plot of the number of fully developed pore pairs in each plate series of the anterior petals against test width for *Taimanawa pulchella* sp., nov. and *T. greyi* (Hutton) showing the separation of the two species. Ordinate values have been estimated for many points and are accurate only to ± 5 mm.

Remarks. Mortensen (1951) also recorded fragments of this species from Station 44 of the Danish Expedition to the Kei Islands (1922), but the material is poor (Dr. F. Jensenius Madsen, private communication) and has not been examined in the preparation of this report. *T. mortenseni* is conformable in all its principal characters with the fossil *T. pulchella* and *T. greyi* but represents a discrete species. The possession of an internal fasciole and a strong frontal notch shows that *mortenseni* must be referred to *Taimanawa.* Indeed, the very close resemblance between the mid-Tertiary New Zealand species and the present form, which is living in the Kei Island area of the Indonesian region, is remarkable.

The holotype represented by the most complete set of fragments would have measured approximately 140 mm in width. The test height cannot be accurately estimated, but the aboral surface is more inflated than that of either *T. pulchella* or *T. greyi,* and the ambitus is more rounded than in either of the fossil species. The anterior petals resemble those of *T. greyi* in the number of pore pairs, but the anterior interambs agree with those of *T. pulchella* in the number of primary tubercles. The present species is readily distinguished from either of the fossil species in that its primary tubercles are much less distinctly crenulated and possess a much wider platform (Fig. 2a, b).

Although the Kei Island fragments clearly represent a new species, more complete material is needed before it can be adequately defined.

Genus *BRISSOPATAGUS* Cotteau, 1863

Type species. B. caumonti Cotteau (1863: 144, pl. 8, figs. 3-7); by subsequent designation (Cotteau 1886: 135).

Brissopatagus Cotteau, 1863: 144; Pomel, 1883: 32, *pars;* Duncan and Sladen, 1884: 226, *pars;* Duncan, 1889: 250, *pars;* Lambert and Thiery, 1924: 491, *pars;* Cooke, 1942: 57, *pars;* Mortensen, 1951: 453, *pars;* Cooke, 1959: 92, *pars;* Phillip, 1966: 114, *pars;* Fischer, 1966: 584, *pars.*

Brissospatangus Cotteau, 1886: 135, *pars.*

non Brissospatangus: Cotteau, 1890: 18.

Diagnosis. Test small, with the test height approximately half the test length, bearing subanal and peripetalous fascioles. Frontal ambulacrum narrow and lightly depressed, forming a narrow, shallow frontal notch. Petals lightly depressed with subparallel pore series; anterior pair widely splayed, posterior pair less so. Anterior interambs with conspicuous depressions confluent with depressions of the anterior petals. Primary tubercles present on the anterior plate series of the frontal interambs.

Remarks. Brissopatagus is a poorly defined genus. It was proposed for two incompletely known species: *B. caumonti* from the Eocene of France; and *B. javanicus* Cotteau (1863: 144), originally described as *Spatangus?* sp. by Herklots (1854: 13, pl. 3, figs. 2, 2a, 2b). The latter was reported from the Eocene of Java by Cotteau, but Gerth (1922: 520) revised the age to middle Miocene. Each of the species is apparently known from a single specimen; that representing *B. javanicus* is an internal mould and shows no tuberculation, whereas that representing *B. caumonti* is an eroded, somewhat deformed specimen. So far as their morphology can be observed, the two species show good agreement in test shape and in the nature of the ambulacra.

B. caumonti, the type species by subsequent designation, forms the basis of *Brissopatagus* and is redescribed and refigured below. The specimen shows traces of a peripetalous and a subanal fasciole which have not hitherto been recorded. Cotteau's figures of the specimen, as typical of fossil echinoid illustrations of that time, are idealized. The distribution of primary tubercles is of particular significance. Those shown in Cotteau's figures are fictitious; the original specimen shows traces of a few primaries on the anterior plate series of the anterior paired interambs, but the remainder have been removed by erosion.

Brissopatagus, in the sense of the type species, is closely related to *Eupatagus,* with which it has been grouped as a subgenus by some authors (Dames, 1878; Cooke, 1959). It is also closely related to *Macropneustes.* The only character by which it can adequately be differentiated from these two genera is the depressions of the anterior interambs. The genus is also affiliated with *Gillechinus* Fell (based on *G. cudmorei* Fell, 1964, p. 213, pls. 1, 2), which is discussed in detail below. Phillip (1966: 114) has proposed that *Gillechinus* be treated as a synonym of *Brissopatagus.* A comparison of the type species of the two genera shows at once that such a view is untenable. *G. cudmorei* lacks the interambulacral depressions of *B. caumonti,* an essential character of *Brissopatagus,* as Fischer (1966) indicates. Further, *G. cudmorei* is clearly distinct from *B. caumonti* in that its primary tubercles are restricted to the posterior plate series of the paired interambs. If *Brissopatagus* is to be taken as including forms lacking interambulacral depressions and possessing primary tubercles on the anterior plate series of the paired interambs, then it is transitional to *Eupatagus* through species like *E. lamberti* Fourtau and *E. cordiformis* Duncan and Sladen and is indistinguishable from *Macropneustes.*

Subsequent to its erection, a number of species have been referred to *Brissopatagus*. Several possess characters of both *Brissopatagus* and *Gillechinus*, so that their correct generic assignment is not immediately apparent. For the reasons given in the discussion of *Gillechinus*, those with primary tubercles restricted to the posterior plate series of the paired interambs are referred to that genus. The remaining species are *B. colligoni* Lambert (1933: 37, pl. 4, fig. 21) from the Eocene of Madagascar and *B. sundaicus* Böhm (1882: 365, pl. 2, figs. 2a, b) from Madura Island north of Java. *B. sundaicus* is no older than Miocene in age, as no Lower Tertiary rocks are known to crop out on Madura Island (van Bemmelen, 1949: 106). This species, like *B. javanicus*, possesses distinct interambulacral depressions, but both species are represented by internal moulds alone, so that the nature of their tuberculation is not known and they cannot be referred to either *Brissopatagus* or *Gillechinus* with certainty. *B. collignoni* was described from crushed material that shows primary tubercles on both plate series of the paired interambulacra, and thus it agrees with *Brissopatagus* rather than *Gillechinus*. However, its interambulacral depressions are very weakly developed, and it may prove to be best included in *Eupatagus* or *Macropneustes*. The existence of transitional species showing characters of more than one genus is, of course, an inevitable consequence of evolution, since intermediate stages must often persist after generic stocks have differentiated. While such species are valuable indications of the relationships and origins of generic stocks, it becomes a matter of practical convenience to tolerate these transitional inter-generic taxa, whilst maintaining the validity of the formal genera which they seem to link. Any other course would result in the fusion of large groups of species in ever larger generic categories, as more intermediate forms are discovered from intermediate horizons, and as clines are elucidated from wider geographic sampling. Under the Linnaean system of taxonomy, we are compelled to base our generic diagnoses upon the characters seen in the original genotypes. In the case of *Brissopatagus* and *Gillechinus*, these characters are given by the type material, and they confirm the opinions of Mortensen (1951), Fell (1964), and Fischer (1966).

In summary, *Brissopatagus* as here restricted has but a single undoubted representative, *B. caumonti* from the Eocene of Biarritz, France. It is doubtfully represented in the Eocene of Madagascar (*B.? collignoni*) and may occur in the Miocene of the Javanese area (*B.? javanicus, B.? sundaicus*).

BRISSOPATAGUS CAUMONTI Cotteau

Plate 5, figs. 2-4.

Brissopatagus caumonti Cotteau, 1863: 144, pl. 8, figs. 3-7.
Brissospatangus caumonti; Cotteau, 1886: 136, pl. 30, figs. 1-4.

Holotype. 409- 1A- Co 1-2- b 132 (École des Mines, Paris).

Description. Test of moderate size, low vaulted, elongate; apical system anteriorly excentric, apex near the posterior margin. Anterior ambitus broadly rounded and cut by a narrow, shallow, frontal notch. Posterior ambitus somewhat tapered and more narrowly rounded. Apical system cannot be clearly seen but appears to possess four gonopores. Traces of peripetalous and subanal fascioles are present, the former not indented between the petals and the latter complete and reniform. Peristome small, crescentic, anterior; periproct vertically elongate and situated on the truncated posterior test surface.

Aboral surface: Frontal ambulacrum depressed on the adambital half of its length; its pores not preserved. Paired petals distinctly depressed with ovate pores. Anterior pair short, widely splayed, and anteriorly concave; each has about 12 well-developed pore pairs. Posterior pair somewhat longer, set close together, and straight, with about 20 well-developed pore pairs. Interambulacra 2 and 3 with conspicuous depressions forming concavities in the test continuous with those of the anterior paired petals. Ornament almost entirely lacking due to erosion of the specimen; a few primary tubercles preserved on the anterior plate series of interambulacra 2 and 3. The few patches that have escaped severe erosion suggest that much of the adoral surface was originally ornamented with small, dense, secondary tubercles.

Oral surface: Not well preserved. Plastron with a well-developed median keel and ornamented with dense secondary tubercles. Labrum appears to be long and narrow. Other interambulacral areas also bear dense secondaries. Ambulacra adjacent to the plastron appear to be narrow and, like the anterior ambulacral areas, naked except perhaps for miliary tubercles.

Remarks. The specimen is badly eroded and somewhat deformed. The interambulacral depressions adjacent to the anterior petals, although undoubtedly natural structures, have been accentuated by deformation. As far as can be deduced from Cotteau's descriptions, the specimen to hand is the only known representative of *B. caumonti.* The illustrations given by Cotteau are strongly idealized, as may be suspected from the discrepancies between those given in the two reports. The nature of the apical system and arrangement of the plates on the oral surface as depicted by Cotteau are fictitious. On the original specimen, the groove of the frontal ambulacrum does not reach as close to the apical system as depicted by Cotteau, nor are the posterior petals as divergent.

Genus *GILLECHINUS* Fell, 1964

Type species. G. cudmorei Fell (1964: 213, pls. 1, 2); by original designation.

Gillechinus Fell, 1964: 213; Phillip, 1966: 114; Fischer, 1966: 584.

Diagnosis. Test of moderate size, with the test height approximately half the test length, bearing peripetalous and subanal fascioles. Frontal ambulacrum weakly depressed, frontal notch broad and shallow. Petals lightly depressed, narrow, with subparallel pore series; anterior petals widely splayed, posterior pair less so. Interambulacra of the aboral surface ridged at or near the suture of the two plate series, with ridges of the paired interambs subtending flattened or concave surfaces posterior to the adjacent ambulacral depressions. Primary tubercles restricted to posterior plate series of the paired interambulacra within the peripetalous fasciole.

Remarks. As already pointed out, *Gillechinus* cannot be synonymised with *Brissopatagus*, as advocated by Phillip (1966), because the interambulacral depressions diagnostic of *Brissopatagus* are not shown by the type species of *Gillechinus*. A further distinction is provided by the restriction of primary tubercles to the posterior plate series of the paired interambs of *Gillechinus*, a feature not shown by *Brissopatagus*. There are, however, a number of species that have previously been referred to *Brissopatagus* and that possess both interambulacral depressions and tuberculation of the *Gillechinus* style. To classify these forms, it is necessary to decide which of the two characters is taxonomically significant. The species concerned are as follows:

- *G. alabamensis* (Cooke) (1942: 58, pl. 4, figs. 7, 8) from southeast U.S.A. and possibly Cuba. = *B. georgianus* Cooke (1942: 58, pl. 7, figs. 8-11) and possibly *B. avilensis* Sánchez Roig (1951: 45, pl. 33, figs. 2, 3). Eocene and possibly Oligocene.
- *G. beyrichi* (Dames) (1878: 82, pl. 11, figs. 2a, b) from north Italy. Eocene.
- *G. humei* (Fourtau) (1908: 218, pl. 2, fig. 8) from north Africa. Eocene.
- *G. lunmani* (Castex) (1930: 82, pl. 4, fig. 1) from France. Eocene.

- *G. sindensis* (Duncan and Sladen) (1884: 226, pl. 38, figs. 19-21) from India. Eocene.

One further species, originally referred to *Macropneustes,* must be added:

- *G. mexicanus* (Dickerson and Kew) (1917: 134, pl. 24, fig. 3, pl. 25, figs. 1a, b) from northeast Mexico. Upper Oligocene or Lower Miocene.

Gillechinus georgianus was synonymised with *G. alabamensis* by Cooke (1959: 92). *G. avilensis* is not well known, but the grounds for maintaining it as distinct, given by Sánchez Roig (1951) as its more depressed petals and less pronounced groove for the frontal ambulacrum, are slight and likely to be due to infraspecific variation. *G. lumnaui* and *G. alabamensis* may prove to be synonymous; *G. lumnaui* appears to be less inflated, and its anterior interambs have more primary tubercles than those posterior, while the reverse is true of *G. alabamensis.* The first distinction could be due to the slight crushing evident from Castex's (1930) figure, and the second could be due to infraspecific variation. *G. mexicanus* is closely related to *G. cudmorei,* differing mainly in its less inflated posterior oral surface. *B. sindensis* is more elongate than any of the other species, and *B. humei* is likewise readily distinguished by its more depressed frontal ambulacrum and deeper frontal notch. *G. beyrichi* is characterized by possessing more prominent interambulacral depressions than any of the other species.

The six species show considerable variation in the development of interambulacral depressions. In *G. beyrichi* they are well developed, apparently forming actual concavities on the test surface. The anterior depressions of *G. sindensis* are recorded by Duncan and Sladen (1886) as forming concavities on the test. However, in the remaining species the paired interambulacra appear to possess flattened surfaces subtended posteriorly from a tumid zone near the median suture of the two plate series. The flattened surfaces pass into confluence with the depressions of the paired petals and give the impression of interambulacral depressions. Homologous structures are well developed in *Taimanawa* and *Plagiobrissus,* and can be recognized on the type species of *Gillechinus, G. caumonti.* Such structures cannot be regarded as identical with the strong interambulacral concavities of *Brissopatagus.* It is significant that the interambulacral depressions of all six species are developed in all four of the paired interambs, whereas in *Brissopatagus* these structures are restricted to the anterior paired interambs. There is little doubt that the six species are closely related; it must be concluded that interambulacral depressions are a variable character in this species group, and the point at which they can be regarded as present or absent is not easily defined.

The restriction of the primary tubercles to the posterior plate series of the paired interambs is a conspicuous feature of all six species and is highly unusual for members of the *Brissidae*. This feature not only shows the six species to be very closely affiliated with *G. cudmorei* but provides a convenient diagnostic character for *Gillechinus*, separating it from all other brissid genera with the exception of *Lajanaster* Sánchez Roig. *Lajanaster* differs in possessing an elongate, strongly flattened test, and its oral surface, like that of *Plagiobrissus*, has a narrow plastron and very narrow ambulacral areas. In consequence, the six species here discussed are referred to *Gillechinus*.

Brissopatagus vilanovae Cotteau (1890: 19, pl. 2, figs. 9-13) is somewhat transitional between *Gillechinus* and *Eupatagus*. It has primary tuberculation of the *Gillechinus* style, but its petals are spatangiform with curved pore series rather than with subparallel pore series as in *Gillechinus*. For this reason the species is probably best referred to *Eupatagus*, whereupon it becomes a homonym of *B. vilanovae* Cotteau (1890: 10, pl. 1, figs. 1-4) and has been renamed *E. ibericus* by Lambert.

Gillechinus enjoyed a wide distribution in tropical and subtropical seas during Eocene time. It may range as high as the Miocene, but the Oligocene age given for *G. avilensis* by Sánchez Roig (1951) and the Upper Oligocene — Lower Miocene age given for *G. mexicanus* by Dickerson and Kew (1917) are unsupported and must be treated with caution.

TABLE I

DIMENSIONS OF TAIMANAWA AND BRISSOPATAGUS

	tl	tw	th	aa	apl	apw	aps	ap	ppl	ppw	pps	pp	at	pt	nw	nd
*OU. 8568c	c70.0	c67.0	c19.0	c30.0	19.0	4.0	35.0	14	20.0	4.0	19.5	14	7	10	13.5	c6.7
*OU. 8590	c110.0	c108.0	c30.0	55.0	34.0	6.3	c60.0	18	29.0	6.0	31.0	16	12	15	17.0	14.0
*EC. 426		c109.0	c30.0	c64.0	34.0	6.2	59.5	19	31.0	6.0	34.0	17	14	16		
†EC. 474	c58.0	c54.0		c31.5	17.0	3.3	29.0	20	15.0	3.2	17.0	17	10	12	10.0	5.5
†EC. 615	c123.0	c114.0		c58.0	37.0	5.0	c58.0	25	35.0	4.8	c38.5	24	c20	c22		
†OU. 8547	c123.0	c116.0		64.0	35.0	5.0	c62.0	24	34.0	5.0	c36.0	20	24	27	14.5	13.0
†OU. 8598	133.5	c114.0	43.0	65.5	42.0	6.0	68.0	25	40.0	6.0	41.5	23	31	34	15.0	14.0
†OU. 8545		c115.0	c35.0	c71.0	39.0	6.4	65.0	24	38.0	6.4	38.5	23	24	28	15.0	16.0
†EC. 471	134.0	119.0		68.0	41.0	6.5	69.5	23	41.0	6.0	41.0	22	27	23	15.5	16.0
†OU. 8601		124.0		65.0	42.0	6.0	67.5	23	37.0	6.0	c38.5	22	24	27	17.5	13.0
†OU. 8606	151.0	136.0		77.0	43.0	7.0	73.0	23	40.0	6.5	44.0	20	24	35	17.0	15.5
B. caumonti	40.5	35.0	19.5	14.5	10.5	2.5	18.5	12	13.5	2.5	c8.0	20			7.5	0.6

* *T. pulchella;* † *T. greyi.* Test length (tl); test width (tw); test height (th); distance from apical system to anterior margin (aa); length of anterior petals (apl); width of anterior petals (apw); distance between distal tips of anterior petals (aps); number of fully developed pore pairs in each anterior petal (ap); length of posterior petals (ppl); width of posterior petals (ppw); distance between distal tips of posterior petals (pps); number of fully developed pore pairs in each posterior petal (pp); number of primary tubercles in each anterior interamb (at); number of primary tubercles in each posterior interamb (pt); width of frontal notch (nw); and depth of frontal notch (nd). All measurements in millimeters.

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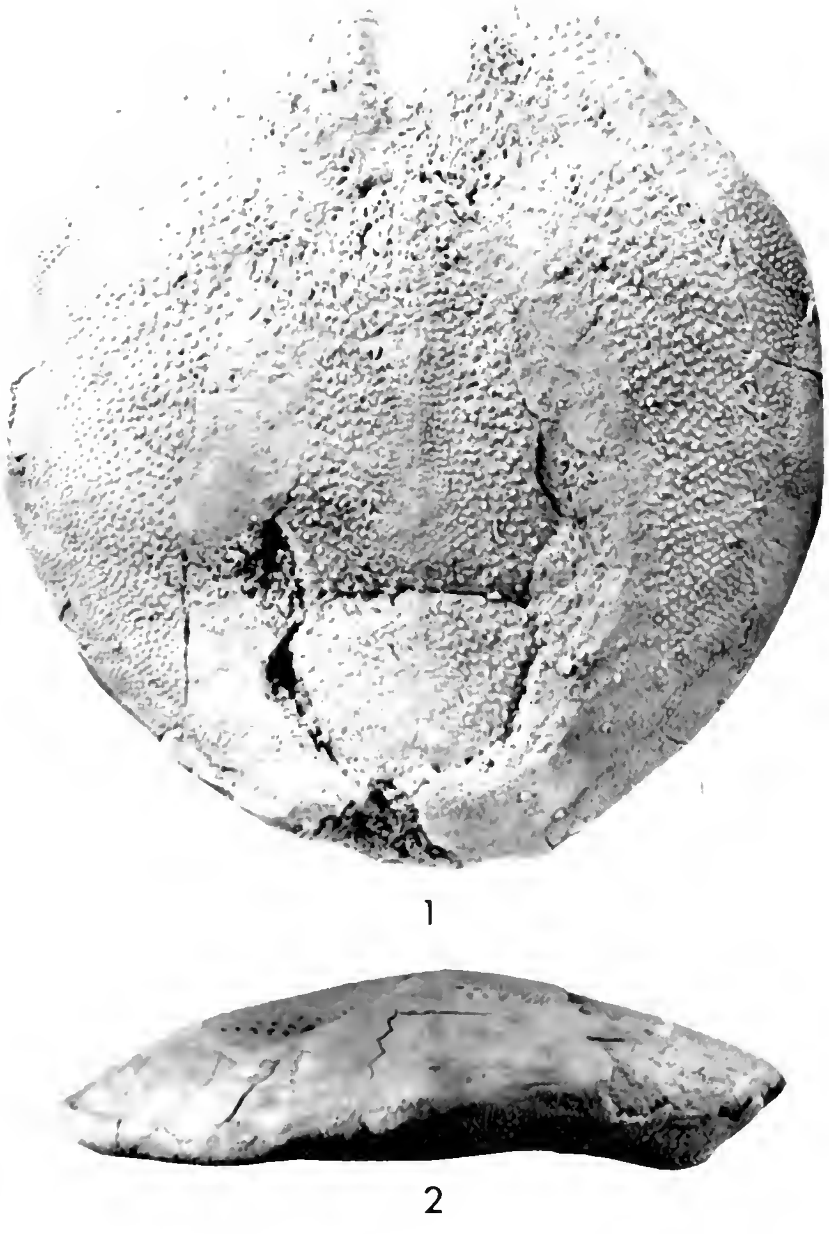
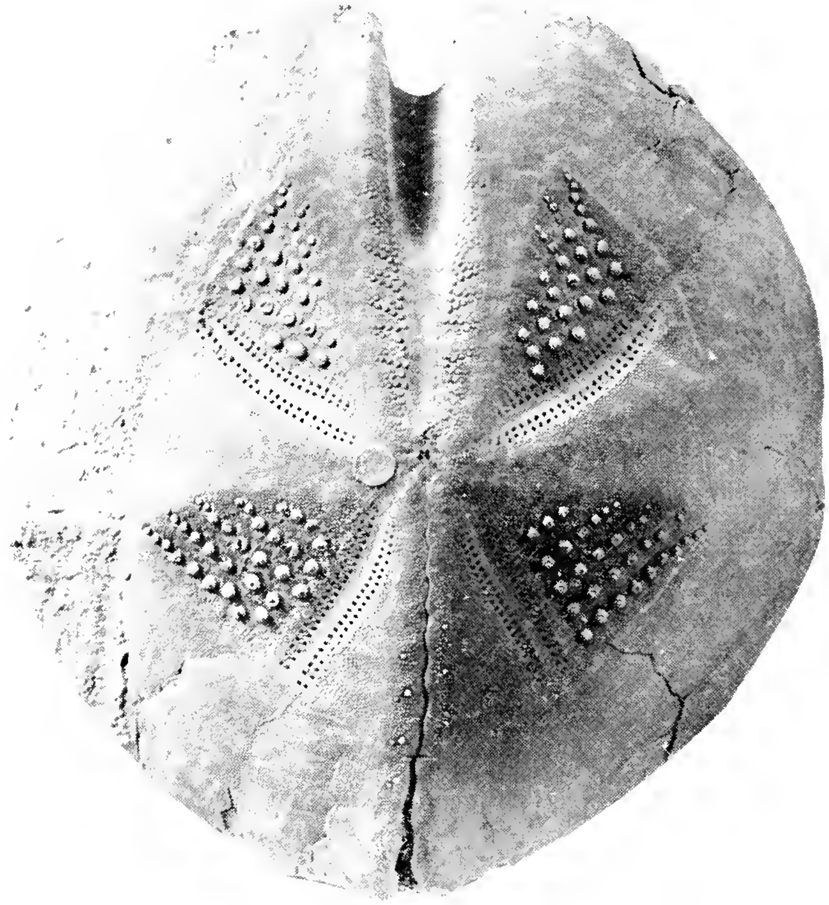


PLATE 1

FIGS. 1, 2. *Taumanawa greyi* (Hutton), dorsal view (Fig. 1), lateral view (Fig. 2). OU. 8598, test length 135.5 mm; (×⅔).



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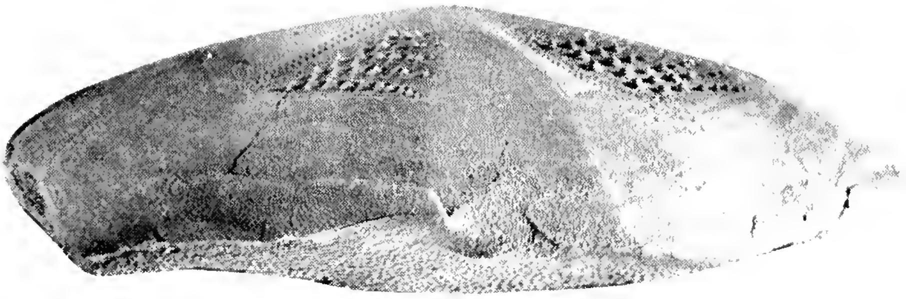

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PLATE 2

FIG. 1. *Taimanawa greyi* (Hutton), ventral view. OU. 8598, test length 133.5 mm; (×⅔).

FIG. 2. *Taimanawa pulchella* sp. nov., lateral view. Holotype, OU. 8590, test length *c* 110.0 mm; (×⅔).

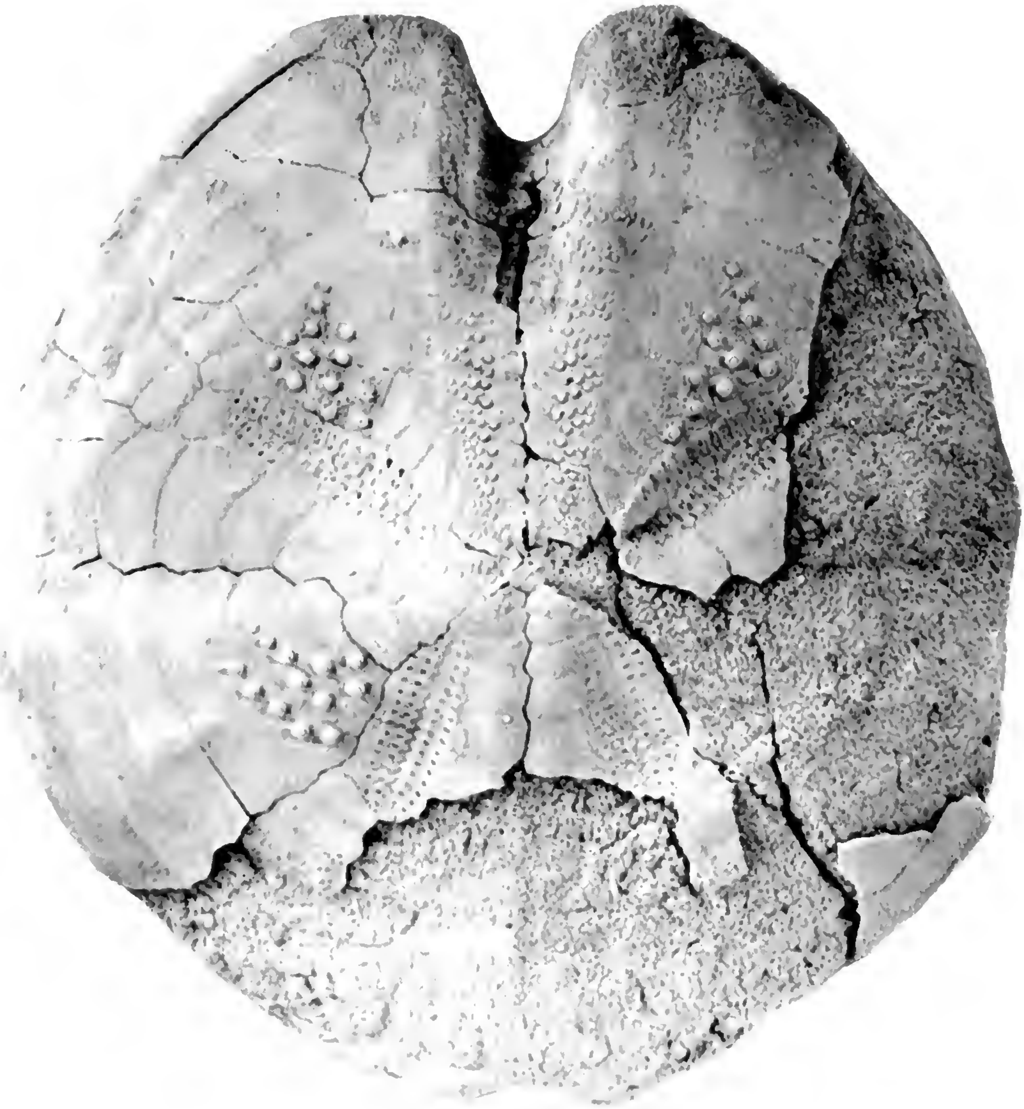
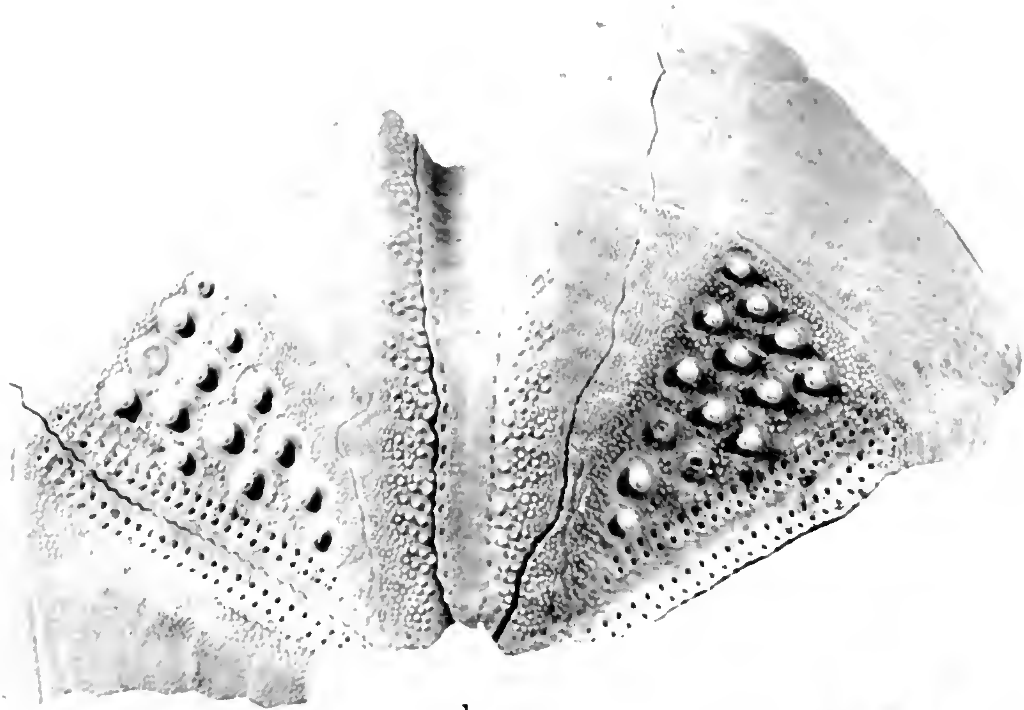


PLATE 3

Taimanawa pulchella sp. nov., dorsal view. Holotype, OU. 8590, test length c. 110.0 mm: (× 1).

PLATE 4

Taimanawa pulchella sp. nov., ventral view. Holotype, OU. 8590, test length *c* 110.0 mm; (×1).



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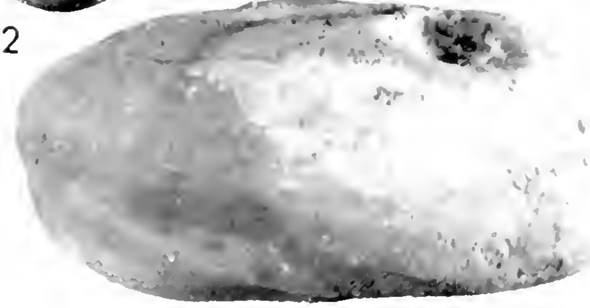

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PLATE 5

FIG. 1. *Taimanawa mortenseni* sp. nov., dorsal view. Holotype, fragments of a specimen from Station 32 of the Danish Expedition to the Kei Islands (1922), University Zoological Museum Copenhagen, width of fragment 105 mm; (× *c* 1).

FIGS. 2-4. *Brissopatagus caumonti* Cotteau, dorsal view (Fig. 2), ventral view (Fig. 3), lateral view (Fig. 4). Holotype, 409- 1A- Co 1-2- b 132, École des Mines, Paris, test length 40.5 mm; (X*c*1).

BREVIORA

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OBSERVATIONS ON THE AGONISTIC AND BREEDING BEHAVIOR OF *LEPTODACTYLUS PENTADACTYLUS* AND OTHER AMPHIBIAN SPECIES IN VENEZUELA

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and

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Abstract. Observations were made of breeding aggregations of *Leptodactylus pentadactylus, Phyllomedusa trinitatis, Engystomops pustulosus, Phrynohyas venulosa* and *Hyla minuta* in northeast Venezuela. *L. pentadactylus* makes hollows near the water's edge and produces a foam nest where the eggs are deposited. During amplexus and oviposition, the male moves the feet in alternate, coordinated movements over the cloacal openings of the embracing pair, apparently assuring, in this way, proper fertilization and distribution of the eggs, besides beating the foam into the proper consistency. During amplexus, the male shows definite agonistic behavior towards other members of his species or to any other object that may touch him. Quite often fights between males occur. These may last several minutes and consist of standing up and hugging the opponent with the thumb tubercles, pushing, toppling, and apparently embracing, and pulling the adversary towards the breast tubercles.

Engystomops seems to prefer road puddles and fouled water for breeding. Its voice is similar to that of a puppy, and a group of this species will stop calling simultaneously, and for relatively long intervals, when approached by an observer.

Phyllomedusa was extremely abundant in *Dieffenbachia* and other broad-leaved plants. Egg clusters were found on leaf surfaces only. It appears that when leaves of the right size are not found, *Phyllomedusa* does not need to make the leaf nests (funnels) described for many of the species. Besides its normal mating call, the male has a particular release call. It is possible that spent females produce a similar sound.

Phrynohyas venulosa were occupying approximately equidistant positions in a shallow pool. Both this species and *Hyla minuta,* which were extremely common during the first night of observation, had completely disappeared the following night.

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INTRODUCTION

On June 25, 1968, the authors made a trip to the region of Güiria, Estado Sucre, in the Península de Paria of Venezuela, and collected extensively in the vicinity of the village of Río Salado and on Pica del Mango at a slightly higher elevation (100 m). The conditions near Güiria are xerophytic to mesophytic, but higher up on Pica del Mango the vegetation is quite luxuriant and there is a great abundance of heliconias, Araceae and Marantaceae. Most of the observations reported here were made at Pica del Mango.

The excursion to Pica del Mango was made at night after a heavy rain during the afternoon. As a result of the rain, a depression in the forest had been filled with water to a depth of a few inches. The pool, of about ten by three meters, was undoubtedly temporary, but it may have been in existence prior to the rainy period of that afternoon. The margins, three to five meters beyond the edge of the water, were more or less clear of any vegetation except at one end, where there were a number of broad-leaved Marantaceae and *Dieffenbachia* growing in a thicket. The forest, with its heavy undergrowth of heliconias, *Costus* and Araceae, commenced at about five meters from the edge of the pool. The pool was, however, shaded by two or three large trees that grew near its margins.

The roar produced by frogs calling from the pool could be heard at a distance of about 200 meters. Upon approaching, the noise increased in intensity and became almost deafening. Calling from the leaves of plants were *Hyla minuta*, sometimes three, four, or five to each leaf of *Dieffenbachia*. It was often possible to get three specimens with one sweeping movement of the hand over the leaf surface.

When flashlights were pointed at the water, *Phrynohyas venulosa* were seen to be occupying the pool, spaced in a pattern at a distance of about three to four feet from one another. As there was no vegetation inside the pool, this "formation" could be easily observed.

Also contributing to the uproar coming from the pool were *Leptodactylus pentadactylus* and *Phyllomedusa trinitatis* in great abundance, *Engystomops pustulosus* in lesser abundance, and a few specimens of *Leptodactylus p. petersii*.

LEPTODACTYLUS PENTADACTYLUS

Most attention was given to *L. pentadactylus*, since it was hoped that the following night could be dedicated to the other species breeding in the pool. Large specimens of *L. pentadactylus* were everywhere; occasionally one would even step on them. In one place, eight breeding pairs were counted in a space about three meters by one meter, a condition reminiscent of the breeding rookeries of some shore birds. Nests were sometimes eight to ten inches apart, but more commonly they were about one foot from one another. As the eyes of *L. pentadactylus* shine red at night, it was not difficult to survey the area and locate and count specimens. Remaining stationary and moving the flashlight around the pool, we counted 60 individuals, but, if it is considered that nests were more abundant in the *Dieffenbachia* thicket, that females in nests were probably not seen, and that many specimens were protected from view by other obstructions, the total number may easily have been double that. More specimens, especially females, were pouring in from the forest all the time.

Most specimens were males, however. Apart from the mated specimens, which were usually quiet in their nests, unattached individuals were moving all the time, the jumps being short and frequently changing in direction. When the butt end of a flashlight was presented to a free male, the animal would move away, and no attempt was made at amplexus (in contrast to what a *Bufo* would

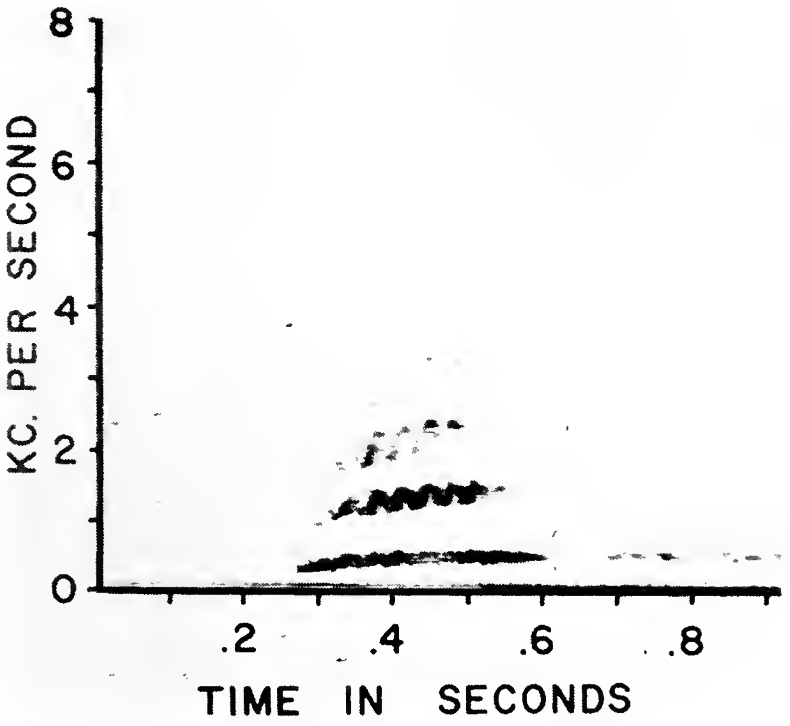

Fig. 1. — Audiospectrogram of the breeding call of *Leptodactylus pentadactylus*, Pica del Mango, Estado Sucre, Venezuela, 25 June 1968.

do). Males were often seen fighting, the two animals rising on their rear legs and attempting to puncture the adversary with their thumb spines by inward embracing movements of their powerful forelimbs. The movements were brisk, and the fight did not usually last more than a few seconds, one of the frogs moving away, or being pushed away, after the first "round." On other occasions, the fight lasted for five or ten minutes, and there was much pushing, toppling (from the raised position), and embracing before the fight was over.[1] These fights created considerable turmoil, and the noise could be heard at a distance of 15 or 20 feet without difficulty. In the plant thicket there was much movement of the plants as the wrestling animals pushed against them.

The male attached to a female showed agonistic behavior towards anything of the right size. If a frog of a smaller species was brought close to the male by the observer, the male would not usually release its hold but would try to push the animal away with one or both arms. If the "attack" were more persistent, or if a bigger animal were involved, it would release its hold and fight the intruder in the usual manner, trying to puncture it with the strong inward movements of the forearms. If the intruder went away, or if it was moved away, the male — if it had been displaced — would give a few short hops near or around the nest, call, and then come back, either to the original female or to any other neighboring female that was nesting and was not pre-empted by another male. If the male had not been displaced, he would just sit above the female, turn around and call repeatedly.

It appears that a male does not have any strong attachment to any particular female, and, if it happens to step on something having the proper consistency, it gives a few short hops, turns around several times, and then attempts amplexus. During this time the female is completely passive.

During the period of observation, it was the authors' impression that the female does not respond, locally, to an individual male's call. Females were coming to the pool, apparently attracted by the males' calls, but once there they did not seem to go to calling males and, when they were moving freely, the males did not pay any attention to them. In practically all cases of matings observed, the females were flat on a depression apparently made by them, and

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[1] Similar fights have been described for dendrobatids (Test, 1954; Sexton 1960; Duellman, 1966), *Rana* (Brode, 1959) and *Hyla* (Lutz, Bertha, 1960), but only the latter and *Leptodactylus* are reported to use their thumb spines as offensive weapons.

the meeting — or rather the stepping of the male over the female — was apparently fortuitous, a situation that may explain the continuous and erratic movements of unattached males. To be sure, males were sometimes seen calling from shallow depressions, but they were never seen making the holes, and no females were seen to be attracted to them. Mated males continue to call regularly during the sexual embrace, an indication that the call may constitute an innate mechanism to call females to the breeding site but may not have any local value. It might have a territorial function, but embracing males are often attacked, and not much respect is apparently given to their call. However, after a male has rejected an intruder, he hops around the nest and calls repeatedly, as if he were looking for another "fight," or as a rooster would, signalling its victory.

As nests (depressions) were sometimes very close together, it was often possible to have several breeding pairs under observation at the same time. In one particular place, there were three breeding pairs about six to eight inches from one another, three unattached males one to two feet away and at approximately that same distance from one another, and two females that arrived from the forest during the period of observation. No foam had been produced in any of the nests as yet. The embracing males were closely attached to the females, with the last finger over the shoulder and the others, including the tubercular thumb, in the axilla. Occasionally there was some shifting movement on the part of the males, perhaps to secure a better position, although it resembled the fondling movements of mammals. One of the males suddenly released its hold and moved away. The female stayed flat (actually slightly concave, the head and posterior ends being higher than the center of the body) in place. After a while, another male came by, apparently by accident, stepped on her, and embraced her. She pushed the mud forward with her forearms, much as a crab would do with its pincers. The occasional "fondling" movements continued.

Another male coming from somewhere else jumped over one of the embracing males, dislodging it. When the attack is sudden in this fashion, the animal is apparently caught by surprise and, if physically displaced, does not usually come back or offer a fight. The intruding male did not, however, take "possession" of the vacant female and, after a while, left the place. In a second case, the attacking male took possession of the female and, in a third, the attacking animal took possession, not of the vacated female, but of another vacant one a few inches away.

The two incoming females wandered into the place at different times. They passed unattached calling males without incident. When a female was captured and offered to a male by an observer, no attempt at amplexus or fight was made. Captured males did not produce a release call or vibrations that could be noticed. No attempt at mating was seen with anything not flat on a depression, although one pair was found in amplexus, not in a depression, but about a foot from the edge of the pool. Probably if a male were to attempt amplexus with another male, the attempt would be met not with a release call, but with strong agonistic behavior. In many instances, males were sometimes found fighting away from nests, but it is possible that the fights originated in nests, as in no case were two unattached males seen to start a fight and neither were males seen fighting females.

One of the observed incoming females settled for a while in a foam nest full of eggs. After some shifting movements, she flattened there for a few minutes but then departed for another depression apparently left by another individual, and settled there. After a while, she was embraced.

The other incoming female did a lot of wandering, trying several sites, passing only inches away from calling, unattached males, and then disappearing for a few minutes. This specimen was probably the one seen later in amplexus near the water's edge. It is not known if this female was grabbed by a male while passing, but this was the only instance in which a mated pair was seen out of a nest (depression).

On one occasion a commotion was heard at the plant thicket and a male was seen trying to clasp the horizontal stem of a *Dieffenbachia* plant. The stem came out of the ground vertically, but about 3 inches from the ground it bent and continued horizontally for about a foot before becoming vertical again. The frog was holding the horizontal portion of the stem (which was about 1½ inches in diameter and quite fleshy) and was trying to clamp it with jerky inward movements of his arms. It is not known if the stem was confused with a female or with a male; it is possible that a fight between two males had been going on and, as one retreated, the other continued to fight with the best possible substitute: the fleshy, slightly raised stem of *Dieffenbachia*. During this unilateral fight, the male was seen to raise its hind legs, first one, then the other, as if attempting to scratch the antagonist with its foot.

When a flashlight butt was pushed at an embracing animal, he released his hold, clasped the flashlight with his arm, moved his arms inward several times, making a noise as the thumb tubercles hit the metal, and apparently pushed the flashlight tube towards the breast tubercles with his clasping arms. Some "scratching" movement of the hind limbs was also noticed, but again it is not known if this was done to produce harm or to be able to have all four legs on top of the flashlight, which was presented in an oblique position.

The nest is a shallow depression apparently made by the female, who flattens out and moves mud forward with her forelimbs. She also makes sidewise movements, as a *Phrynosoma* would do to cover itself with sand, and may also do some pushing with the hind limbs, but this was not observed. The nest depression is round, only slightly bigger than the animal, and, since it is generally made near the edge, but out of the water, it usually has a little water in the bottom. Some foam nests were at the margin of the pool, but inside the water, and one was associated with floating debris. No central depression or opening can be observed in the foam. In fresh nests some radiating and spirally arranged lines can be seen coming from the center, but these soon dissipate, perhaps because the wandering males do not hesitate to step on nests and other females may flatten up in them as if the foam were non-existent.

In the region of La Escalera, Estado Bolívar, where several foam nests were observed in a shallow pool, these were usually in the water (not deeper than one inch) and associated with sticks, leaves, and other debris. A few were out of the water, but under the leaf litter at the edge of the pool.

Unfortunately, the production of foam could not be observed. In many of the nests, foam was already produced, and in others with amplexing pairs no foam was produced during the period of observation. After the foam is produced, male and female seem to be absorbed in their activity. Every few seconds (about ½ minute) the female dumps her head in the foam and raises the posterior end of the body. The male follows her, and for a while both heads disappear in the foam while both posterior ends are raised above it. Then follows a most interesting movement. The male starts a fanning movement with his feet, moving them up and down, one following the other in a rhythmic, well-coordinated fashion. As the toes are moved over the cloacal opening of the male, they may carry sperm down to the cloacal opening of the female, while at the same time they apparently spread the fertilized eggs out into the foam. Foam, by the way, is flowing between the two cloacal openings during the whole procedure. While this process is occurring, the foam may be seen to increase in quantity. It appears that the fanning movement of the feet may have three functions: passing the sperm over the eggs, distributing the fertilized eggs in the foam.

and agitating the water in an egg beater fashion so that it mixes with the sperm fluid and produces a foam of the right consistency. Substances produced with the sperm or eggs or both may contribute to add viscosity to the liquid.

ENGYSTOMOPS PUSTULOSUS

Some *Engystomops* were observed in the forest pool described above, but apparently this is not their preferred kind of site, as only 10 or 12 individuals were seen here. The same fanning movement observed in *Leptodactylus* was seen in *Engystomops pustulosus*, but in this case mating occurred in shallow water and not in nests or depressions out of the water. *Engystomops* has a notable preference for pools made in dirt roads by passing cars. In these muddy and agitated places they seem to be at their best, calling continuously with a voice that reminds one of a puppy recently separated from its mother. In the Andes (near La Azulita and at Isnotú) *Engystomops* was collected in water discharged from latrines, where it was calling together with *Hyla crepitans* and *L. poecilochilus* (Isnotú). Approach to a pool in which *Engystomops* is calling must be made quietly as they can stop calling suddenly, as if by signal, and then keep quiet for a while.

PHYLLOMEDUSA TRINITATIS

Another species breeding in the forest pool together with *Leptodactylus pentadactylus* and *Engystomops* was *Phyllomedusa trinitatis*. If the sight of breeding *L. pentadactylus* was grandiose, that of *Phyllomedusa* was spectacular. The Marantaceae-*Dieffenbachia* plant thicket described above was literally loaded with them. Many leaves were bent as a result of the weight, and others had broken at the stem and hung down with several *Phyllomedusa* attached or walking, in monkey fashion, along the stem. Some *Phyllomedusa* were in amplexus, as well described and photographed by Kenny (1966), but females were relatively scarce; quite often a male would grab another male, only to release him upon the production of his release call and vibrations. A specimen that hung from its hind limbs, dead, was "covered" by a male for about one hour. In some places there were bunches of four or five individuals, all apparently attempting amplexus with a female. These bundles hung like grapes; they were never seen on top of a leaf or on the floor, but embracing pairs were sometimes found on broad leaves or on stems.

The movements of *Phyllomedusa* remind one of those of a monkey. The limbs are moved slowly and deliberately, the fingers and toes grabbing the twigs or branches more or less as a monkey would. Obviously, its walking gait is adapted to moving along twigs and small branches, but, when placed on the floor, it can also walk, although it may jump fairly fast too. When *Phyllomedusa* is placed in the sun, the color first becomes spotted dark green on a lighter green background and later, but in a matter of seconds, it becomes dark, bottle green. In the collecting bag in the shade, most were leaf green, but a few were olive brown, and this latter color is kept after preservation. It is stated by Kenny that the non-breeding color is bright green, whereas the breeding color is olive brown. This could not be confirmed, as most of the specimens observed, including amplexing pairs and unspent females, were green. Calling males from San Casimiro, 850 m, were also of a bright green color.

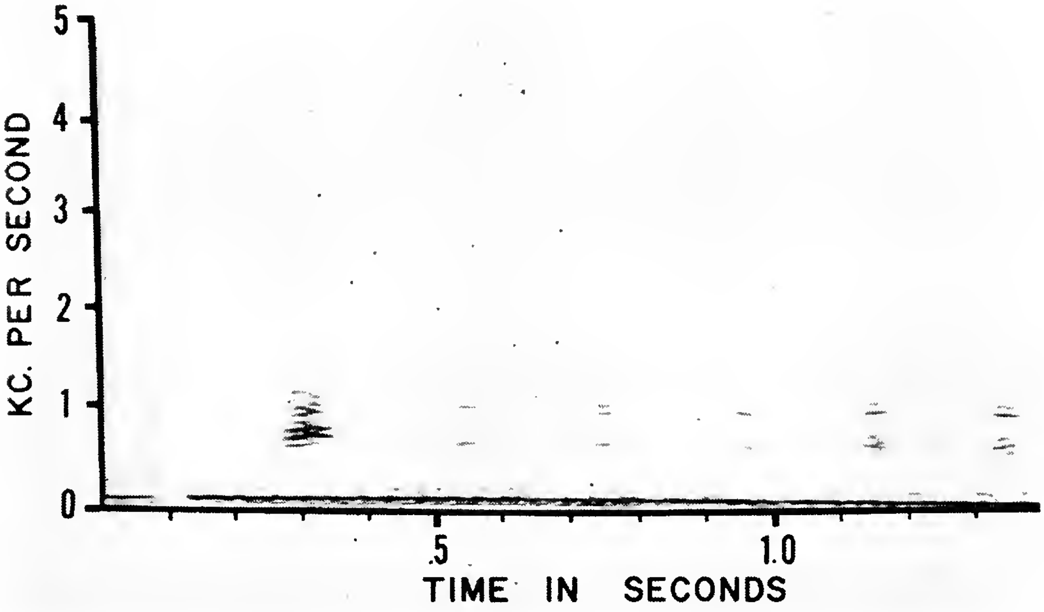

Fig. 2 — Audiospectrogram of the breeding call of *Phyllomedusa trinitatis*, Monte Oscuro, near San Casimiro, Estado Aragua, Venezuela, 15 June 1968.

In one instance a *Phyllomedusa* was seen to be walking along a stem. Suddenly it stopped, more or less "sat," and, while holding the twig with the two feet and one hand, raised the right arm and waved it around as if looking for another twig. On another occasion the animal raised both arms and did a similar operation. It appears that the animal "feels" the twigs and branches rather than sees them, but this may have been as a result of the light pointing at it. This behavior looked so unfroglike that it was thought to be accidental until it was observed on several other occasions.

Only three or four bunches of eggs (of about 25 or 30), all attached to the upper surfaces of broad-leaved plants, were observed. This is contrary to the situation described in other *Phyllomedusa* (Budgett, 1899; Agar, 1909; von Ihering, 1866) or for this species in Trinidad (Kenny, 1966), where a funnel made from one or more leaves is used as a nest. A. and B. Lutz (1939) wrote that a nest of *P. appendiculata* was found in a hollow of a wet block of stone covered by a fallen tree trunk in a mountain brook. It appears that when small leaves are not available, *Phyllomedusa* can adapt to other conditions.

How *Phyllomedusa* made itself heard under the roaring sound of *P. venulosa* and *L. pentadactylus* is difficult to understand. Perhaps it comes earlier to the pool; or perhaps the scarcity of females can be attributed to this factor. Kenny (1966:16) reports that the females of *Phyllomedusa* are also vocal and that males have a mating call ("huh, huh, huh") and a non-mating call which they produce throughout the night. The authors only heard two calls, one the regular mating call, and the other, a release call (and vibrations) produced by males when other males touch them or attempt amplexus with them. This call is also produced when a male is grabbed by a human or when several specimens are placed together in a bag. It is possible that spent females produce a similar sound, although this was not recorded.

PHRYNOHYAS VENULOSA

Few observations were made on *Phrynohyas venulosa*, in the hope of paying more attention to this species the next day. However, it was observed that they occupy equidistant positions in the pool, that they retain amplexus after capture, that one was seen to grab a *L. pentadactylus* in amplexus and ride it until they both disappeared, and that even when not calling, the two vocal sacs seem to act as floaters, looking as if the animal were wearing water-wing life preservers.

The voice of *Phrynohyas venulosa* has been described by a number of authors. The call can perhaps best be described as like the bleating of a goat, but when many specimens are calling together, the noise produced can be compared to that of a low-flying helicopter or to that produced by automobiles with holes in their mufflers.

The following afternoon, the surface of the pool was seen to be almost completely covered with what, at first sight, appeared to be the pupae of giant mosquitoes; these were the eggs of *P. venulosa.* That same night both *P. venulosa* and *Hyla minuta* had disappeared completely. And they were neither seen nor heard in another pool a few kilometers away, where they were heard abundantly the night before.

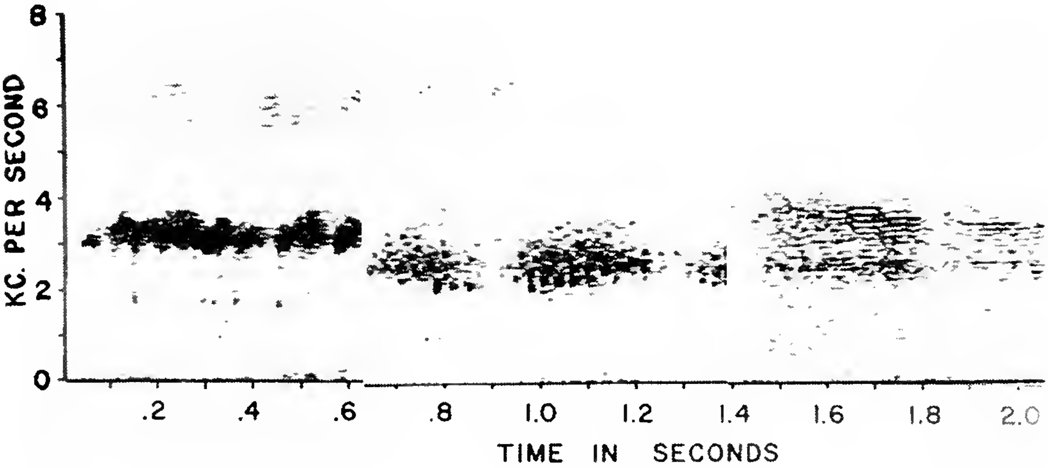

Fig. 3 — Audiospectrograms of breeding choruses. Left, *Leptodactylus podicipinus petersii*, El Pilar, Estado Sucre, Venezuela, 27 June 1968. Center, *Pseudis paradoxus*, Río Salado, Estado Sucre, Venezuela, 25 June 1968. Right, *Phrynohyas venulosa*, Pica del Mango, Estado Sucre, Venezuela, 25 June 1968.

It is not known when the forest pool described above was filled with water. If it was during the afternoon rain preceding our visit, then the breeding of *Phrynohyas venulosa* lasts only one night. During the periods of observation, no ordinary frog predators were seen. *Leptodactylus* can easily swallow *Engystomops*, but it was probably too active, breeding and fighting, to bother about eating. On the first night, two enormous pigs were observed grabbing frogs and apparently eating them (the actual eating was not seen, as the pigs were immediately scared off by the observers, but their insistence on coming back left little doubt about their "intentions"). Three of the *P. venulosa* seen were dead, the other came out of the water dying. The cause of this is not known, but it is not improbable that they accidentally bumped into a male *Leptodactylus,* which can be a dangerous adversary. In one instance, Esteves' hand was accidentally grabbed by a male *Leptodactylus* and, before he could remove it, the animal tried to puncture it with its thumb tubercles by jerky inward movements and did its best to push the hand against the breast spines. A *P. venulosa* would probably be in serious trouble if similarly treated.

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THE FOSSIL RECORD OF AMPHIUMID SALAMANDERS[1]

Richard Estes

ABSTRACT. The first pre-Pleistocene records of amphiumid salamanders are described here. *Proamphiuma cretacea,* n. gen., n. sp., from the late Cretaceous Hell Creek Formation of Montana, differs from *Amphiuma* in having less well-developed vertebral muscle crests, basapophyses, and neural spines. The species is represented only by vertebrae. *Amphiuma jepseni,* n. sp., from the late Paleocene Polecat Bench Formation, Wyoming, is the earliest record of the modern genus. Its vertebrae do not differ from those of Recent *Amphiuma,* but its skull lacks the facial elongation characteristic of the modern species. It is represented by vertebrae and by a partial skull.

Widespread transgressive seas of the Cretaceous, by providing extensive coastal plains and abundant shallow-water riparian habitat, may have been a major factor in the evolution of amphiumids and other elongated, aquatic salamanders.

INTRODUCTION

No previous fossil record for the salamander family Amphiumidae has been described, except for two Pleistocene records, one reliable, the other spurious. Auffenberg and Goin (1959) and Brattstrom (1953) have correctly ascribed to *Amphiuma* specimens from Florida Pleistocene localities. An unusual zoogeographic record was described for the Pleistocene of Germany by Brunner (1956), as a new species, *Amphiuma norica.* This specimen may be the parasphenoid of a teleost; it bears no resemblance to that of *Amphiuma*, and there is no basis for the identification (Fig. 3g-h).

Study of a North American Cretaceous floodplain herpetofauna (Estes, 1964) has disclosed ancestors of some lower vertebrates now living only on the Gulf Coastal Plain of North America. The

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[1] Fossil vertebrates from the late Cretaceous Hell Creek Formation, Montana: Contribution No. 3.

fauna of the latter region today differs in many ways from the ancient floodplain fauna, but both share the presence of the fishes *Amia, Lepisosteus, Acipenser*, a polyodontid, sirenid salamanders, crocodiles, the turtle *Trionyx*, and alligators. These animals today are all relicts of forms once widely distributed on floodplains of late Cretaceous epicontinental seas, the relict drainage of which is the Mississippi River system. The description here of another Gulf Coast element in the fossil fauna of the late Cretaceous of Montana and Paleocene of Wyoming is further indication of the relict nature and former wide distribution of the Gulf Coast forms noted above.

ACKNOWLEDGMENTS

I am grateful to Dr. Francis Rose for helpful suggestions. Dr. Glenn Jepsen has provided the Silver Coulee specimens, which are described here in advance of a collaborative paper on Silver Coulee lower vertebrates, and I take pleasure in naming the new species for him. Collection of the Princeton material was supported by the Scott Fund, Princeton University. This research has been supported in part by National Science Foundation Grant GB-7176. The figures are by Mr. Laszlo Meszoly.

FAMILY AMPHIUMIDAE

Proamphiuma cretacea, n. gen., n. sp.

(Figs. 1, 2)

Holotype. MCZ 3504, vertebra.

Paratypes. MCZ 3506-3509, 3627-3636, vertebrae; 3505, 3637, atlantes.

Locality. Bug Creek Anthills (BCA), 80 feet below the Tullock Formation in the west half of Section 9, T 22 N, R 43 E, McCone County, Montana; collected by A. D. Lewis and party.

Horizon. Hell Creek Formation.

Age. Late Cretaceous.

Diagnosis. An amphiumid with neural arch of atlas horizontal rather than dorsally-pointing posteriorly; vertebrae relatively narrower, more constricted medially, and with muscle crests, basapophyses, and neural spines less prominent than in Recent *Amphiuma* of comparable size; shares with *Amphiuma* described below the relatively more constricted centrum and neural arch.

Description. Centra amphicoelous, cotyles teardrop-shaped with thin internal coating of calcified cartilage; subcentral keel prominent or low, with or without channels for the segmental blood vessels; prominent or flattened anterior basapophyses usually projecting beyond anterior centrum margin; indications of two closely-appressed rib-bearers appearing on the four anterior vertebrae, the

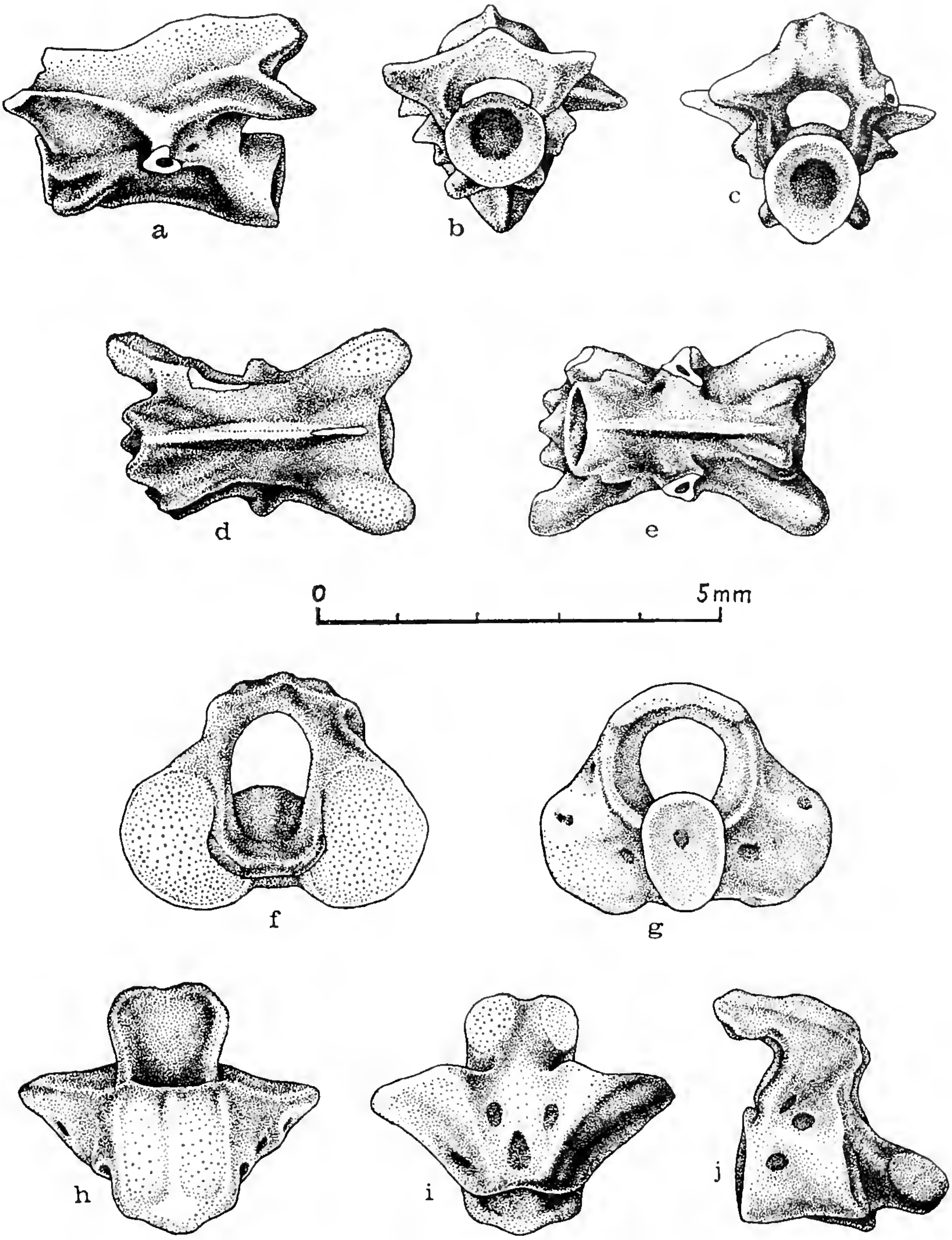

FIG. 1. *Proamphiuma cretacea*, n. gen., n. sp.: *a*, left lateral, *b*, anterior, *c*, posterior, *d*, dorsal, and *e*, ventral views of holotype vertebra, MCZ 3504; *f*, anterior, *g*, posterior, *h*, dorsal, *i*, ventral, and *j*, right lateral views of atlas, MCZ 3505.

others with only one; ventral lamina of rib-bearer present but apparently not well developed anteriorly; zygapophyses anteroposteriorly elongate, prominent, widely separated; posterior zygapophyses with keeled crests dorsally, extending forward to level of root of transverse process, these crests more medial in presumed anterior vertebrae and more lateral in presumed posterior vertebrae; neural spine relatively low, but prominent, thin and keeled, squared-off in lateral view; posterior border of spine slightly forked, often in three-pronged fashion. Atlantes with rounded anterior cotyles and prominent intercotylar process; centrum short; neural arch relatively high and blunt, with dorsal surface horizontal; neural spine only a faint ridge.

Discussion. The vertebrae are distinctively amphiumid in the combination of anterior basapophyses, subcentral keel, and posterior zygapophyses with prominent distinctive crests on their dorsal

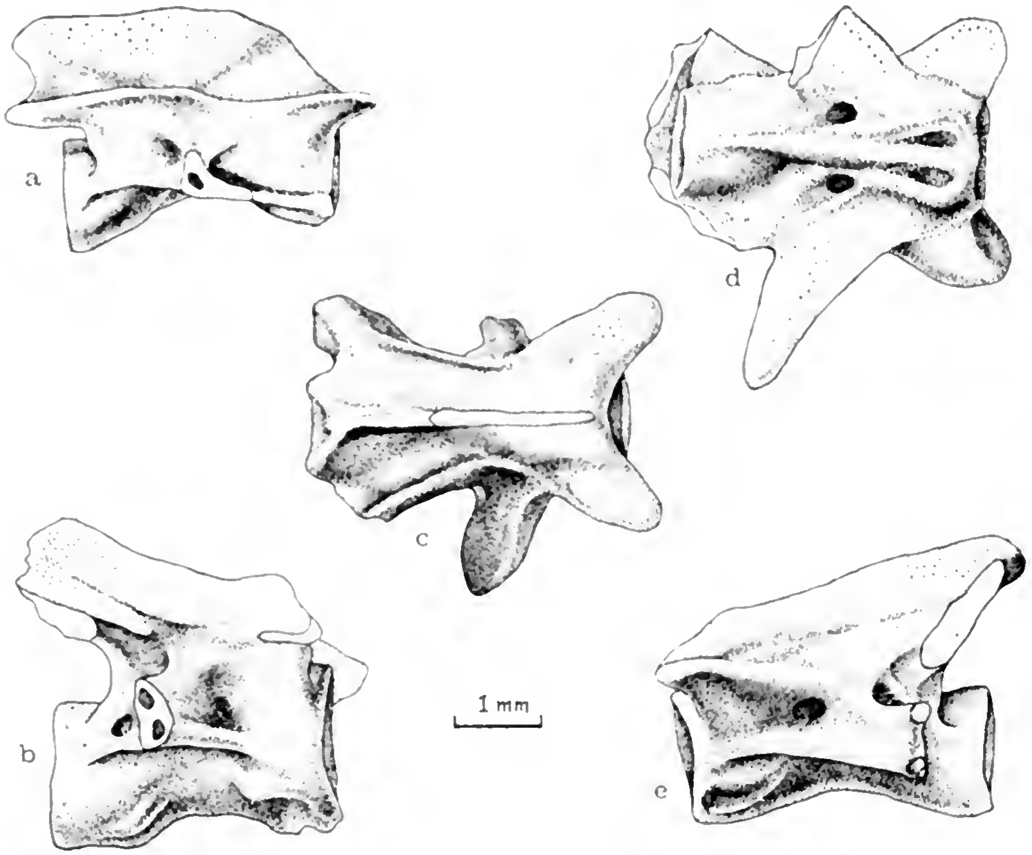

FIG. 2. *Proamphiuma cretacea*, n. gen., n. sp.: *a*, MCZ 3507, right lateral view of trunk vertebra; *b*, MCZ 3508, right lateral view of anterior trunk vertebra; *c*, MCZ 3506, dorsal view of trunk vertebra; *d* and *e*, MCZ 3509 — *d*, ventral, and *e*, left lateral views of trunk vertebra, probably near anterior end of column. White = broken surfaces.

surfaces that reach anteriorly to the roots of the transverse processes. There is close resemblance to vertebrae of *Amphiuma,* but specimens of equal size of the latter and of *Proamphiuma* differ in that the Cretaceous species has relatively narrower centra, less prominent zygapophyses, and weaker muscle crests. These are small differences but are on the order of those in closely-related modern salamander genera. Presence of posterior zygapophyseal crests implies development of the specialized IV-6 intervertebral muscle fibers found in Recent *Amphiuma* (Auffenberg, 1959).

No skull parts are known for this species, but the Paleocene *Amphiuma* described below has a less elongated snout than Recent *Amphiuma,* and probably a similar short skull was present in *Proamphiuma* as well. The two genera are closely related; *Proamphiuma* is structurally an ancestor of *Amphiuma* and there is no impediment to considering it a real ancestor, as well. It resembles the Paleocene *Amphiuma* described below in having relatively narrow, constricted centra. This is the earliest record of the Amphiumidae.

Amphiuma jepseni, n. sp.

(Figs. 3-5)

Holotype. Princeton University (PU) 14666, at least fourteen associated but dislocated vertebrae in a single block of matrix; associated left quadrate and left dentary.

Paratypes. PU 14668, partial skull and associated mandibles.

Locality and collector. Silver Coulee Quarry, S21, T 57 N, R 100 W, Park Co., Wyoming; collected by G. L. Jepsen and party.

Horizon. Polecat Bench Formation, Silver Coulee beds.

Age. Late Paleocene (Tiffanian).

Etymology. Named for its collector, Dr. G. L. Jepsen, Princeton University.

Diagnosis. Vertebrae relatively narrow as in *Proamphiuma,* crests and basapophyses well developed as in modern *Amphiuma;* snout short and blunt in contrast to modern *Amphiuma;* vomers less larval, with fewer and relatively more pointed teeth than in modern *Amphiuma.*

Description. Vertebrae amphicoelous, cotyles suboval anteriorly, teardrop-shaped posteriorly; anterior basapophyses strong, ventrally flattened, crested on their posterior surfaces, subcentral keel well defined, subcentral foramina simple, elongate; rib-bearers of posterior vertebrae unicipital, blunt distally, no rib articulation facet; anterior vertebrae with bicipital but closely approximated

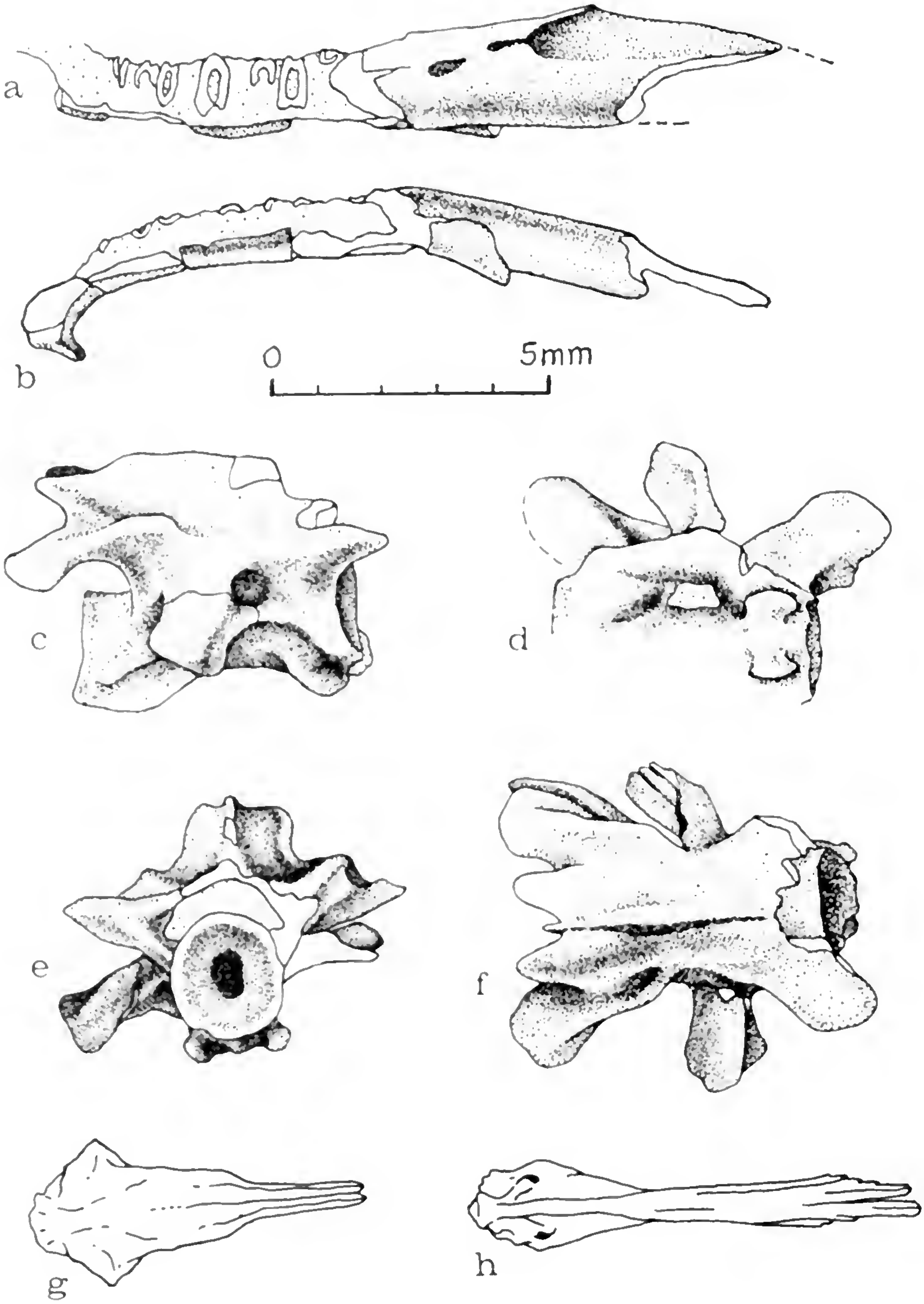

FIG. 3. *a - f*, *Amphiuma jepseni*, n. sp., PU 14666: *a*, labial, and *b*, ventral views of left dentary associated with holotype; *c*, right lateral, *d*, ventral, *e*, anterior, and *f*, dorsal views of best-preserved vertebra from holotype series. *g*, *A. means*, ventral view of parasphenoid; *h*, *A. norica* Brunner, ventral view of parasphenoid (?), after Brunner; *g*, *h*, × about 4. Coarse stipple = matrix, white area = broken surface.

rib-bearers; ventral lamina of transverse process prominent in posterior vertebrae, absent or reduced in anterior vertebrae; zygapophyseal ridge little developed near midpoint of vertebrae, neural arch narrow, pinched in at level of transverse process; well-developed keels on posterior zygapophyses reaching anteriorly to the level of transverse process; neural spine prominent, thin, squared off dorsally; posterior border of neural arch forked, a median septum bisecting the fork in three-pronged fashion.

Only anterior part of skull present, crushed and flattened, but restoration indicates a snout relatively wider and shorter than in *Amphiuma;* premaxilla unpaired, flattened dorsally, elongated posteriorly, a strong median septum formed, total actual tooth number not determinable because of breakage, but presence of a median tooth and six left lateral ones indicating a total of 13; ethmoid processes of frontals visible in section posteriorly; nasals not preserved, prefrontals sculptured, elongated, a long prefrontomaxillary

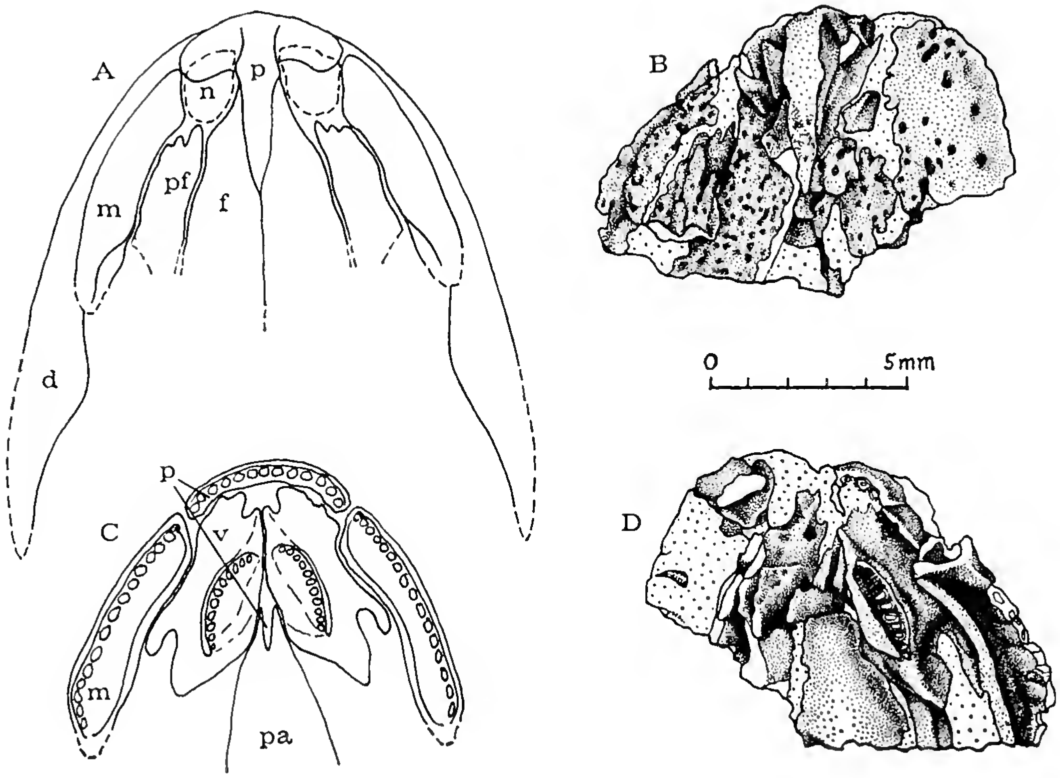

FIG. 4. *Amphiuma jepseni,* PU 14668, anterior portion of skull: A, restored dorsal view of snout and dentaries; B, dorsal view of fossil as preserved, right maxilla dislocated and flattened; C, restored palatal view; D, palatal view of fossil, elements of left side in approximately natural articulation. Abbreviations: d = dentary, f = frontal, m = maxilla, n = nasal, p = premaxilla, pa = parasphenoid, pf = prefrontal, v = vomer.

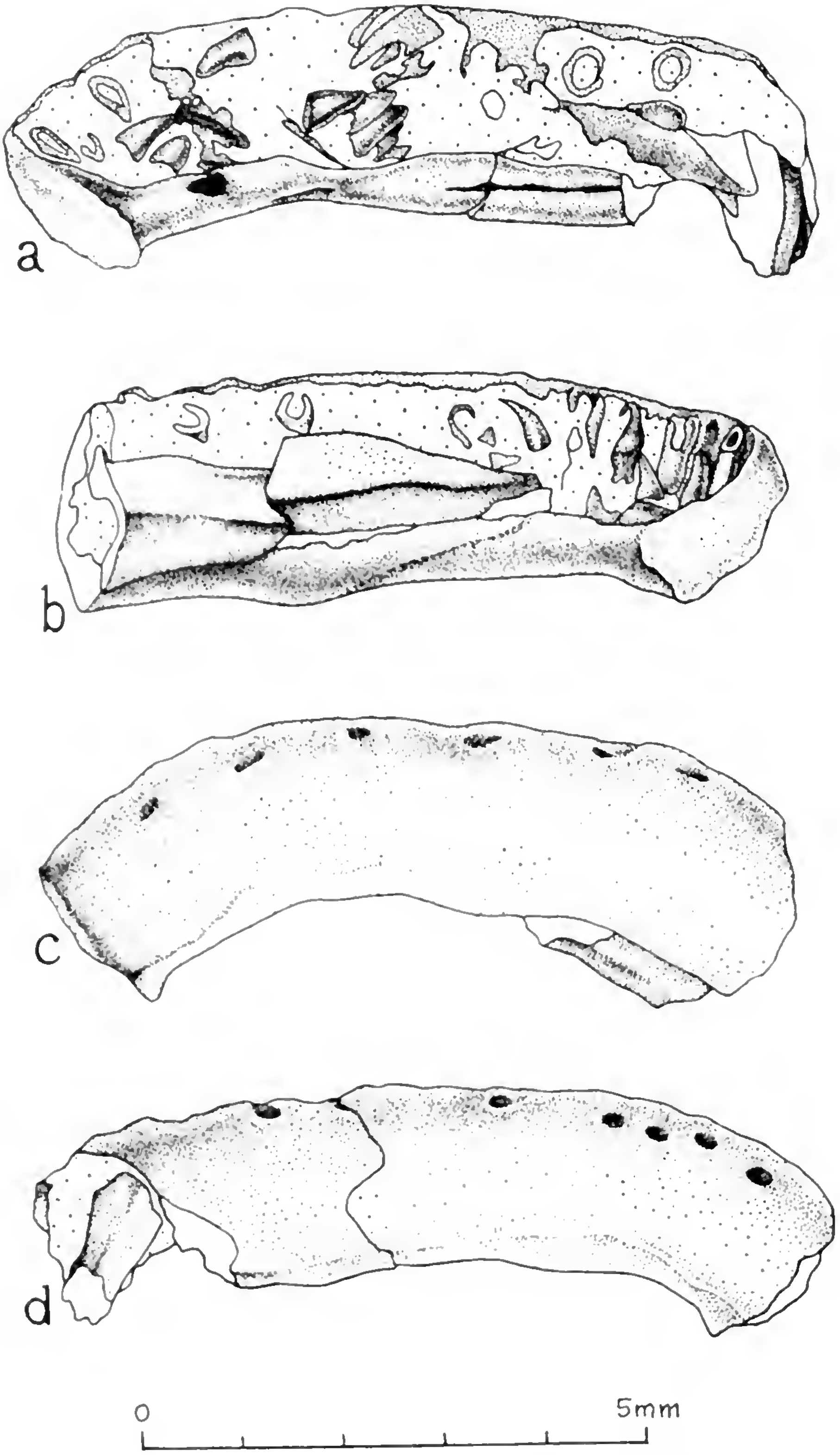

Fig. 5. *Amphiuma jepseni*, PU 14668, fragmentary dentaries originally in articulation with skull and removed to prepare palate: *a*, right lingual, *b*, left lingual, *c*, left ventral, and *d*, right ventral views.

suture extending posteriorly to orbit; frontal broken, dislocated, a strong sculpture present; maxilla bluntly curved, sculptured on nasal process, a row of foramina present exteriorly; teeth placed in a deep, channelled *sulcus dentalis;* teeth pedicellate, sharply pointed, and with recurved crowns, total tooth number unknown because of breakage; vomer expanded anteriorly, a small hollowed-out *sulcus dentalis* present near the midline, 10 or 11 teeth present, choanal excavation present laterally in vomer, reaching to level of seventh tooth from front; ethmoid visible medial to vomer, an anterior ethmoid foramen visible on the left; blunt parasphenoid extending anteriorly, covering ethmoids and separating vomers to anterior end of *sulcus dentalis;* orbitosphenoids missing, but grooves for them present on ventral surfaces of ethmoid; flange of vomer covers orbitosphenoid area ventrally.

Dentary strongly curved with deep *sulcus dentalis;* teeth as in upper jaw; symphysis flat, prominent; tooth number unknown, but comparison of dentary associated with type and PU 14668 indicates about 18; prearticular robust, medially crested, reaching anteriorly to about sixth tooth from symphysis; prominent fossa for adductor muscle attachment posterior to last tooth; blunt coronoid process present.

Quadrate blunt, robust, articular surface gently concave, palatoquadrate and hyoid connections well separated.

Discussion. Vertebrae of *Amphiuma jepseni* do not differ significantly from those of Recent species in general features, and are especially similar in degree of muscle crest development. Vertebrae of *Proamphiuma cretacea* have substantially less well-developed muscle crests relative to those of *A. jepseni* and Recent *Amphiuma* of equal size. The relatively constricted centra resemble those of *P. cretacea,* a resemblance not unlikely in view of their close geographic and temporal association.

The snout of *Amphiuma jepseni* is less elongated than that of Recent *Amphiuma,* although the specialized enclosure of olfactory tracts by the frontal is as well developed as in the Recent species. Tooth crowns of the fossil are less chisel-shaped than those of Recent species. Tooth number of premaxilla and dentary is within the range of Recent *Amphiuma,* but the number of vomerine teeth is significantly less (10-11 rather than 17-18; Rose, 1968). The latter condition and the greater development of vomers anterolateral to the tooth row indicate a lesser degree of paedomorphosis in *A. jepseni* than in Recent *Amphiuma.*

These skull differences probably reflect no more than specific difference from the Recent species. The lack of complete skeletons of the fossil form and the existence of only two closely-related modern amphiumid species for comparison makes the differences somewhat difficult to assess. However, some substantiation of this conclusion can be drawn from the fact that *Proamphiuma cretacea* differs substantially in development of vertebral muscle crests when compared with *Amphiuma jepseni* and with Recent individuals of equal size. I consider these muscle crests to be useful in defining generic boundaries, since their development reflects muscle difference of greater adaptive significance to the animal than is elongation of the snout.

EVOLUTION AND FAUNAL ASSOCIATES

Other Cretaceous records of modern and extinct families of elongated, aquatic salamanders have also been described (Estes, 1964, 1969). The addition of amphiumid salamanders to this record suggests that the widespread epicontinental seas of the Cretaceous were an important factor in evolution of this abundant salamander fauna, by providing extensive coastal plains with slow drainage and abundant shallow-water, riparian habitats.

The presence of these amphiumids in Cretaceous (Maestrichtian) and Paleocene (Tiffanian) sediments in Wyoming and Montana implies an origin of the Amphiumidae earlier than the late Cretaceous. The family is thus almost equally as ancient as the Sirenidae, the earliest record of which occurs in rocks of late Cretaceous (Campanian) age in Wyoming (unpublished record of *Habrosaurus;* Estes, 1964, p. 170).

The reduction in size and numbers of dinosaurs and the presence of plant fossils of Paleocene aspect imply warm-temperate rather than sub-tropical conditions for the Bug Creek locality, which is stratigraphically close to the arbitrary Cretaceous-Paleocene boundary in Montana (Sloan and Van Valen, 1965).

The fauna at the Paleocene Silver Coulee locality is unusual for late Cretaceous and early Paleocene localities in that fish remains are lacking. However, the aquatic salamanders *Scapherpeton* and *Opisthotriton* occur at both Silver Coulee and Bug Creek localities.

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BREVIORA

Museum of Comparative Zoology

CAMBRIDGE, MASS. 10 JUNE, 1969 NUMBER 323

ON THE EARTHWORMS OF ASCENSION AND JUAN FERNANDEZ ISLANDS[1]

G. E. Gates[2]

ABSTRACT. Recent collections enable addition of several species to lists of earthworm faunas of the two oceanic islands. As all species are widely distributed anthropochores. differences in the two faunas may be due mainly to climatic factors.

ASCENSION ISLAND

Ascension is a small island in the South Atlantic with an area of only 38 square miles. Green Mountain, reaching a height of 2,817 feet, is surrounded by a table land with a height varying from 1200-2000 feet. The island was discovered by Joao da Nova in 1501 but probably was first settled only in 1815 when Napoleon was exiled to St. Helena, some 500 miles distant, the nearest land. Previously the island was bare except for vegetation at the summit of Green Mountain.

Only two megadrile species had been recorded (Sims, 1964) from the island. Through the efforts of herpetologist Arthur Loveridge, who retired to St. Helena, a small collection was secured from Ascension.

LUMBRICIDAE

Allolobophora Eisen, 1874

Allolobophora sp.

The aclitellate worm (Sims, 1964) was not further identified.

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[1] From research financed by the National Science Foundation.

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MEGASCOLECIDAE

Pheretima Kinberg, 1866

Pheretima californica Kinberg, 1866

Green Mountain, 30 August 1962, (3?)-1-6. John Packer *per* A. Loveridge.

Pheretima hawayana (Rosa, 1891)

Green Mountain, 30 August, 1962, (3?)-1-1. John Packer *per* A. Loveridge.

Pheretima morrisi (Beddard, 1892)

Three of the four specimens of this species previously available (Sims, 1964) were from garden soil.

OCNERODRILIDAE

Green Mountain, 30 August, 1962, 2-0-0. John Parker *per* A. Loveridge.

Setae, closely paired. Gizzards, probably lacking. Calciferous glands, long, seemingly extending through ix-x, deeply constricted by 9/10, opening into the gut posteriorly in x, the anterior half more firm. Prostates, one pair, very long, external apertures unrecognizable. Spermathecae, none found.

These worms (*ca.* 1mm thick) were so softened that further information was unobtainable. No other ocnerodrile is known to have glands of the kind indicated above. Although reference to any known genus is impossible, the worms obviously were ocnerodrile.

Remarks. The pheretimas are widely distributed anthropochores. They almost certainly were brought from the Orient to the island, directly or indirectly, by man. Any lumbricids on the island probably were brought, also by man, from England. Evidence to be presented elsewhere suggests that the pheretimas may be better adapted than the lumbricids to the climates of tropical islands such as Ascension.

P. californica and *hawayana* have been collected on St. Helena, the nearest land. *P. morrisi* was once recorded from St. Helena but was not present in any of the various collections which were made on that island by Loveridge and others during the last twenty years.

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THE JUAN FERNANDEZ ISLANDS

The Juan Fernandez islands, all small, are three: Mas a tierra (36 square miles), Mas Afuera (33 square miles), and Santa Clara. The first is inhabited. The islands were discovered by the man for whom they are named in 1563. The first settlement to become permanent was in 1877.

Prior to Dr. Y. Kondo's visit, four species had been recorded from Juan Fernandez: *Allolobophora caliginosa* (Savigny, 1826), *Dendrobaena rubida* (Savigny, 1826), *Eiseniella tetraedra* (Savigny, 1826), *Eukerria saltensis* (Beddard, 1895). In the absence of any indication to the contrary, all presumably were found on Mas a tierra. Collections made by Dr. Kondo on Mas a tierra, enable the listing of three more species.

LUMBRICIDAE

Allolobophora Eisen, 1874

Allolobophora tuberculata Eisen, 1894

Quebrada, Portozuela East, 200m, 2.xi.1966, 4(+25?)-5-2. No. 31, 11. xi. 1966, 5-0-1.

A. tuberculata is one of at least four species long retained in a classical congeries known as *A. caliginosa*. Worms previously recorded from Juan Fernandez as *A. caliginosa* may well have been *A. tuberculata*.

Dendrobaena Eisen, 1874

Dendrobaena octaedra (Savigny, 1826)

No. 31, 11. xi. 1966, 1-0-2.

Dendrobaena sp.

Asondalan, 29. x. 1966, 1-0-0.

This small juvenile is not of *D. octaedra,* but its condition was too poor to permit a positive identification, and it may be of *D. rubida* (Savigny, 1826), previously recorded from the island.

Octolasion Oerley, 1885

Octolasion tyrtaeum (Savigny, 1826)

No. 31, 11. xi. 1966, 2-0-1.

MONILIGASTRIDAE

Drawida Michaelsen, 1900

Drawida bahamensis (Beddard, 1892)

No. 31, 11. xi. 1966, 0-1-1.

The left copulatory chamber, of one of the posterior amputees, is everted and the penis is protruded. Apertures of the other three chambers are tightly closed.

Gizzards, in xii-xiv (1), in xiii-xiv (1). Ovisacs, confined to xii.

DISCUSSION

Mas a tierra is only two square miles smaller than Ascension. Both islands are in the Southern Hemisphere. The Atlantic island has a known megadrile fauna of five species, and the Pacific island has seven; each island has one ocnerodrile. *E. saltensis* originated in southern South America, but in which part is unknown. The Ascension ocnerodrile could have evolved in South America or even in Africa. Ascension pheretimas, like the San Juan moniligastrid, originally were from the Orient. Lumbricids, of course, came from Europe.

Each species of the two islands is more or less widely distributed throughout the world. Each very probably was brought to the islands accidentally by man. Lumbricids, so far as can be indicated by the samples, seem to be dominant on Mas a tierra. Megascolecids, according to a smaller sample, seem to be dominant on Ascension. The Juan Fernandez Islands are well south of the tropics, Ascension well within them. The difference in dominance may, then, be due to climatic factors. Nevertheless, the pheretimas, like the lumbricids, probably are from the Temperate Zone of the Northern Hemisphere.

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B R E V I O R A

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POLYMORPHISM AND EVOLUTION OF THE HISPANIOLAN SNAKE GENUS *UROMACER* (COLUBRIDAE)

Henry S. Horn[1]

ABSTRACT. Four species of the endemic genus *Uromacer* are recognized: *catesbyi, frenatus, oxyrhynchus,* and *dorsalis*. All save *dorsalis* show a remarkably discrete di- or trimorphism in a color pattern that is apparently cryptic. The adaptive significance of this polymorphism is discussed using an intuitive model that draws on the theory of Levins.

The species are linearly ordered on the basis of body shape. Surprisingly, the stomachs of the stoutest species contain arboreal lizards and frogs, while the slimmer species take progressively more terrestrial lizards. The linear order suggests a pattern of geographic speciation occurring at the time when the northern and southern portions of Hispaniola were separate islands. Thus the pattern is consistent with patterns of evolution and migration proposed for other Hispaniolan reptiles by Williams and others. Speculations about the origin of *dorsalis*, endemic to Île de la Gonâve, may explain why the fauna of that islet is a curious mixture of species characteristic of the northern and southern portions of Hispaniola.

INTRODUCTION

The snakes of the genus *Uromacer* are endemic to Hispaniola and the surrounding islets. Some years ago A. Stanley Rand discovered a color polymorphism in several local populations of *Uromacer oxyrhynchus*. Examination of the other species has shown that several of them are also polymorphic. Since the same morphs of different species are superficially more similar than are different morphs of the same species, this polymorphism sometimes results in the misidentification of museum specimens. Consequently, the polymorphism has obscured the pattern of distribution

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of the forms of *Uromacer*, making it difficult to relate their distribution to that of other Hispaniolan reptiles.

The recent concentration on the herpetology of Hispaniola at the Museum of Comparative Zoology (MCZ) has provided large, synchronous collections of *Uromacer* from several localities. The geographical coverage of even these large collections is not yet extensive enough to warrant a definitive discussion of intraspecific variation. However, the available collections allow me to assess the validity of the described species of *Uromacer*, to suggest the pattern of their relationships, to document their striking polymorphism in some detail, and to comment on some interesting evolutionary problems posed by the genus. Though I have studied only preserved material, I have made inferences about the ecology of the species from their stomach contents. However, I must leave several questions unanswered because I lack field knowledge of Hispaniola, particularly of seasonal changes during the year.

Where MCZ material was insufficient, I have examined specimens from the American Museum of Natural History (AMNH), the British Museum (Natural History) (BMNH), the Field Museum of Natural History (FMNH), the Yale Peabody Museum (YPM), the Albert Schwartz Field Series (ASFS), and the United States National Museum (USNM). I am grateful to the curators of these collections for allowing me to examine specimens in their charge.

I thank A. Stanley Rand and Ernest E. Williams for discussion and criticism throughout this study. Dr. Rand introduced me to *Uromacer*, and his unpublished notes on their polymorphism were the starting point for my work. Dr. Williams sponsored part of this study as my undergraduate thesis at Harvard College in 1962. My ideas on polymorphism developed from discussions with Richard Levins and Robert H. MacArthur. For criticisms of several manuscripts, I am indebted to Thomas H. Frazzetta, Elizabeth G. Horn, Thomas W. Schoener, Albert Schwartz, and George G. Simpson. Dr. Schwartz kindly compiled the faunal list for Île de la Gonâve.

MATERIAL AND METHODS

Cochran (1941) recognized six species of *Uromacer: catesbyi, scandax, frenatus, wetmorei, dorsalis,* and *oxyrhynchus.* There is reason to doubt the specific distinctness of *scandax* and *wetmorei*, which Cochran recognized as respectively allied to *catesbyi* and *frenatus.* For reasons given in the Appendix, I consider *scandax*

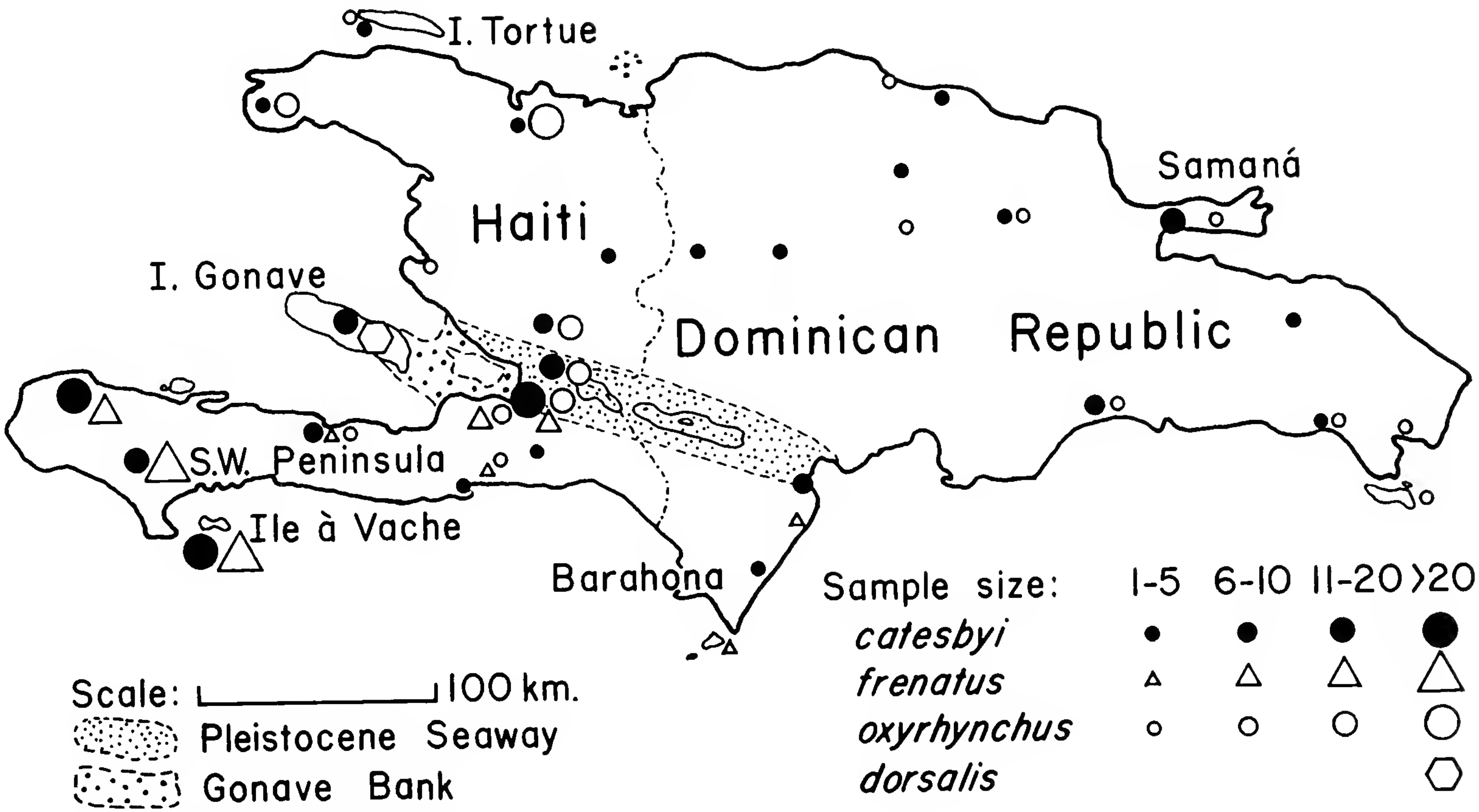

Figure 1. Hispaniola, showing locality records for *Uromacer*.

to be identical with *catesbyi*, and *wetmorei* to be a subspecies of *frenatus*. The remaining species are easily separated by the diagnostic characters of Cochran's key: snout length relative to eye diameter, ventral scale count, and midbody scale rows. The ranges of snout length and ventral scale count overlap between species, but these characters are usually sufficient for tentative identification of single specimens. The number of scale rows at midbody is constant in each species, but is diagnostic only for *oxyrhynchus*. The subcaudal scale count for each species has a large range, and though there may be significant differences between the means of different populations, it is seldom useful in identifying a single specimen. Similarly, the presence or absence of an anterior loreal may be used to infer relationships among populations, but it is useless as a diagnostic character.

Stomach contents of the MCZ and YPM specimens were removed and identified. The snakes had fed primarily on *Anolis* whose ecology is relatively well known, so inferences about the ecology of *Uromacer* may be made on the basis of these stomach contents. Schwartz (in litt.) and Mertens (1939) have observed that freshly caught *Uromacer* often swallow the cohabitants of a collecting bag, but even those stomach contents that were not eaten by free snakes will reflect the syntopic fauna in which the snakes were collected. To minimize this difficulty, those stomach contents that were undigested were ignored in analysis.

Where different color morphs are described for a single species of *Uromacer*, these morphs are entirely distinct, with no intermediates except between the gray and the striped gray forms. There was never any hesitation in assigning any well-preserved specimen to one of three alternative morphs: *green*, green above and below, lighter below; *gray-green*, green above, mottled gray below; or *gray*, gray above and below. A detailed description of each morph and its variations in each species is given in the Appendix.

RESULTS AND INTERPRETATIONS

The ranges of the species of *Uromacer* are mapped in Figure 1 and listed in Table 1.

External metric characters are listed in Table 2, and there are photographs of the several species in Figure 2. The species may be linearly ordered, as in the table, on the basis of characters that are correlated with slimming and lengthening the body. *U. catesbyi* is typically colubrid in shape, with a short, blunt snout, low

TABLE 1

Ranges of the species of *Uromacer*

Species	*Southwest and Barahona Peninsulas*	*Port-au-Prince and vicinity*	*N. and E. Dominican Republic*	*Île de la Gonâve*
catesbyi	*	*	*	*
frenatus	*	*		
oxyrhynchus		*	*	?
dorsalis				*

TABLE 2

Metric morphology of the species of *Uromacer*

Species	*Number examined*	*Snout length relative to eye diameter*	*Ventral scales*	*Subcaudal scales*	*Scale rows at midbody*	*Anterior loreal*
catesbyi	254	2.0	167 ±0.7	183 ±1.0	17	—
		*	*	*		
frenatus	102	2.6	187 ±0.5	204 ±1.9	17	—
		*	*		*	*
oxyrhynchus	129	3.0	200 ±0.5	199 ±1.1	19	present in 25
				*	*	*
dorsalis	84	2.9	200 ±1.2	210 ±2.2	17	+

Entries are the means for each character ± the standard error of the mean. The standard error of the mean snout length (±0.01) was, in all cases, less than the reading error of each measurement (±0.2). Numbers separated by * are significantly different at the .05 level by a one-tailed t test (Snedecor, 1956), for snout length, ventral count, and subcaudal count, or a binomial test (Siegel, 1956), for scale rows at midbody and anterior loreal.

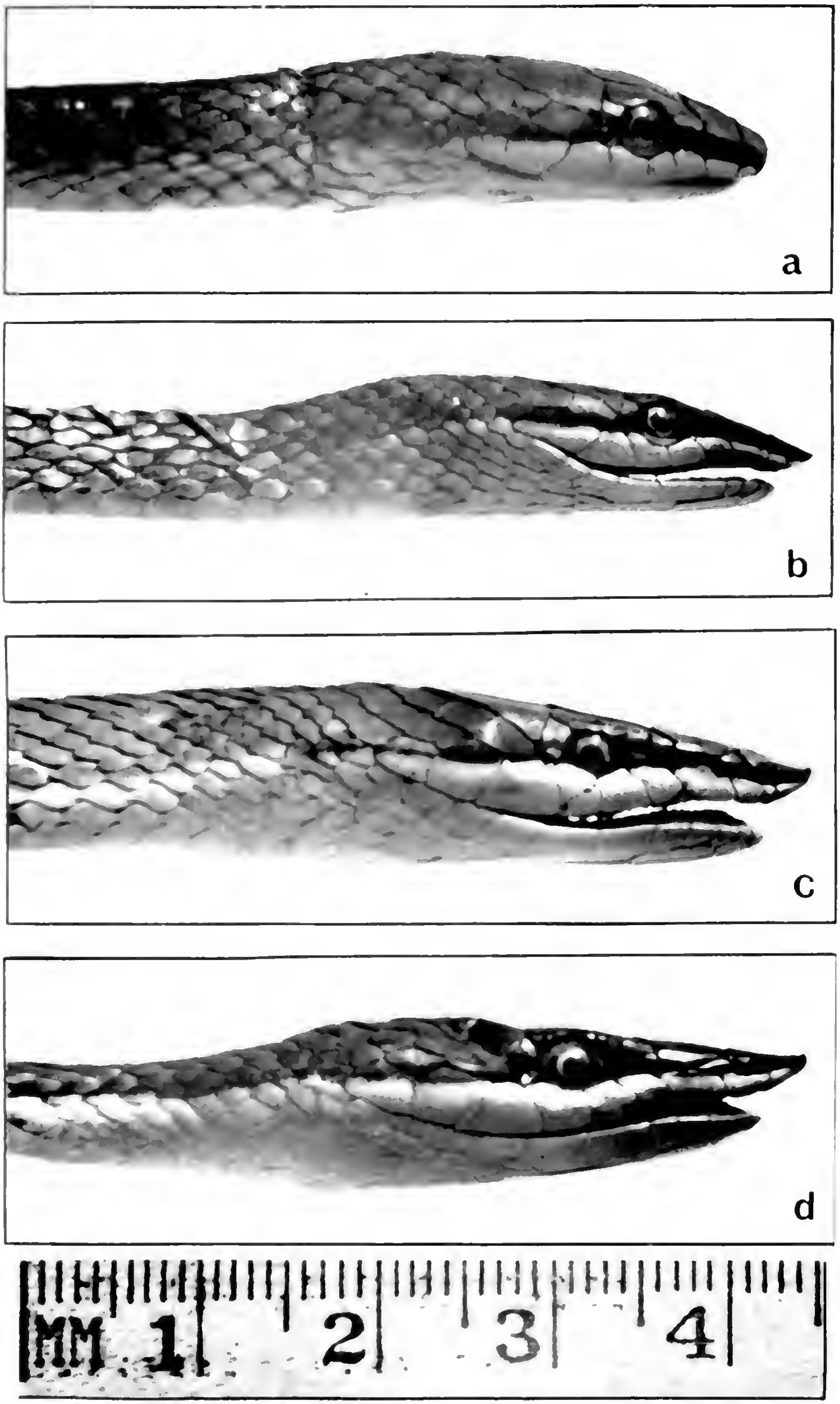
a
b
c
d
MM 1
2
3
4

Figure 2. a, *Uromacer catesbyi* MCZ 57764 nr. Carpintero, Dominican Republic; b, *U. frenatus* MCZ 65530 Perrine nr. Jérémie, Haiti; c, *U. oxyrhynchus* MCZ 62713 Bombardopolis, Haiti; d, *U. dorsalis* MCZ 80815 Pointe-à-Raquettes, Île de la Gonâve, Haiti.

ventral and subcaudal counts, and a relatively thick body covered with rhomboidal scales that are nearly square. *U. oxyrhynchus* and *dorsalis* are shaped more like typical tree and vine snakes, with long, pointed snouts, high ventral and subcaudal counts, and more slender bodies covered with obliquely rhomboidal scales. *U. frenatus* is intermediate between these extremes.

The stomach contents of *Uromacer* are listed in Tables 3 and 3a. In Table 3 the stomach contents of the snakes are pooled within

TABLE 3

Habitat of food taken by the species of *Uromacer*

Habitat	*catesbyi*	*frenatus*	*oxyrhynchus*	*dorsalis*
Trees	7	3	1	2
Tree trunks and bushes	9	5	11	4
Grass and open areas		2	4	11
Ground and rocks		4	4	10

TABLE 3a

Stomach contents of the species of *Uromacer*

Habitat and species eaten	*catesbyi*	*frenatus*	*oxyrhynchus*	*dorsalis*
TREES				
Hyla pulchrilineata	1			
dominicensis	3			
Anolis chlorocyanus	2		1	2
coelestinus	1	3		
TREE TRUNKS & BUSHES				
Anolis cybotes	4	4	8	3
brevirostris				1
distichus	5	1	3	
GRASS & OPEN AREAS				
Anolis semilineatus		2	3	
olssoni			1	11
GROUND & ROCKS				
Ameiva taeniura		1	2	1
chrysolaema				6
Leiocephalus melanochlorus		2		
vinculum				3
schreibersii			2	
Sphaerodactylus sp.		1		

common habitats of the food species; the habitat groupings were made by referring to Mertens (1939), Williams and Rand (1961), and Rand (1962). Since the groupings are only generalizations, and the samples are small and heterogeneous, the data do not fully characterize the diets of the species of *Uromacer*. However, the differences among the diets are so striking, when compared to the uniformity of diets within each species, that crude relative characterizations can be made with confidence.

U. catesbyi takes arboreal food almost exclusively, and *dorsalis* feeds primarily on terrestrial food, whereas *f. frenatus* and *oxyrhynchus* are intermediate and more similar to each other than either is to *catesbyi*. The tendency for the colubrid-like *catesbyi* to take arboreal prey, and for the longer-snouted species to take progressively greater proportions of terrestrial prey, is the opposite of expectations based on the morphology of the species (e.g. Mertens, 1939, who suggest that *oxyrhynchus* is the most arboreal species of *Uromacer*).

Polymorphism. Of the four species of *Uromacer*, only the gray *dorsalis* is not demonstrably polymorphic in at least one locality (see Table 4). Green *U. catesbyi* occur throughout the range of the species, but with a pattern unlike the corresponding morph of any other species; *catesbyi* is polymorphic, with a gray form, near Miragoâne, in the middle of the southwest peninsula of Haiti.

TABLE 4

Distribution of the color morphs of the species of *Uromacer*

Species	*Green*	*Gray-green*	*Gray*	*Gray (striped)*
catesbyi	ENTIRE RANGE		Miragoâne	
f. frenatus		Ile à Vache	mainland	Île à Vache
f. wetmorei		Barahona		Isla Beata
oxyrhynchus	ENTIRE RANGE	Haiti & Eastern D.R.	Haiti	
dorsalis				ENTIRE RANGE

U. f. frenatus is monomorphic gray on the mainland, and polymorphic gray and gray-green on Île à Vache. The gray form on Île à Vache resembles that of *dorsalis* more than that of mainland *frenatus* or *oxyrhynchus*. *U. f. wetmorei* on Barahona may be polymorphic, but the few poorly-preserved specimens presently available from scattered localities are insufficient evidence.

U. oxyrhynchus is apparently monomorphic green through much of the Dominican Republic, but it is dimorphic green and gray-green throughout the Haitian portion of its range. In scattered Haitian localities it is trimorphic, green, gray-green, and gray. *U. oxyrhynchus* may in fact be trimorphic throughout the Haitian portion of its range, perhaps in parts of the Dominican Republic as well. The gray morphs are rare enough to be found only in large, synchronous collections from Haiti; no such collections have been made in the Dominican Republic.

The discreteness of the morphs in all the polymorphic species, and the lack of intermediates, suggests that the mechanism controlling the polymorphism is an allelic switch at a single genetic locus. In the trimorphic *oxyrhynchus*, the distribution of the morphs is consistent with the interpretation that the green and the gray forms are homozygotes and that the commoner gray-green form is the heterozygote; i.e. in all the localities from which both green and gray specimens have been taken, gray-green specimens have been taken as well.

The distribution of the color forms among the localities of the polymorphic species and among the species of the genus suggests that the various forms are cryptic for different surroundings. *U. catesbyi* is green throughout its range, darker in the western portions of Hispaniola than in the eastern, with some gray individuals on the southwest peninsula in the Miragoâne area. *U. frenatus* is gray on the southwest peninsula and polymorphic on Île à Vache, while its ecological counterpart, *oxyrhynchus*, has green, gray-green, and gray morphs in Haiti, but a preponderance of green morphs in the Dominican Republic (see Table 5). These distributions correspond roughly to the pattern of humidity and vegetation on Hispaniola, as described by Wetmore and Swales (1931: 2-7).

TABLE 5

Geographical distribution of the color morphs of *frenatus* and *oxyrhynchus*

Species	*Area*	*Green*	*Gray-green*	*Gray*
f. frenatus	Île à Vache		15	22
f. frenatus	Haitian mainland		2	56
f. wetmorei	Barahona		4	1
oxyrhynchus	Haiti	47	48	4
oxyrhynchus	Dominican Republic	17	4	

The grayer and darker (i.e. less bright green) forms are associated with the drier, western portion of the island. The presence of the gray-green morph of *frenatus* on Île à Vache and the brighter green of the *catesbyi* from the islet are correlated with the presence of denser woodland on the islet than on the adjacent mainland. This correlation of the distribution of the color morphs with foliage density suggests cryptic coloration as a possible function of the different morphs.

The two most strictly monomorphic species, *catesbyi* and *dorsalis*, are characterized by the most restricted diets. The green *catesbyi* takes only arboreal prey, while the gray *dorsalis* takes predominantly terrestrial prey. This additional correlation of color pattern with ecology suggests again that the coloration of *Uromacer* is cryptic, concealing the snake as it stalks agile prey.

Polymorphism in a cryptic pattern of coloration poses an interesting evolutionary question. If a specific color pattern is indeed cryptic, why is more than one pattern present at all? The theory of polymorphism provides some likely answers and suggests the kinds of data that should be sought to choose between alternatives. Levins (1962-6; Levins and MacArthur, 1966) has examined the adaptive significance of polymorphism, using an abstract mathematical model of extreme generality. I shall develop a much simpler model to examine polymorphism in the special case of cryptic coloration, but the intellectual basis and results are the same as those of Levins. This model is almost absurdly simple, but the concepts illustrated are quite general and are not easily apparent without the model.

The environment is a checkerboard with black and white squares and the cryptic animals are checkers. Later I shall introduce reproduction and "fitness" into the model, but first let us look at crypticity alone. If we randomly place black or white checkers on the squares of the checkerboard, roughly half the black checkers will fall on black squares and half the white checkers, on white. Thus half the population of either black or white checkers will be cryptic. However, if we throw gray checkers on the checkerboard, none of them will be cryptic, unless, of course, the checkers are very large and the squares of the checkerboard are so tiny that it looks like the gray of a halftone illustration. Thus if two alternative morphs are to be cryptic, the environment must be a mixture of large patches of different kinds, each with an extreme morph that is more cryptic than an intermediate morph.

I assume that "adaptation" is achieved through natural selection, which favors that individual whose offspring form the greatest proportion of breeders in the next generation. Correspondingly the "fitness" of an individual is defined as the number of his offspring that breed in the next generation, and the individual with the greatest fitness in a given environment is the "best adapted" to that environment.

We now allow each checker to reproduce an average of X offspring in each generation; in each reproductive period we throw checkers onto the board and give each checker X+d offspring if it is cryptic but only X−d offspring if it is not cryptic. Black checkers have black offspring; white checkers have white offspring. We define "polymorphic" checkers to have either black or white offspring with a 50-50 chance, whether the phenotype of the "polymorphic" checker is black or white. The genetic or developmental basis of this polymorphism need not be specified, so I shall call it "sibling polymorphism," since it requires that the offspring of a given morph may include both morphs. If the checkerboard has an equal number of black and white squares, then the offspring of black, white, or polymorphic checkers have an equal chance of being cryptic or non-cryptic, and the fitness of each type is an average of X+d and X−d, or simply X. (You can easily show that if the environment is an uneven mixture of black and white squares, the morph that is cryptic in the commoner square has a higher fitness than the other morph or the polymorph.) Thus, if the environment is a spatial mixture of large patches of two types, a monomorphic population is better adapted than a polymorphic population, or at least as well adapted.

If, instead of throwing the checkers onto the board randomly, we allow each of the checkers to choose and reproduce in its appropriate habitat, then the white squares will be occupied predominantly by white checkers and the black squares by black checkers. On sampling a large and heterogeneous area, we then obtain both morphs, and the population appears to be polymorphic. However, the two morphs could represent two species, rather than a polymorphic species. In fact, the average fitness of individuals of the two separate species would be higher than that of a polymorphic species, unless the polymorphism continually adjusted the ratio of the morphs to match the proportions of the corresponding patches in the environment. Since this polymorphism may result from sampling a heterogeneous environment and does not require that a given individual be capable of having polymorphic offspring, I shall call it "sampling polymorphism" as distinct from "sibling polymorphism." (Under certain restricted conditions the two kinds of polymorphism are convergent, and sampling polymorphism may evolve a genetic basis. See Levins, 1965, for a discussion.)

Now instead of throwing the checkers onto a checkerboard, we throw them alternately onto a white board or a black board for each generation. That is, the environment is a temporal mixture of different habitats, rather than a spatial mixture. The black and white checkers are alternately cryptic and non-cryptic. Each individual in a cryptic generation has $X+d$ offspring, each of whom has $X-d$ offspring in the next generation; thus the average fitness of black or white checkers over two generations is $(X+d)(X-d) = X^2-d^2$. On the other hand, the "polymorphic" checkers have an equal number of cryptic and non-cryptic offspring in each generation and their average fitness is $\frac{1}{2}(X+d)+\frac{1}{2}(X-d) = X$ in each generation; then the average fitness of polymorphic checkers over two generations is X^2, which is always greater than X^2-d^2. If the black and white environments alternate several times within each generation, fitness is averaged over the two environments for each generation, and the results are the same as in the case of spatial heterogeneity. However, sibling polymorphism yields a higher average fitness than monomorphism when the environment varies drastically with a period of the same order of magnitude as the time between generations.

What does the checkerboard model predict about *Uromacer*? If the polymorphism of *Uromacer* is simply a sampling polymorphism, then the different morphs should be associated with distinctly different habitats or microhabitats. The habitats might be different types of vegetation, in each of which one of the morphs is most cryptic.

If the polymorphism of *Uromacer* is a sibling polymorphism, the alternative morphs should still be cryptic in distinctly different habitats, but the habitats will alternate in an inescapable temporal pattern, e.g. wet-dry season. Therefore, if the polymorphism is a genetic or developmental adaptation to a temporally heterogeneous environment, the different morphs will often be found in habitats in which they are not cryptic.

Documenting the adaptive significance of polymorphism in *Uromacer* is a difficult, long-term project. It is first of all a field, not a museum project. It is necessary to define the habitats in which each of the morphs is most cryptic. Then the alternatives of genetic and sampling polymorphism must be separated by determining the distribution of the morphs among the several habitats, over a time equal to several generations of *Uromacer*. As interesting as the problem is, it will probably not be quickly solved, perhaps not even quickly undertaken, since the required study is longer than the lifetime of the average research grant.

Relationships within the genus. There has been no previous discussion of the relationships of the species of *Uromacer*.

It is at once tempting to suggest that the morphological and dietary series described corresponds to an evolutionary series as well; that *catesbyi* is the most primitive of the *Uromacer*, *oxyrhynchus* and *dorsalis* the most recently derived, and that *frenatus* represents an intermediate step. When the present ranges of the species, the physiographic history of Hispaniola, and the mechanisms of geographic speciation are taken into account, this suggestion is strengthened.

During the Pleistocene, Hispaniola was divided by an arm of the sea into two large islands, a northern island, Haiti north of the Cul-de-Sac Plain and the Dominican Republic exclusive of the Barahona peninsula, and a southern island, the southwest peninsula of Haiti and the Barahona peninsula (Schuchert, 1935; Weyl, 1966; Williams, 1961). The ancestral colubrid (Maglio, in prep., suggests something similar to *Alsophis*) had given rise to a *catesbyi*-like form, to be called "proto-catesbyi," and to "proto-frenatus," autochthons of the northern and southern islands respectively. Proto-frenatus invaded the northern island, and as it came into contact with the well-established proto-catesbyi, the characteristics that distinguished the two species were intensified (character divergence of Mayr, 1963, after Darwin). By its increased divergence from proto-catesbyi, the invading proto-frenatus gave rise to "proto-oxyrhynchus," ancestor of *oxyrhynchus* and *dorsalis*.

The proposed sequence accounts for the presence in *dorsalis* of characters similar to both *frenatus* and *oxyrhynchus*. The progenitor of *dorsalis* on Gonâve was presumably proto-oxyrhynchus, which would have retained similarities to proto-frenatus and thus to *frenatus*, while differentiating in the direction of *oxyrhynchus*. Alternatively, *dorsalis* could have been derived directly from proto-frenatus, and its similarity to *oxyrhynchus* could represent parallel evolution of the species. Lack of evidence relevant to these alternatives is in itself sufficient reason for provisionally calling *dorsalis* a separate species.

This evolutionary sequence is only an interpretive hypothesis and cannot be tested, but it embodies processes that have been suggested to account for the present distribution of other Hispaniolan reptiles. The postulated distinction of proto-catesbyi and proto-frenatus, as the respective autochthons of the northern and southern islands, is paralleled by the distinction of *Anolis coelestinus* and *Anolis chlorocyanus*, of *Anolis aliniger* and *Anolis singularis*, and perhaps of the *Anolis* of the *monticola* group and the subspecies of *Anolis ricordii* (Thomas and Schwartz, 1967; Williams 1965a, 1965b). The subsequent invasion of the northern island by proto-frenatus is paralleled by the *Anolis* of the *semilineatus* group. Williams (1961) suggests that *Anolis olssoni* and *A. semilineatus* are indigenous to the northern and southern islands respectively and that their present distributions are the result of the relatively recent invasion of the northern land mass by *semilineatus*. Similarly, Schwartz (1967) suggests that *Ameiva taeniura* originated on the southern island and has since invaded the northern land mass.

There are probably other patterns of radiation that are consistent with the present ranges of the species of *Uromacer*, and almost as simple in the changes of morphology that they would require. However, several conclusions will remain unchanged given such alternative patterns. *U. catesbyi* is clearly more different, in morphology and diet, from the other species than they are from one another. It is then significant that only *catesbyi* is broadly sympatric with the other species of the genus. *U. frenatus*, *oxyrhynchus*, and *dorsalis* are similar in morphology and may provisionally be considered allopatric ecological replacements.

Explaining the origin of *dorsalis* on Gonâve as more than a historical accident requires bold speculation in the absence of critical data. This speculation is justified, however, as it also suggests a possible derivation for the problematical fauna of Gonâve.

Present knowledge of the fauna of Gonâve is scanty, but it is already apparent that the fauna is an odd mixture of species characteristic of the northern and southern islands of the Pleistocene (See Table 6). During part of the Pleistocene, Gonâve was reduced to about one fourth of its present area (Butterlin, 1960). When the northern and southern islands were rejoined, Gonâve may have been connected to the mainland by a spit at least 3 km wide to the north and 7 km wide to the south (Fig. 1; also Woodring et al., 1924), which would have allowed the fauna of both regions to invade Gonâve. When Gonâve became insular again, those species whose presence had depended on continuing invasion would be eliminated, leaving only those best adapted to the restricted habitats of Gonâve and those potential competitors that were most divergent. The geographic origin of the invading species would be irrelevant to their subsequent persistence.

TABLE 6

Reptiles of Gonâve and their areas of origin

Species	*Origin*[1]	*Reference*
Gonatodes albogularis		
Sphaerodactylus cinereus		
Aristelliger cochranae		
Anolis brevirostris (end. subsp.)		
chlorocyanus	North	Williams, 1965a
cybotes		
olsoni	North	Williams, 1961
singularis	South	Williams, 1965a
Cyclura cornuta		
Leiocephalus vinculum (end. subsp.)		
Ameiva chrysolaema (end. subsp.)	North	Schwartz & Klinikowski, 1966
taeniura	South[2]	Schwartz, 1967
Diploglossus curtissi		
Amphisbaena gonavensis (end. subsp.)	South?	Thomas, 1965
Typhlops capitulatus (end. subsp.)		
pusillus	North	Richmond, 1964
Epicrates angulifer		
fordi		
Tropidophis haetianus		
Dromicus parvifrons		
Hypsirhynchus ferox		
Ialtris dorsalis		
Uromacer catesbyi	North[2]	
dorsalis (endemic)	North	

[1] North and south under this heading refer to the northern and southern islands into which Hispaniola was periodically divided during the Pleistocene. See Fig. 1.

[2] Island of origin of parent species, though invasion may have been from a population on the other island.

In particular, if proto-catesbyi, proto-frenatus, and proto-oxyrhynchus all reached peninsular Gonâve, the ultimate persistence of the most divergent pair, and the elimination of the intermediate proto-frenatus is predictable. The dietary divergence of *dorsalis* and *catesbyi* confirms the role of interspecific competition in the origin of *dorsalis*. *U. dorsalis* clearly differs from *catesbyi* in foraging habitat, if not in foraging behavior, to a greater extent than *frenatus* and *oxyrhynchus* differ from *catesbyi* (Table 3). Interspecific competition may necessitate this increased divergence of *dorsalis* and *catesbyi* on Gonâve, whereas less divergence insures the coexistence of two sympatric *Uromacer* on the more extensive and heterogeneous Haitian mainland.

If the history above is wrong, Gonâve deserves intensive study as an extraordinary example of an island colonized from two comparable and equidistant sources. If the suggested history is correct, then Gonâve is a model of the faunal transformations of a continental island that when peninsular had the full complement of species of the adjacent mainland: while several closely related species could persist when immigration from the mainland was easy, fewer were able to persist after their populations became insular. Those that did persist on the island had to be strongly divergent ecologically. According to such a model, an interpretation of the fauna of a continental island must emphasize the ecological compatibilities of the potentially resident species, rather than their relative vagilities and routes of invasion from the adjacent mainland.

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APPENDIX

SYSTEMATICS

The synonomy of each species cites only the original description and additions to the synonomy of Cochran (1941). The data for the cited geographical range are given in Figure 1. The extreme measurements of the snakes examined are given for each metric character; the standard error for each measurement is listed in Table 2. A list of all specimens examined, their localities and color morphs, and the stomach contents listed in Table 3 are filed with the specimens at the Museum of Comparative Zoology.

UROMACER CATESBYI (Schlegel)

Dendrophis catesbyi Schlegel, 1837, Essai sur la physionomie des serpens, 2: 226 (type loc. "L'île de St. Dominque").

Uromacer scandax Dunn, 1920, Proc. New England Zool. Club, 7: 43 (type loc. Tortuga Island).

Range. Hispaniola: the coastal area north of the Cul-de-Sac Plain, the southwest peninsula of Haiti, upland valleys of the interior of the island, Ile à Vache, Île de la Gonâve, and Île de la Tortue. It is sympatric with every other species in the genus.

Diagnosis. Snout 2.0 (range: 1.7-2.7) times eye diameter; scale rows at midbody 17; ventrals 167 (range: 160-180); subcaudals 183 (range: 163-205); anterior loreal absent. 254 specimens were examined: 14 AMNH, 79 ASFS, 6 BMNH, 21 FMNH, 126 MCZ, 8 USNM.

Color pattern. Green morph: dark green above, light yellow-green below, the colors meeting on the 3rd scale row; head dark green above, cream below, a light line above the eye and a dark line from the snout to the end of the head (after MCZ 64800). A few specimens have a light lateral line on the 2nd and/or 3rd scale row. The dorsal dark green varies geographically, from a dark, brownish green in western Haiti to a very light green in the eastern Dominican Republic. Specimens from Ile à Vache are somewhat lighter than those from the adjacent mainland.

Gray morph: gray above, cream below, the colors meeting on the 3rd scale row; head gray-green above, cream below, a light line above the eye (after MCZ 66350). This morph has been found in 5 specimens from the Miragoâne area.

Nomenclature. Dunn (1920) defines *scandax* as "like *Uromacer catesbyi* but with 19-11 scale rows and 181 ventrals." Examining the holotype (USNM 59438), I count 17 scale rows at midbody and 180 ventrals, with 19 scales around the neck persisting to within 5 cm of midbody. A count of 19 scale rows persists for some distance down the body in six of the 254 *catesbyi* examined; there are also three typical *catesbyi* from scattered localities with ventral counts of 177, 178, and 179. Two *catesbyi* typical in scale characters (MCZ 37607, USNM 59920) have been taken from Île de la Tortue, but larger collections may reveal an endemic subspecies of *catesbyi* for which the name *scandax* would be appropriate.

UROMACER FRENATUS (Gunther)

Ahaetulla frenata Gunther, 1865, Ann. Mag. Nat. Hist., Ser. 3, 15: 94 (type loc. "not known").

Uromacer wetmorei Cochran, 1931, Proc. Biol. Soc. Washington, 44: 91 (type loc. Isla Beata).

Range. Southwest peninsula of Haiti east and north to the Cul-de-Sac Plain, Ile à Vache, Isla Beata, and the eastern coast of Barahona Peninsula. Records outside this area have been based on misidentifications (Cochran, 1941). It is sympatric with *catesbyi* throughout its range and with *oxyrhynchus* at the base of the southwest peninsula.

Diagnosis. Snout 2.6 (range: 2.1-3.0) times eye diameter; scale rows at midbody 17; ventrals 187 (range: 177-196); subcaudals 204 (range: 185-212; but AMNH 51416 has 135 and its tail appears intact); anterior loreal absent. 102 specimens were examined: 4 AMNH, 39 ASFS, 2 BMNH, 46 MCZ, 11 USNM.

Color pattern. Gray-green morph: Gray-green *frenatus* from Île à Vache are dark blue (probably green in life) above, mottled gray to gray-brown below, the colors separated by a white line on the 2nd and 3rd scale rows from four head lengths down the neck to the vent; head blue (probably green in life) above, cream below, a light line above the eye, dorsal edge of upper labials black (after MCZ 37630). The posterior extent of the white line is variable; on some specimens it fades as far anteriorly as midbody. Gray-green *f. wetmorei* from Barahona are as above, but the white line is on the 4th and 5th scale rows from the snout to one head length behind the vent (after AMNH 51421). One specimen (MCZ 43806) is not mottled ventrally and may represent a green morph, but it has been so blackened by the preservative that it is impossible to infer its color in life.

Gray morph: Mainland *f. frenatus* are finely mottled gray above and below; a trace of green on the top of the head, light green on upper labials, chin, and ventral neck (after MCZ 65530). Gray *frenatus* from Île à Vache and the type specimen of *f. wetmorei* (USNM 83891, Isla Beata) are the same as above but with the 4th and 5th scale rows very light, thus giving the appearance of a wide, dark gray dorsal stripe (after MCZ 37629).

Nomenclature. Cochran (1931) described *wetmorei* on the basis of a single specimen (USNM 83891) from Isla Beata, noting its close relationship to *frenatus*. I have re-identified 5 specimens from the Barahona mainland (MCZ 43806, AMNH 51416, 51419-21) as *wetmorei*. These additional specimens narrow the morphological distinction between *frenatus* and *wetmorei*. *U. f. wetmorei* has a significantly lower ventral count (180) than *f. frenatus* (189) (t=5.7, 45d.f.), although there is extensive overlap. The color patterns of *f. wetmorei* are unlike that of mainland *f. frenatus*, but are quite similar to those of *f. frenatus* from Île à Vache. Until enough specimens are available to characterize the Barahona population, I prefer conserving the name *wetmorei* to designate a subspecies of *frenatus*.

Specimens of *frenatus* from Diquini show some characteristics that might be attributed to introgression by *oxyrhynchus*. BMNH 1913.7.17.29 has a ventral count of 196; USNM 117282 has the anterior loreal scale; MCZ 8683, USNM 117282, and 117346 differ from typical *f. frenatus* in coloration, being gray with a broad stripe of gray-green down the back. Each of these specimens can be definitely identified as an aberrant *f. frenatus*, but it seems strange that all the *frenatus* from Diquini are aberrant. Recent collections from the Diquini area include no *frenatus*, but typical *frenatus* and *oxyrhynchus* are found together in the Jacmel and Miragoâne areas, and in Port-au-Prince, adjacent to Diquini, with no evidence of interbreeding. Without a larger sample, further speculation on the significance of the Diquini population seems pointless.

UROMACER OXYRHYNCHUS Duméril and Bibron

Uromacer oxyrhynchus Dumeril and Bibron, 1854, Erpétologie Générale, 7: 772 (type loc. "Senegal").

Range. Hispaniola: coastal area north of the Cul-de-Sac Plain, southwest peninsula of Haiti west to Miragoâne, Ile de la Tortue, and Isla Saona. It is sympatric with *catesbyi* throughout its range, and with *frenatus* at the base of the southwest peninsula. *U. oxyrhynchus* is not known to occur with *f. wetmorei*, though Mertens (1939: 79) reports seeing an *oxyrhynchus* and a *frenatus* in the same bush at "Camberlen" (near San Cristóbal, D.R.); he did not catch the *frenatus*, however, so that it is not possible to be sure that the snake was not a gray *oxyrhynchus*. One specimen of *oxyrhynchus* (USNM 75927), collected by J.S.C. Boswell in 1928, is reported as taken from Anse à Galets, Gonâve. Exceptional localities of other specimens in Boswell's 1928 collection have been attributed to labeling errors (Schwartz, 1965). Collections from Ile de la Gonâve in the last ten years contain many *catesbyi* and *dorsalis*, but no *oxyrhynchus*.

Diagnosis. Snout 3.0 (range 2.5-3.7) times eye diameter; scale rows at midbody 19; ventrals 200 (range: 189-212); subcaudals 199 (range: 183-211); anterior loreal present in 25 of the 129 specimens examined: 6 AMNH, 8 BMNH, 2 FMNH, 97 MCZ, 15 USNM, 1 YPM.

Color pattern. Green morph: dark green above, light yellow-green below, the colors separated by a white lateral line on the 1st and 2nd scale rows from the snout to two headlengths beyond the vent, ventral edge of the scales in the 1st row black; head green above, cream below, a light line above the eye, dorsal edge of upper labials black (after MCZ 62701). There are variations in color intensity. The lateral line may be edged by black, yellow, both, or neither. In a few specimens, as much as the anterior half of the lateral line is indistinct or lacking.

Gray-green morph: like the green morph, but with the ventral surface finely mottled gray to gray-brown from the neck to the tip of the tail (after MCZ 62703). This morph has been found in Haiti and in the eastern Dominican Republic. Variations are as in the green morph.

Gray morph: finely mottled gray above, more coarsely mottled gray below, 2nd, 3rd, and 4th scale rows lighter gray, dorsal edge of scales in the 5th row black from midbody to vent; head as in the green morph (after MCZ 62702). Four specimens of this morph have been taken from scattered localities in Haiti.

UROMACER DORSALIS Dunn

Uromacer dorsalis Dunn, 1920, Proc. New England Zool. Club, **7**: 43 (type loc. Gonave Island).

Range. Île de la Gonâve. It is sympatric with *catesbyi*.

Diagnosis. Snout 2.9 (range: 2.5-3.7) times eye diameter; scale rows at midbody 17 (19 in MCZ 93146); ventrals 200 (range: 192-210); subcaudals 210 (range: 197-228); anterior loreal present (absent in MCZ 93139). 84 specimens were examined: 7 ASFS, 65 MCZ, 12 YPM.

Color pattern. The species is monomorphic: finely mottled gray above and below, the dorsal region between the 5th scale rows darker; head green above, light green below (after MCZ 61043). In very light specimens the dorsal stripe is indicated only by black spots on the dorsal edge of scales in the 4th row.

Nomenclature. U. dorsalis is more similar to *oxyrhynchus* than to *frenatus* in general body form, snout length, ventral count, and the presence of the anterior loreal scale, but more similar to *frenatus* in midbody scale count, subcaudal count, and color pattern. Since *dorsalis* is unique in its diet and morphologically intermediate between two distinct mainland species, I retain it as a distinct species. Although I admit a close relationship between *dorsalis* and *oxyrhynchus,* the evidence is not compelling enough to warrant calling *dorsalis* a race of *oxyrhynchus*.

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THE GENUS *PHENACOSAURUS* (SAURIA: IGUANIDAE)

James D. Lazell, Jr.[1]

> *The members of this order are the animals the Lord of the Hebrews did not create to grace his Eden; they are not among the products of the six days' labor. These are the sports, the offthrows, of the universe. . . . These are the weird children of the lust of the spheres.*
>
> *Charles Finney*

ABSTRACT: A complete revision of the Andean genus *Phenacosaurus*, using all available museum specimens, is presented. The genus is separated from *Anolis* on the bases of pelvic osteology and digital pad structure. Of four previously described species, two are retained: *heterodermus* (including *"richteri"* and *"paramoensis"*) and *nicefori*. A new species, *P. orcesi*, is described from Ecuador.

Among the strange and varied productions of the high Andes is a small assemblage of grotesque, big-headed, short-legged, prehensile-tailed lizards: the genus *Phenacosaurus*. Since Dunn's (1944) work on this genus in Colombia, it has not been re-examined as a whole. Through the efforts of E. E. Williams, Museum of Comparative Zoology (MCZ), it has now been possible to amass at one time and place the majority of specimens of all the species of this genus and thus attempt a complete review. Without the cooperation of the curators of many institutions, of course, this would not have been possible. I express here my gratitude to the curators of the following institutions: Instituto de La Salle, Bogota (ILS), British Museum (Natural History) (BMNH), Museum of Vertebrate Zoology (MVZ), University of Michigan Museum of Zoology (UMMZ), Stanford University Museum of Natural History (SU), Field Museum of Natural History (FMNH), Philadelphia Academy of Natural Sciences (PANS), Fundación La Salle

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de Ciencias Naturales, Caracas (FCN), United States National Museum (USNM), American Museum of Natural History (AMNH), Vienna Museum (WIEN), Munich Museum (MUN), Senckenberg Museum (SMF), Berlin Museum (ZMB), Museum National d'Histoire Naturelle de Paris (MHNP), and Universidad Nacional de Colombia (UNC).

Professor Gustavo Orces-V, Esquela Politécnica Nacional, Quito, Ecuador, has very kindly donated the first phenacosaur recorded from Ecuador, which I take great pleasure in designating as the type of a new species named in his honor (see below).

Dr. Fred Medem, Cartagena, Colombia, has made available an excellent collection of Colombian phenacosaurs, including the type and paratypes of *P. richteri* Dunn. Those specimens actually collected by him are fresh alcoholics and combine color retention with very accurate data — including elevations. Dr. George Gorman, Museum of Vertebrate Zoology, Berkeley, has recently collected series in the Bogota area.

The Orsono-Mesas (1946) have provided an informative treatment of several aspects of phenacosaur ecology and behavior.

Color photographs of living phenacosaurs taken around Bogota have been provided by Fred Medem and Jose Muñoz, Hans Zenke, and Victor Hutchison.

In addition to the problems posed by the species-group level taxonomy of *Phenacosaurus,* it seems necessary to re-examine the status and validity of the genus. *Anolis heterodermus* Duméril (1851) was included by Boulenger (1885) in his concept of *Xiphocercus* Fitzinger (1843). "*Xiphocercus*" was then separated from *Anolis* (and *Chamaeleolis*) on the character combination of tricuspid lateral teeth plus a prehensile tail, and from "*Norops*" on the character of a raised terminal phalanx. Barbour (1920) separated *heterodermus* from the West Indian form ("*Xiphocercus*" [= *Anolis*] *valenciennii*) on the basis of body squamation, dorsonuchal crest, elevated rim of head plates (= circumoccipital swelling or casque of Dunn, 1944), digital dilations, and tail structure. "*Xiphocercus*" *heterodermus* thus became the type of the new genus *Phenacosaurus* Barbour (1920). However, Williams (1962) has shown "*Xiphocercus*" to be a synonym of *Anolis;* the validity of *Phenacosaurus* may be questioned also. Certainly neither body squamation nor dorsonuchal crest is useful in separating *Phenacosaurus* from *Anolis.* Caudal vertebrae that lack autotomy septa are found in such distantly related *Anolis* as *darlingtoni* and *latifrons;* though no *Anolis* has yet been demonstrated definitively to use its tail in a prehensile manner, it seems reasonable to infer from structure that some, like *darlingtoni,* do.

The "circumoccipital swellings," or "casque," referred to is indeed a striking feature of adult male *heterodermus.* Actually posterolaterally directed flanges of the parietals, this "casque" is but weakly developed in juveniles and females of *heterodermus,* or in most specimens of *P. nicefori,* regardless of sex, and is reduced in the new form from Ecuador. In addition, some species of *Anolis* (e.g. *richardi* of the Lesser Antilles) develop similar parietal flanges; there is, admittedly, still a definite degree of difference between the condition in some *Phenacosaurus* and that shown even by adult male *Anolis richardi,* but one would hesitate to accept a genus wholly based on such a degree of difference.

The digital dilations of *Phenacosaurus* are distinctive. The toes are comparatively shorter than the toes of *Anolis* of similar size; the digital pad is expanded not only beneath the second and third phalanges of the fourth toe, but beneath the first phalanx as well; proximal continuation of the expanded digital pad is the rule with all the toes, and produces a rather gecko-like appearance of the foot. Although this condition is not matched by any species of *Anolis,* the variation in structure and dilation of the digital pad in *Anolis* is sufficiently great (see Williams, 1963) so that any degree of difference shown by the phenacosaur condition is surely of diminished importance.

After examination of skeletal material of more than 70 species of *Anolis* in the MCZ, I have discovered that not only is the structure of the ilium remarkably constant in that genus, but that it is strikingly different from the condition seen in all forms of *Phenacosaurus.* I therefore propose a redefinition of the genus *Phenacosaurus* and provide the following definition of *Anolis* for comparative purposes:

Anolis is a genus of iguanid lizards without femoral pores; subdigital lamellae bear cuticular hairs; pre- and post-zygopopheses of trunk vertebrae not expanded to form great lateral flanges; angular absent; lateral teeth cusped; ilial shaft subcylindrical, dorsal border forming an obtuse angle with the acute or nodular, elongate, anterior iliac process (see Figure 6).

PHENACOSAURUS Barbour

Anolis (part), Duméril, 1851, Cat. Meth. Rept., p. 59.
Xiphocercus (part), Boulenger, 1885, Cat. Lizards Brit. Mus. II, p. 10.
Phenacosaurus Barbour, 1920, Proc. New England Zool. Club 7, p. 62.

Type species. Anolis heterodermus Duméril, 1851.

Definition. Iguanid lizards without femoral pores; subdigital lamellae bear cuticular hairs; pre- and post-zygopopheses of trunk vertebrae not expanded to form great lateral flanges; angular absent; lateral teeth cusped; ilial shaft compressed and bladelike, inclining smoothly into a blunt, subrectangular anterior iliac process (see Fig. 6).

The condition of the ilium can be readily checked without undue damage to the specimen by merely lifting the skin above one hind limb and separating the muscle attachments from the bone. This has been done for all of *P. nicefori* and the new species, as well as many *P. heterodermus.* The only dry skeletons of *Phenacosaurus* examined are ILS 55d and MCZ 17111, both *heterodermus.*

Polychrus have femoral pores present in males and lack an anterior iliac process.

Anisolepis and *Aptycholaemus* (nearly or quite synonymous, *fide* Etheridge, *pers. comm.*) have an ilium basically similar to that of *Phenacosaurus,* but possess a "fairly large" angular, *fide* Etheridge (*in litt.*). *Anolis* and *Phenacosaurus* lack an angular bone.

The remaining anoline genera (*sensu* Etheridge, 1959) have an ilium like that of *Anolis.* In addition, *Tropidodactylus* is unique in lacking cuticular hairs on the lamellae; *Chamaeleolis* has simple, peglike lateral teeth and a small angular; *Chamaelinorops* has trunk vertebrae bizarrely modified by expansion and amalgamation of the pre- and postzygopophases to form great lateral flanges.

The usefulness of separating *Phenacosaurus* from *Anolis* may be questioned, and Dr. R. A. Etheridge (*in litt.*) has questioned the separation in principle. This, certainly, is the place to make a case for the genus, especially as I regard it as valid. Etheridge notes that phenacosaurs are an early offshoot of "alpha *Anolis* stock in South America that have developed some peculiar behavioral specializations and assorted anatomical specializations." In that, we concur; what alarms Etheridge, however, is that "*Phenacosaurus heterodermus* (for example) is much more closely related to *Anolis jacare* than *Anolis jacare* is to *Anolis nebulosus* (for example)." That is also true, but it in no way invalidates the genus *Phenacosaurus.* The difficulty, and the principle at stake, is the old bugbear of relationship. It is perfectly true that birds are, in a very real sense, more closely related to crocodilians than crocodilians are to lizards, and far more closely than crocodilians are to therapsids (for example). Yet, birds are not included within the Reptilia; they belong to a distinct class of their own. Simpson

(1961, pp. 129-132 and 140-145) has given detailed consideration to this problem. Its solution lies in defining taxa in higher categories in a way that best expresses their evolutionary position and adaptive similarities. In the present case, *Anolis jacare* and *A. nebulosus* are members of a presumably monophyletic group that have so much in common, from an adaptive and evolutionary point of view, that they are best regarded as congeneric despite obvious differences. Also, a plethora of other *Anolis* species spans the gap between them, and thus helps to unite them. The species of *Phenacosaurus,* on the other hand, are sharply distinct, in important adaptations, from any *Anolis;* the gap is not spanned by living intermediates. Of course, intermediates must once have lived, and this leads us to recognize a compelling truth: Any taxon at the level of a higher category (genus or above) must — either now or in the past — contain some member more closely related to members of some other taxon than that member may be to some members of its own taxon. I draw a line by defining the genus *Anolis:* the species of *Phenacosaurus* are outside that line.

It is only my opinion that *Phenacosaurus* — an apparently natural group of species — qualifies for the rank of genus; no definition of the category genus exists to tell me whether *Phenacosaurus* is one or not. I rest my case, therefore, on the evolutionary and adaptive significance of the characters that separate the groups: the structure of the ilium and the digital dilations. These seem to me to be quite as important as the distinctions, noted above, which separate the other anoline genera.

PHENACOSAURUS HETERODERMUS (*Duméril*)

Anolis heterodermus Duméril, 1851, Cat. Meth. Rept., p. 59. Syntypes: MHNP 1664, A1664, B1664, 6798, A6798.

Xiphocercus heterodermus, — Boulenger, 1885, Cat. Lizards Brit. Mus. II, p. 10.

Phenacosaurus heterodermus, — Barbour, 1920, Proc. New England Zool. Club 7, 61-63.

Phenacosaurus richteri Dunn, 1944, Caldasia 3, p. 60. Type: MCZ 69120.

Phenacosaurus paramoensis Hellmich, 1949, Dtsch. Aquar.-u. Terrar.-Ztschr. 2, p. 91. Type: MUN 118/37.

Diagnosis. A *Phenacosaurus* with large dorsal scales: 8-19 dorsals contained in the standard distance[1] (not counting interstitial

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[1] Defined as the distance from the center of the eye to the tip of the snout.

granules); head plates large: interparietal sometimes as long as distance across head between orbits, but often shorter; subdigital lamellae under second and third phalanges of fourth toe 18-24.

Lectotype. MHNP 1664, an adult male with 14 dorsals in the standard distance and 19 subdigital lamellae.

Type locality. "Nouvelle Grenade" (= Colombia), here restricted to the vicinity of Bogotá, Colombia.

Discussion. The extreme variability of this species has led to taxonomic difficulties and confusions, and to the naming, therefore, of two additional species — *richteri* Dunn (1944) and *paramoensis* Hellmich (1949).

Dunn, in his 1944 review, used the following characters to separate *"richteri"* and *heterodermus:*

Dorsal crest squamation. Dunn separated *"richteri"* (and *nicefori*) from *heterodermus* on the basis of single, rather than double, dorsal crest scale row. In attempting to make sense out of the remarkable variation I found in this character, I assigned numbers, from one to ten, to the various sorts of crest scale arrangements noted. In Table 1 each specimen is graded according to the sort of crest scale variant it possesses. Where specimens showed more than one sort of arrangement, the two or more grades are indicated. The following ten grades of variation were noted:

1. Undifferentiated middorsal scales; *i.e.*, no dorsal crest at all, except sometimes a median series of single, enlarged scales on the nape or tail.
2. Some enlarged scales along the middorsum, but not arranged in a particular pattern.
3. Enlarged, tectiform to carinate scales along the middorsum, but separated from each other by undifferentiated smaller scales.
4. Single row of enlarged, tectiform to carinate scales in contact with each other along the middorsum.
5. Single row of spike-like scales in contact with each other along the middorsum.
6. Staggered series of tectiform to carinate scales, every other one separated by undifferentiated smaller dorsals, but each usually contacting the scale immediately adjacent at the dorsal midline.
7. Alternating series of tectiform to carinate scales, continuously in contact with each other.
8. Double row of spike-like scales on anterior body combined with alternating tectiform to carinate scales posteriorly.
9. Alternating series of spike-like scales.
10. Double row of spike-like scales.

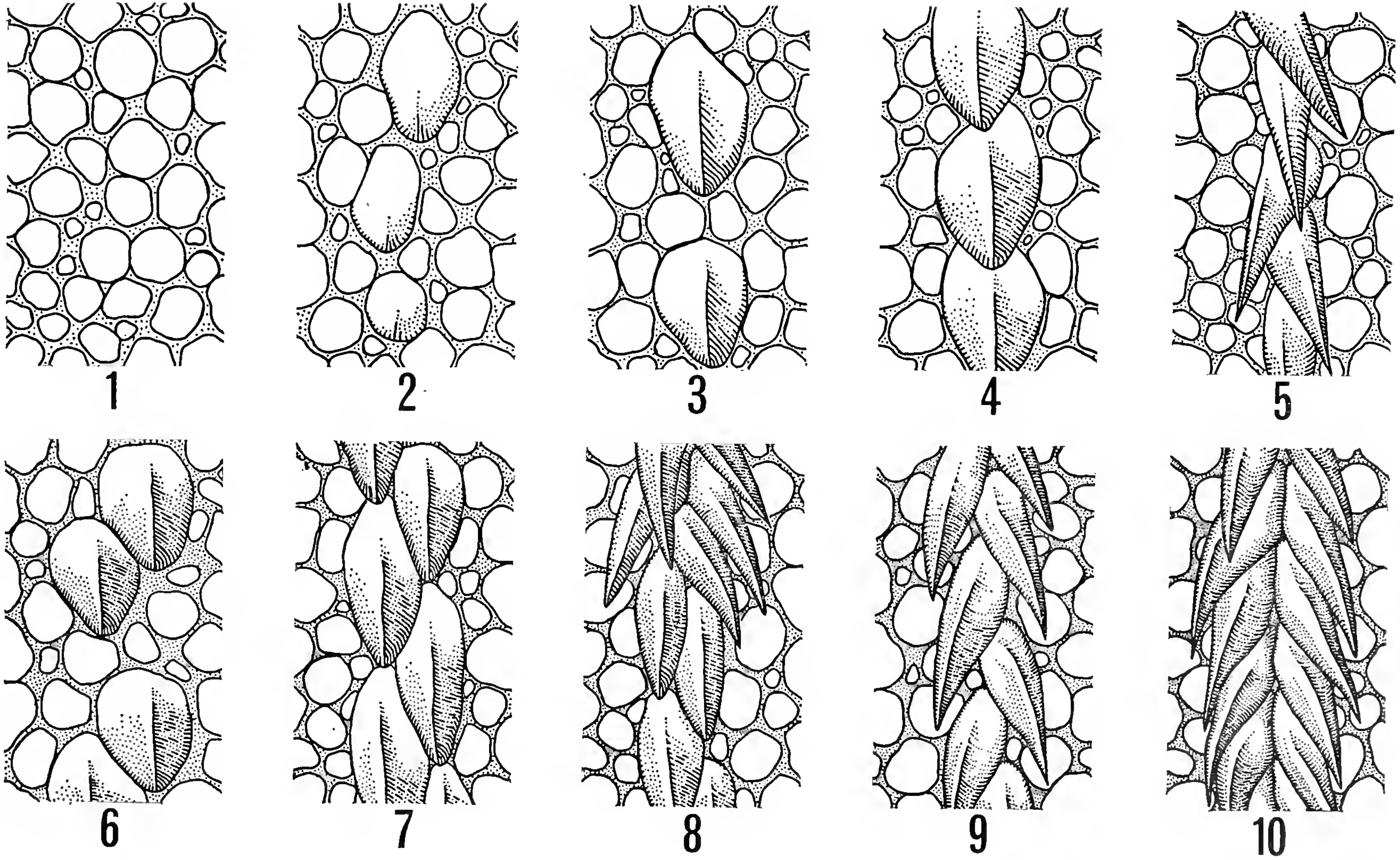

Figure 1. Variations in middorsal crest squamation in *Phenacosaurus*. See text for explanation.

In Figure 1 each of these ten variants is pictured. I do not find the condition of the dorsal crest squamation diagnostic for any of the named forms.

Cranial ridges. Dunn (1944) differentiated both of his new species from *heterodermus* on the basis of the structure of the circumoccipital and postocular ridges. *P. heterodermus* was supposed to have swollen scales making up these ridges, whereas *"richteri"* and *nicefori* were said to have swollen bone structure underlying the scales; the scales themselves were not supposed to be swollen in the latter two forms. Of *"richteri"* he states: "nor are they [these scales] enlarged" except slightly in old males (p. 60). In all the specimens I have seen, including the entire type series of *"richteri"* and the syntypes of *heterodermus*, the scales of the circumoccipital and postocular ridges are greatly enlarged, tectiform to carinate, and, in addition, lie on bony ridges of the skull. This character, therefore, fails to separate taxa.

Chin shields. Dunn (1944) separated *"richteri"* from *heterodermus* on the basis of the extent of contact between the enlarged chin shields and the infralabials. Anteriorly, the chin shields and infralabials are always in contact, posteriorly they are separated by small sublabials. The point at which separation begins is very variable, and the condition supposedly representative of *heterodermus* is to be found in the type series of *"richteri."* I could not correlate variation in this character with any of the others mentioned by Dunn.

Contact of dorsal scales. As with the preceding characters, Dunn recognized two conditions: enlarged dorsal scales either contacting each other, or separated. Both conditions do, admittedly, occur, but very often on the same lizard. I could not correlate this condition, even when clear-cut, with any of the other characters.

Leg length. As noted by Aleman (1953), leg length is variable and will not separate taxa unequivocally. In general, however, *nicefori* do tend to have much shorter legs in the southern part of their range (*e.g.*, Pamplona); *heterodermus* appear to have longer legs; in the northern part of their range (*e.g.*, Saota, Paz del Río). Therefore, though leg length cannot be used to diagnose the forms, it may indicate character divergence between *heterodermus* and *nicefori*, and is discussed further under the latter species. Leg length cannot be used to divide *heterodermus* as here defined into taxa, and *"richteri"* is, therefore, not separable from *heterodermus* on any character or combination of characters discernible by me.

Scale size. As may be noted from the above diagnosis of *heterodermus,* I do regard scale size as useful in separating forms. I have used two indices to scale size: the size of the head plates is here indicated by the length of the interparietal plate compared to the distance between the orbits across the top of the head. As noted, *heterodermus* has rather large head plates; the interparietal plate may be as long as the distance between the orbits, though it is usually somewhat shorter. The size of the dorsal scales, indicated by the number contained in the standard distance just lateral to the midline at midbody, separates *nicefori* and *heterodermus.* The new form from Ecuador combines scale size measured by both indices in a way that is radically different from either of the previously named forms. Both *nicefori* and the new species are discussed fully below. Dorsals in the standard distance just lateral to the midline at midbody are tabulated for *heterodermus* and *nicefori* in Table 1.

Coloration and pattern. Although not utilized taxonomically by Dunn (1944), coloration and pattern are obviously subject to some striking variation, at least in *heterodermus* as here defined, and must be considered more fully. Hellmich (1949) described a single specimen from Paramo de Sumapaz, 3750 meters, as a new species, *P. paramoensis.* The coloration and pattern of this individual are striking (see Figs. 2 and 3). Two other specimens I have seen match this condition: the smaller of ZMB 4256, a female (as is MUN 118/37, the type of *"paramoensis"*), and AMNH 91752, a male. Numerous other specimens approach this condition.

Two specimens, MUN 9/49 and MVZ 68686, from Tambo, Cauca, and San Antonio, Valle, respectively (the most southwestern localities for *P. heterodermus*), are pale ash-grey with very broad, brown bands across the dorsum. Excellent color transparencies taken at Bogotá by Hutchison show that the colors noted occur in living individuals at the type locality. Hutchison further notes (*pers. comm.*) that individuals are capable of changing their patterns as well as their colors.

Range. Phenacosaurus heterodermus, as may be seen in Figure 4, occurs in both the Cordillera Oriental and the Cordillera Central. The species occurs at least in the extreme southern Cordillera Occidental near the head of the Cauca River, at San Antonio, Valle. Because the Cauca River, which separates the Cordillera Occidental from the Cordillera Central, is nowhere as great a barrier as is the Magdelena, which separates the latter

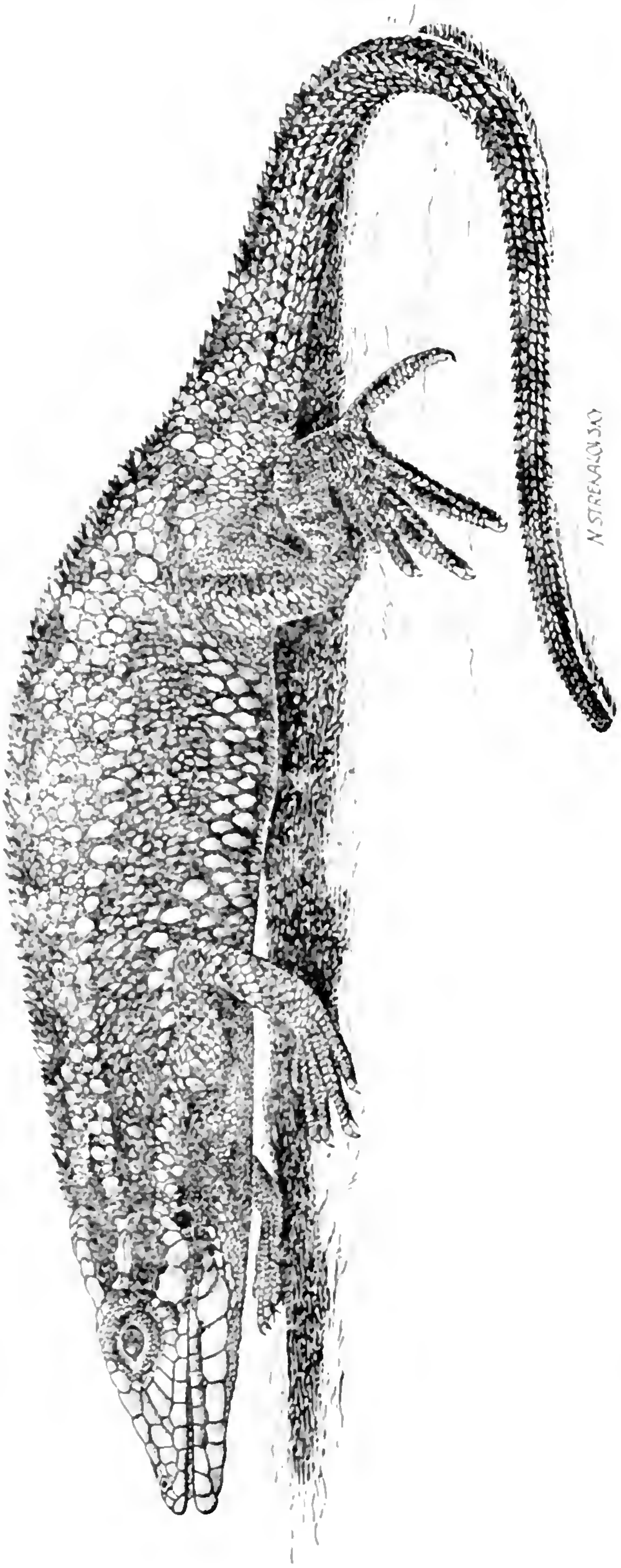

Figure 2. *Phenacosaurus heterodermus.* Specimen MUN 118/37, the type of "*paramoensis*" Hellmich.

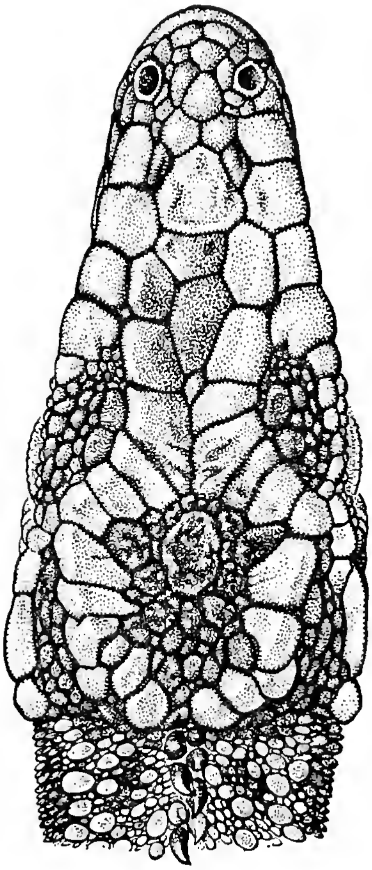

Figure 3. *Phenacosaurus heterodermus,* top of head. Specimen MUN 118/37, the top of "*paramoensis*" Hellmich.

from the Cordillera Oriental, and because all three Cordilleras merge in southern Colombia (*e.g.*, vicinity of Tambo, Cauca), I expect the total distribution of the species, at least in the western range, to be greater than is presently known. Dunn (1944) gives the altitudinal range as from 1800 m to 3500 m. Hellmich (1949) cites the elevation for "*paramoensis*" (= *heterodermus*) as 3750 m. This is the highest recorded elevation for the species.

Size. The largest specimen measured is MCZ 78531, from Paz del Río, Boyaca. It is 86 mm snout to vent. Remarkably, it is a female. In the more southern populations of *heterodermus* males seem to average larger than females, and reach 83 mm snout to vent (male of ZMB 5211) in the Bogotá area; females in the Bogotá area reach 80 mm (MHNP 1923.55). I therefore expect some males from the northern part of the range to be larger than any specimen here recorded. Size is discussed comparatively under the following species:

PHENACOSAURUS NICEFORI Dunn

Phenacosaurus nicefori Dunn, 1944. Caldasia 3, p. 59. Type: ILS 64.

Diagnosis. A *Phenacosaurus* with small dorsal scales: 21-34 contained in the standard distance (not counting interstitial granules); head plates small, interparietal much shorter than the distance across head between orbits; subdigital lamellae 16-20.

Type. ILS 64, an adult female with 24 dorsals in the standard distance and 17 subdigital lamellae.

Type locality. Pamplona, Norte de Santander, Colombia.

Discussion. On the basis of the eight specimens I have seen, this species is quite closely allied to *heterodermus.* The only definitive difference I have been able to discern is dorsal scale size. With respect to this character, it must be noted that for both *nicefori* and *heterodermus* the range of variation within the species, respectively, is greater by far than the gap which separates them. I have indicated in my discussion of *heterodermus* that I believe there is some evidence for character divergence between these two forms as they approach the area of potential sympatry. Though *heterodermus* and *nicefori* have not yet been demonstrated to be sym- or parapatric at any point (see Fig. 4), what evidence for character divergence we do have should be considered in full. Specimens of both forms have been arranged in Table 1 in a north-south sequence from Cerro Tetari (northernmost locality for *nicefori,* and the genus) to Tambo (the southernmost locality for *heterodermus*). Thereafter, in Table 1, the sequence is northward through the more western *heterodermus* localities in the Cordilleras Occidental and Central. Characteristics of dorsal scale size, dorsal crest type, and subdigital lamellae are tabulated; these, with the exception of dorsal crest type (which I do not regard as indicative of either taxon or character displacement), are included in the discussion below:

Dorsal scale size. Although the numbers of specimens in the samples do not permit any meaningful statistical analysis, *nicefori* and *heterodermus* do seem to become more different as they approach one another. The smallest dorsals in *heterodermus* (19 in the standard distance) are in FMNH 69673, from San Antonio, Huila, one of the southernmost examples. Similarly, the largest dorsals in *nicefori* (only 21 in the standard distance) are in FCN 664, from Cerro Tetari, Venezuela — the northernmost representative of that form. The differences between the more nearly adjacent populations — Pamplona (with one specimen of *nicefori* with 22) and Saota (*heterodermus* with 14) — are not spectacular, but with more evidence might prove meaningful.

Subdigital lamellae. In this case the situation is not indicative; assuredly, the Cerro Tetari *nicefori* has the highest number of lamellae found in that species, but the highest counts in *heterodermus* come from the southern part of that range. The more nearly adjacent populations hardly differ with respect to this character.

Leg length. As mentioned previously, leg length does seem to provide an example of character divergence. However, females of both forms seem to be shorter-legged than males, and I can find little difference between them. Fortunately, the three southernmost *heterodermus* localities (San Antonio, Huila; Tambo; and San Antonio, Valle) are represented by males. In all of these the appressed hind limb barely reaches the axilla. In most males from around Bogotá, the one male from Paz del Río, and in the Saota specimen, the appressed hind limb extends beyond the axilla. In Pamplona males of *nicefori* (2) the hind limb is, as in females, shorter than the distance to the axilla, whereas in the Cerro Tetari male, as noted by Aleman (1953), the hind limb is quite as long as this distance. Even in a case like this, however, where the evidence seems clear cut on the face of it, the number of individuals involved is much too small for any sort of surety.

Size. Here again there is but little evidence. The largest *heterodermus* examined, as noted, was from a northern locality, one of the two closest to a *nicefori* population. Similarly, the largest *nicefori*, FCN 664, is 86 mm snout to vent, and from the northernmost locality, farthest removed from the known range of *heterodermus*. Because all phenacosaurs begin life small, and because I have such a paucity of specimens and information about living animals, I cannot claim that this is necessarily meaningful.

Coloration and pattern. Most of the specimens of *nicefori* are formalin specimens, and show nothing in the way of coloration or pattern. FCN 664, however, is well preserved and appears to have been rather uniform green with a white stripe from the supralabials to the shoulder, as in many *heterodermus*. There is nothing about any of the other specimens of *nicefori* that could contradict the assumption that this is how they all look.

In the foregoing discussion I have tacitly assumed that FCN 664 actually represents a *nicefori*. If it does, it is by far the largest representative seen; those from around Pamplona are all less than 65 mm snout to vent. Also, it has the largest dorsals, the highest number of subdigital lamellae, and the longest legs of any *nicefori* seen. I have suggested that these differences may be attributable to character divergence in two species. On the basis of present information I see no alternative; if FCN 664 is not a *nicefori*, then a great deal of additional material will be required to demonstrate its true relationships. Certainly *heterodermus* and *nicefori*, whether they are distinct species or geographic representatives of the same species, are closely related.

Extreme with respect to major characters, the relationships of the new form from Ecuador are in no way so clear. I describe it as:

PHENACOSAURUS ORCESI sp. nov.

Type. MCZ 38937, collected iv. 1957 by Jorge Olalla.

Type locality. Mt. Sumaco, Napo Pastaza Province, Ecuador.

Paratype. USNM 16533, collected by James Peters between L'Alegría and La Bonita, Ecuador.

Diagnosis. A *Phenacosaurus* with very small dorsals, 38-48 contained in the standard distance (no interstitial granules present); head plates very large, interparietal much longer than the distance across the head between the orbits; subdigital lamellae under second and third phalanges of fourth toe 16-18.

Description of the type. MCZ 38937 is a female measuring 58 mm snout to vent, with a 61 mm tail. Both the foot structure and the ilium (dissected on left side) are typically phenacosauran.

Figure 4. Localities for three species of *Phenacosaurus*. Names are not cited here for localities in the immediate vicinity of Bogotá but are tabulated in north-south order in Table 1.

There are three large plates across the snout at the level of the second canthals. Two scales, the right one of which appears to be two smaller scales anastamosed, border the rostral. The nasal is entire, in contact with the first supralabial, and separated from the rostral by a single, subrectangular prenasal.

The supraorbital semicircles are composed of large plates, three of which are broadly in contact at the midline. The supraocular disks are composed of several large plates, two or three of which border directly on the supraorbital semicircles, that decrease in size laterally. There are no supraciliary scales distinguished from the orbital granules.

There are two rows of loreals. The interparietal is very large, ca. 1.3 times as long as the distance between the orbits across the top of the head, and is in contact with the supraorbital semicircles. The circumoccipital ridges are reduced to the point of absence. The suboculars are in contact with the supralabials. The mental is sutured, bordered posteriorly by the infralabials, sublabials, and four gular granules — eight scales in all.

A single series of sharply tectiform crest scales, separated by undifferentiated dorsal granules, begins on the nape and continues to the rump; this is a "3" type crest scale pattern. The dorsal scales are granular and of rather uniform size; there are 38 contained in the standard distance at midbody. The ventrals are smooth, slightly swollen, and subimbricate medially.

There are 18 subdigital lamellae under the second and third phalanges of the fourth toe. The digital dilations are very broad and become only gradually narrower proximally.

The tail is very slightly compressed; there is a single row of slightly enlarged, tectiform scales middorsally beginning somewhat posterior to the level of the vent. There are no scale whorls or other indications of autotomy septa.

There is apparently not a functional throat fan in this female. This is a formalin specimen; it has been rendered a dark, disagreeable, mud-brown all over; no trace of coloration or pattern remains.

The type is illustrated in Figure 5.

The paratype. The only other specimen of *P. orcesi* currently available is a male 60 mm, snout to vent, with a 67 mm tail. The digital pads of both fourth toes on the hind feet taper more abruptly proximally than is usual in *Phenacosaurus*, but are broader under the first phalanx than in *Anolis* of similar size. The ilium (dissected on the left) is typical of the genus: blade-like, with a blunt, obtuse anterior prominence.

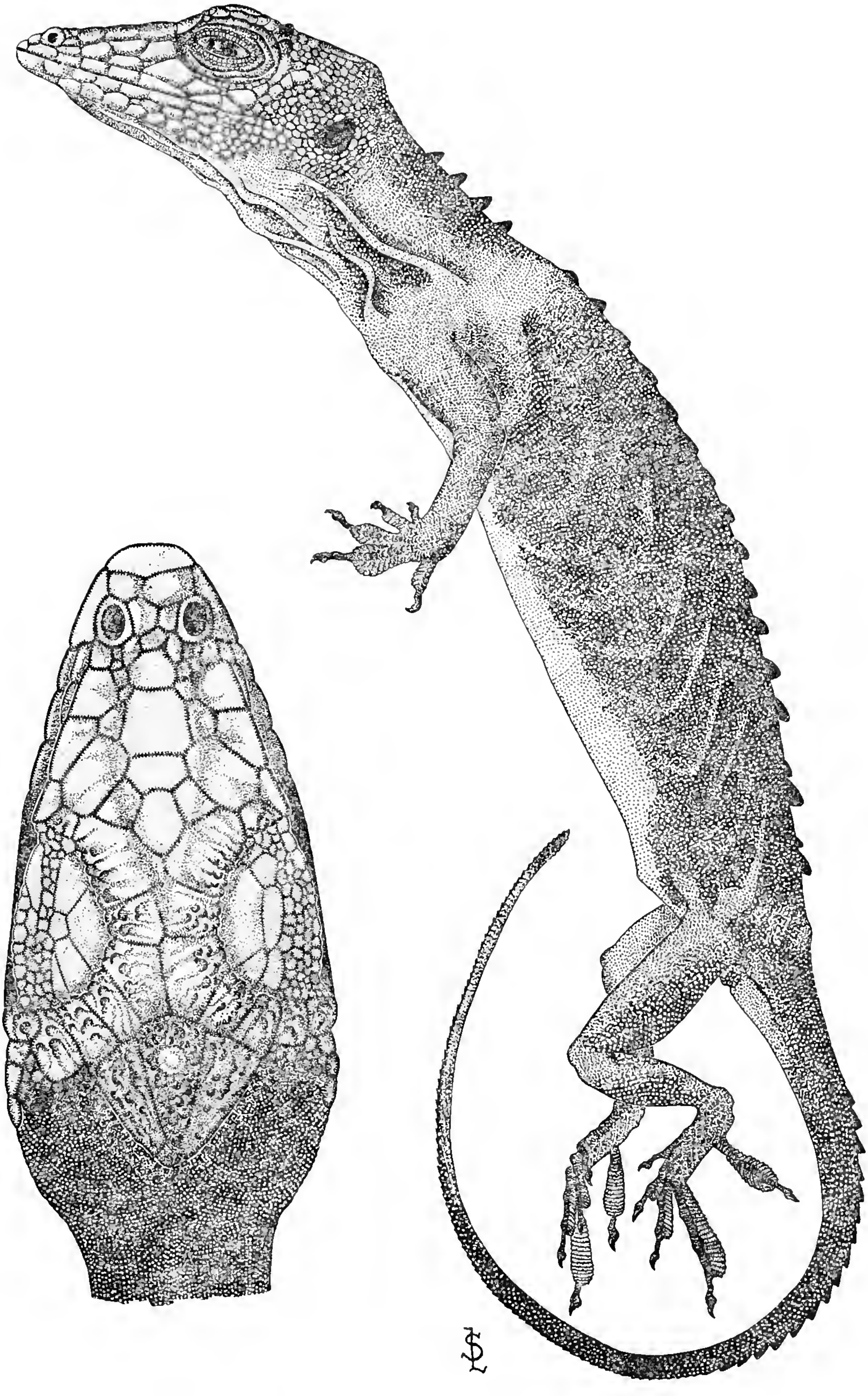

Figure 5. *Phenacosaurus orcesi* sp. nov., type, MCZ 38937, from Mt. Sumaco, Ecuador.

The paratype is similar to the type in all details described above except the following: There are four large plates across the head between the second canthals, and three scales border the rostral posteriorly. Two plates of the supraorbital semi-circles are in contact at the midline. The circumoccipital ridges, though low, are quite evident. Because one row of gular granules fails to reach the mental, only seven scales border it posteriorly. There are no enlarged crest scales on nape or back; this is a "1" type crest scale pattern. The dorsals are granular but variable in size; counts of 46 to 48 can be made in the standard distance at midbody. There are 16 or 17 lamellae under the second and third phalanges of the fourth toe. The tail bears a series of enlarged, tectiform scales, separated by smaller granules, beginning just posterior to the level of the vent; this is a "3" type crest scale pattern. The throat fan appears about as well developed as young males of *P. nicefori* or *P. heterodermus:* not apparently greatly extensible.

Dr. James Peters reports (*in litt.*): "The specimen was picked up by me personally. . . . It was found on the trail between L'Alegría and La Bonita, in Napo Province, Ecuador, high above the river that forms the boundary between Ecuador and Colombia, on the eastern slopes, on June 26, 1962. It was found dead on the trail, in a horse's hoofprint. . . . It was rather badly beaten up . . . — in the state you see it now, unfortunately. The elevation at which it was collected is approximately 5800 feet."

Discussion. While *Phenacosaurus heterodermus* and *P. nicefori* seem quite closely allied forms, *P. orcesi* appears remote. The dorsal squamation lacks the large scales interspersed with granules that both other species exhibit. The dorsals are smaller than in *nicefori*, though the head plates are larger than in *heterodermus*. The general appearance is very much like some *Anolis* (e.g., *solitarius*); the small scales augment this effect. The pelvic girdle, however, is distinctly phenacosauran; *P. orcesi,* in fact, differs from *Anolis* with respect to the ilium in the same ways that *heterodermus* and *nicefori* do, but to an even greater extent; the ilial prominence is very obtuse and weakly developed in both specimens available.

All considered, we know so little about the phenacosaurs in general that any attempt at a reasonable assessment of relationships is pointless. Until series of specimens can be collected from the many crucial areas presumably included within the range of the genus, and until comparisons can be made utilizing such characteristics as coloration in life and behavior in the field — features demonstrably of great importance in the systematics of anoline lizards — our knowledge of *Phenacosaurus* will remain reprehensibly elementary.

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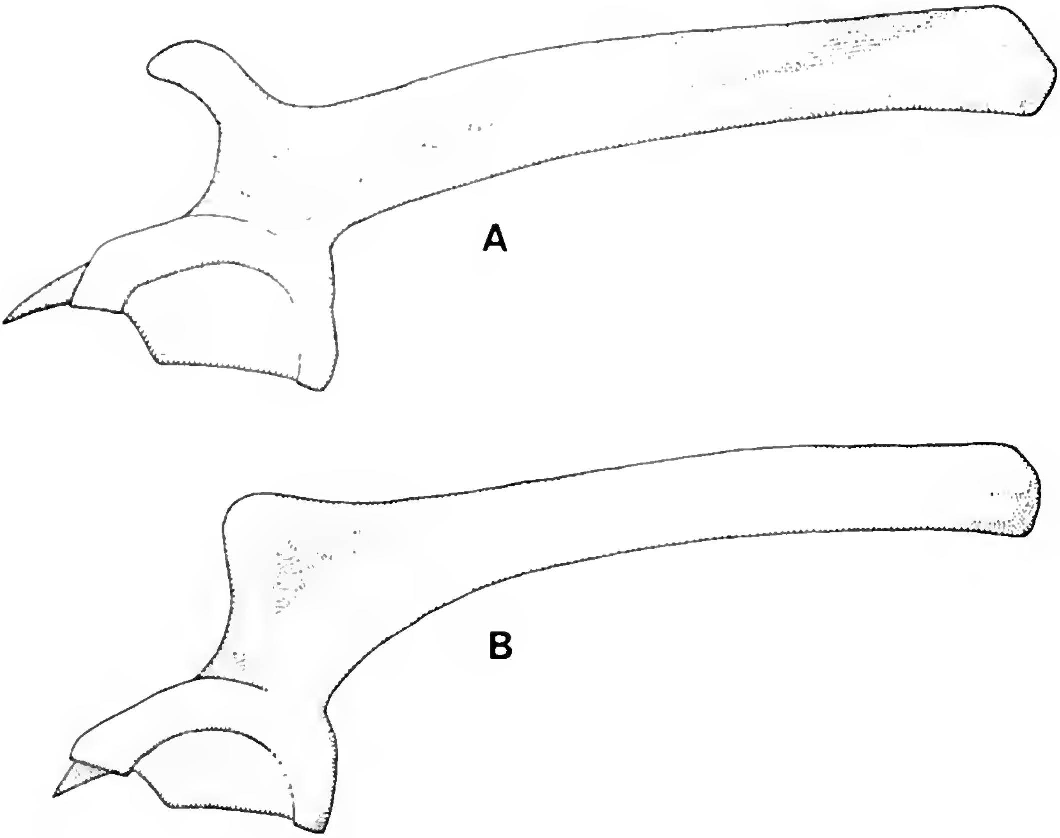

Figure 6. Ilia of two anoline lizard genera: A. *Anolis* (specimen MCZ 61027, *A. richardi*, Tobago, West Indies); B. *Phenacosaurus* (specimen MCZ 17111, *P. heterodermus*, Guasca, Colombia).

TABLE 1: SPECIMENS EXAMINED

Specimens of the three species of *Phenacosaurus* and three of their characters: dorsal scales counted in the standard distance, type of dorsal crest, and number of subdigital lamellae. See text and map (Fig. 5). The locality "Bogotá" is of highly variable precision.

PHENACOSAURUS NICEFORI

Specimen	*Sex*	*Locality*	*Dorsals*	*Crest*	*Lamellae*
FCN 644	♂	Cerro Tetari	21	3	20
FMNH 5684	♀	Paramo de Tana	28	6	17
FMNH 56443	juv.	Pamplona	31	3	18
PANS 25865	♂	"	27	3	17
ILS 64	♀	"	24	3	17
ILS 64a	♀	"	22	3	16
MCZ 6729	♂	"	34	3, 4	17
USNM 72745	♀	Tapatá	33	3	16

PHENACOSAURUS HETERODERMUS

Specimen	*Sex*	*Locality*	*Dorsals*	*Crest*	*Lamellae*
ILS 63	♂	Saota	14	9	18
UNC 692	♀	Paz del Río	10	2, 9	21
UNC 693	♂	" " "	14	5, 7	20
MCZ 78520	♂	Cogua	11	3, 5	20
MCZ 78521	♂	"	12	4	20
ILS 62	♂	Subachoque	13	8	18
ILS 62a	♂	"	15	9	19
MCZ 78524	♂	Cajica	13	5, 4	21
MCZ 78525	♂	"	10	5, 4	21
MCZ 78526	♀	"	9	5	20
MCZ 78527	♂	"	11	5, 3	20
MCZ 78528	♂	"	12	5	20
MCZ 78529	♂	"	14	5, 3	19
MCZ 78534	juv.	"	12	4	20
UNC 705	♀	"	10	5, 4	21
MCZ 104409	♂	Chia	10	4	19
MCZ 110133	♂	"	10	7	10
MCZ 110134	♀	"	12	4	18
MCZ 110135	juv.	"	17	2	20
MCZ 110136	♀	"	8	2	22
MCZ 110137	♀	"	14	2	22
MCZ 110138	♂	"	11	2	20
MCZ 110139	♂	"	11	7	19
MCZ 78522	♀	Usaquen	10	8	19
MCZ 78523	♂	Bosque Popular	16	6	20

Specimen	*Sex*	*Locality*	*Dorsals*	*Crest*	*Lamellae*
MCZ 78519	♂	Tena	12	4, 7	19
MCZ 69120	♂	Tabio	10	4	20
MCZ 69121	♀	"	9	5, 7	19
MCZ 69122	♂	"	12	4	21
MCZ 69123	♂	"	10	5	23
PANS 25074	juv.	"	12	8	19
PANS 25192	♂	"	10	8	20
PANS 25193	♂	"	11	8	18
PANS 25194	♂	"	9	5	19
PANS 25195	♂	"	11	5	20
PANS 25196	♀	"	10	5	19
PANS 25197	♂	"	12	3	20
ILS 55	♂	Sopo	8	5	20
ILS 55a	♀	"	12	5, 6	18
ILS 55b	♂	"	12	5	20
ILS 55c	♀	"	10	5, 6	19
ILS 55e	♂	Sopo	10	5	20
ILS 55f	♀	"	13	5, 6	20
UMMZ 56755	♀	Guasca	10	5, 6	20
MCZ 117111	♀	"	10	10	19
MCZ 117112	♂	"	11	9, 5	20
MCZ 14164	♂	Bogotá	14	4	19
MCZ 14165	juv.	"	14	9, 5	21
BMNH 68.3.3.9	♂	"	13	9, 6	20
BMNH 68.3.3.10	juv.	"	14	9	19
BMNH 1919.3.6.1	♂	"	12	9, 5	19
BMNH 1919.3.6.2	♀	"	10	6	21
BMNH 1919.3.6.3	♂	"	12	5	20
BMNH 1919.3.6.4	♀	"	11	5, 6	20
BMNH 1919.3.6.5	♂	"	13	9, 10	20
BMNH 1919.3.6.6	♂	"	13	9, 6, 4	21
SU 8275	♀	"	12	9	20
SU 8276	♀	"	15	5	20
SU 8277	♂	"	14	5	19
PANS 21058	♂	"	12	1	21
PANS 21059	♂	"	11	8	21
PANS 21060	♀	"	13	1	19
ILS 61	♂	"	13	5, 6, 3	20
ILS 61a	♂	"	11	8, 6	20
ILS 61b	♂	"	12	8	21
ILS 61d	♀	"	14	9, 5	20
ILS 61e	♀	"	11	8	21
ILS 61g	♂	"	14	8	20
ILS 61h	♂	"	13	8	20

PHENACOSAURUS HETERODERMUS

Specimen	*Sex*	*Locality*	*Dorsals*	*Crest*	*Lamellae*
ILS 61i	♀	"	8	9, 5	19
ILS 61j	♂	"	15	9	20
ILS 56	♀	"	10	5, 1	20
ILS 56a	♂	"	11	5, 3	19
ILS 56b	♀	"	9	5, 3	20
ILS 56c	♀	"	10	5	21
ILS 56d	♂	"	15	5, 3	21
ILS 56e	♀	"	14	5, 1	20
MCZ 74314	♀	"	10	8, 5	20
MCZ 74315	♂	"	11	8	20
UNC 687	juv.	"	11	5	20
MUN 119/37	♂	"	13	5	21
MUN 119/37	♀	"	11	5	20
WIEN 72	♂	"	16	9, 4	21
WIEN 72	♂	"	14	9, 4	21
WIEN 72	♂	"	16	6, 9, 4	19
WEIN 72	♂	"	15	6, 9, 4	22
WEIN 72	♂	"	14	9, 5	20
WEIN 72	♂	"	15	9, 6	20
WEIN 72	♂	"	10	5, 7, 2	20
WEIN 72	♂	"	10	5, 7, 6	21
WEIN 72	♀	"	14	9, 7, 6	19
WEIN 72	♀	"	14	8	20
WEIN 72	juv.	"	12	9, 4	20
MHNP 1923-55	♀	"	12	8	21
ZMB 4255	♂	"	12	5, 2	20
ZMB 4255	♂	Bogotá	13	9	19
ZMB 4256	♂	"	10	8	21
ZMB 4256	♀	"	10	9	19
ZMB 5211	♂	"	14	5	19
ZMB 5211	♂	"	13	5, 9, 2	19
UMMZ 56258	♂	"	13	9	23
SMF 10789	♂	"	18	8, 4	22
AMNH 91752	♂	"	14	6, 3	19
AMNH 91753	♂	"	14	7	20
AMNH 91754	♂	"	15	4, 7	18
AMNH 14024	♂	"	9	5	19
AMNH 14023	♂	"	13	9	22
AMNH 27567	♀	"	9	9	22
AMNH 7641	♂	"	17	5, 9	20
AMNH 24215	♂	"	13	9, 10	20
USNM 93225	♂	"	13	9	24
USNM 95923	♂	"	13	9, 10	21
USNM 92495	♂	"	13	9	19

Specimen	*Sex*	*Locality*	*Dorsals*	*Crest*	*Lamellae*
USNM 95922	♀	"	11	9	18
AMNH 44987	♀	no locality	15(?)	8, 6	21
AMNH 44986	♂	"	12	7, 6	19
MHNP 1664	♂	"Nouvelle Grenade"	14	9, 7	19
MHNP A.1664	♂	" "	13	5, 7	20
MHNP B.1664	♂	" "	12	5, 8	19
MHNP 6798	♀	" "	10	10, 7, 2	18
MHNP A.6798	♂	" "	12	5, 7	18
WIEN 12662	♂	" "	17	5	21
WIEN 451	♂	"Alto de los Cruces"	15	9, 6	20
WIEN 12660	♀	Paramo de Cruz Verde	10	6, 4	21
WIEN 12661	♂	" " " "	15	9, 4	20
UNC 680	♂	" " " "	16	5, 7	21
UNC 681	♀	" " " "	16	5, 7	19
UNC 686	♀	" " " "	11	8, 6	19
MCZ 78514	♂	Arracachal	13	5, 2	21
MCZ 78515	♂	"	16	5, 2	21
PANS 24150	♂	Aguadeta	11	5	19
PANS 24151	♀	"	13	9	22
PANS 24152	♂	"	17	8, 6	21
ILS 57	♀	Fusagasuga	11	5	19
USNM 127099	♂	"	13	3	19
USNM 127100	♂	"	16	3	20
USNM 127101	[illegible]	"	8	3, 2	20
MUN 118/37	[illegible]	Paramo de Sumapaz	10	8	20
AMNH 32680	♂	Gutierrez	12	5, 9	19
AMNH 32681	♀	"	9	5, 9	20
FMNH 69673	♂	San Antonio, Huila	19	3, 5	21
MUN 9/49	♂	W. Tambo	16	3, 5	24
MVZ 68686	♀	San Antonio, Valle	16	3, 5	21
PANS 25285	♂	"Laguneta" (?), Caldas	16	5, 2	19
SMF 10443	♂	Río Samana	13	2	22
UMMZ 65209	♀	Sonson	15	5, 4	20
AMNH 35303	♀	"	9	5, 4	21
AMNH 35304	♀	"	14	5	19
AMNH 35305	♂	"	12	5	20
AMNH 35306	♀	Sonson	13	3, 1	21
AMNH 32673	♂	Medellin	14	5	19
ILS 58	♂	San Pedro	17	5	19
ILS 59	♂	" "	9	8, 4	21
ILS 60	♂	" "	14	8, 6, 4	22

PHENACOSAURUS ORCESI

MCZ 38937	♀	Mt. Sumaco	38	3	18
USNM 166533	♂	btwn. L'Alegría and La Bonita	48	1	16