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BREVIORA

MUSEUM OF COMPARATIVE ZOOLOGY

HARVARD UNIVERSITY

NUMBERS 179-230

1963-1965

CAMBRIDGE, MASS., U.S.A.

1965

Edited
By
NELDA WRIGHT

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Museum of Comparative Zoology

CAMBRIDGE, MASS.

JANUARY 16, 1963

NUMBER 179

THE HOLOTHURIANS OF CLIPPERTON ISLAND IN THE EASTERN TROPICAL PACIFIC

By ELISABETH DEICHMANN

Museum of Comparative Zoology
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In 1902 H. L. Clark listed two typical Indo-West-Pacific aspidochirote holothurians from Clipperton Island, though at that time he considered one of them a new species. Later expeditions brought no holothurian material from this island. It was not until 1958 that Deichmann was able to include in her Hancock report some material of a third species, collected by the Scripps Institution's expedition a few years before. Finally, in 1958, the University of California Clipperton Expedition, which used more refined methods, with diving, etc., brought back four species, two of which had never been reported from any locality in the eastern tropical Pacific.

Of the five species now known from Clipperton Island, only one, *Microthele difficilis* (Semper) appears to be well established on the mainland of the Pacific coast of America. Two other species had previously been listed from some of the outlying islands, *Semperothuria atra* (Jaeger) and *Mertensiothuria leucospilota* (Brandt). Of the remaining two forms, *Stichopus horrens* Selenka represents a typical Hawaiian form, while *Semperothuria flavomaculata* (Semper) is considered rare; it was originally described from Samoa and later listed from Tahiti, and (?) Batavia in the East Indies.

The conclusions one can draw from this short list are that more Indo-West-Pacific forms are able to cross, at least intermittently, the "Ekman Barrier" than hitherto assumed, and that some of these forms may have escaped notice because they are living at a greater depth here than that in which they normally live in the more favorable localities of the Indo-West-Pacific.

STICHOPODIDAE

1. STICHOPUS HORRENS (Selenka) 1867

- Stichopus horrens* Selenka, 1867, p. 316, pl. 18, figs. 27-29. H. L. Clark, 1922, p. 64, pl. 2, figs. 19-23.
Stichopus godeffroyi Semper, 1868, p. 75, pl. 130, fig. 4; var. *pygmaeus*, p. 75, var. b, p. 246.
Stichopus tropicalis Fisher, 1907, p. 676, pl. 70, figs. 1-11.

The five specimens secured measure 15-20 cm. in length and agree well with Fisher's description of his material from Hawaii. All the specimens have numerous C-shaped bodies of all sizes in the skin; this is the character which is supposed to separate *tropicalis* (= Semper's var. b.) from the typical *godeffroyi*, but I fully agree with H. L. Clark in regarding the presence or absence of these structures as most unimportant. The typical tables — with a pointed spire — are present, although not in large numbers in some individuals, and likewise the peculiar rosettes could be located in all five individuals.

The color of four of the specimens is indicated to be "mottled with orange and pale cream," while the fifth is "mottled dull greenish," a color range which agrees well with H. L. Clark's observations on *horrens*. Fisher writes: "dark olive green, mottled with deep brownish green." His material, 16 cm. long, in preserved condition, came from tide pools in Hawaii.

While most earlier records (from Samoa, Fiji and Hawaii) are from shallow water, the present material (Clipperton A-588-6) came from 10-20 meters depth, off the edge of "the 10 fathoms terrace" on the northern side of the atoll: it was noted that the species did not occur at greater depth (40 meters) off the edge of that terrace. It was also observed, at similar depth, on the other side of the island, and the species appears therefore to be well established in this locality.

HOLOTHURIIDAE

2. MICROTHELE DIFFICILIS (Semper)

- Holothuria difficilis* Semper, 1868, p. 92, pl. 30, fig. 21.
Microthele difficilis:—Deichmann, 1958, p. 288, pl. 1, figs. 6-9 (list of references).

Four dark brown individuals, 6-7 cm. long, were collected (Clipperton A-588-8) on the reef flats "from the shore out, at least to the weak algal ridge."

The presence of this species in Clipperton is not surprising, since this atoll was the type locality for H. L. Clark's "*Holothuria frequentiamensis*," described in 1902 on the basis of 17 individuals, about 4 cm. long, of which one had immature genital organs.

The species ranges from the east coast of Africa to the Panamic region, where it is known from the Galapagos Islands, northwards to Espiritu Santos Island in the Gulf of California.

3. SEMPEROTHURIA FLAVOMACULATA (Semper)

Holothuria flavomaculata Semper, 1868, pp. 87, 277, pl. 30, fig. 26. Panning, 1934, pt. II, p. 42, text-fig. 35 (list of references).

Semperothuria flavomaculata:—Deichmann 1958, p. 303 (treated in the key for the genus).

Until the present study, there were only a few species belonging to the old genus *Holothuria* of which the Museum of Comparative Zoology did not possess representatives, and *flavomaculata* was one of these. When the key for the few members of the genus *Semperothuria* was worked out in 1958, it was necessary to rely entirely on the literature. It was consequently a satisfaction to discover two specimens of this comparatively rare species in the Clipperton material and to find that they agreed with the key.

Both specimens came from Clipperton A-588-6, from the 10 fathoms terrace, in water varying from 1-20 meters, off the edge of the tidal flat. The species was not noted by divers off the edge of that terrace, in water up to 40 meters depth.

The two individuals (M.C.Z. no. 3008) measure 8 and 12 cm. in length; they are dark, with few feet in scattered rows on the ventrum and more sparingly developed as papillae on the dorsum, here with a yellow area around their base. The spicules agree completely with the earlier descriptions: a crowded layer of tables with no disk, but a base which tapers to a point, four pillars and the spire ending in a double Maltese cross. In the deeper layer are scattered short rods, covered by coarse, rough spines, or clusters of spines.

The type, 11 cm. long, came from Samoa, and according to Panning the species has also been taken in Tahiti and (?)Batavia. It may possibly, when contracted, have been mistaken for *Ludwigothuria atra*, or some of the other dark-skinned forms in the Indo-Pacific. It was at first assumed that the material

represented *atra*, previously known from Clipperton Island, but the roughness of the skin eliminated that possibility, even before the spicules had been examined.

4. MERTENSIOTHURIA LEUCOSPILOTA (Brandt)

Stichopus leucospilota Brandt, 1835, p. 51.

Mertensiothuria leucospilota:—Deichmann, 1958, p. 297, pl. 3, figs. 1-9 (list of references).

Three large, reddish-brown individuals (Clipperton A-588-8) were collected on reef flats, identical in size and spiculation with those taken some years ago by the Scripps Clipperton Expedition, and included in Deichmann's 1958 report.

The species has the same wide range as *Microthela difficilis*, from the east coast of Africa to the Panamie region, but so far it has never been found established on the mainland. The Hancock expeditions reported it from Galapagos, Clarion and Socorro islands. The largest individuals, 20 cm. long, in preserved condition, have all come from Clipperton Island.

5. LUDWIGOTHURIA ATRA (Jaeger)

Holothuria atra Jaeger, 1833, p. 22. Panning, 1934, pt. II, p. 30, text-fig. 22 (list of literature).

Ludwigothuria atra:—Deichmann, 1958, p. 312, pl. 2, figs. 18-23.

Of this species H. L. Clark reported nine specimens from Clipperton Island in 1902. The Hancock expeditions collected thirteen in the Galapagos Islands and one in Cocos Island. The species is known to range from Mozambique to Hawaii; in the latter locality it is stated by Fisher to be "one of the commonest holothurians inhabiting Hawaiian shores."

The fact that the recent expeditions to Clipperton Island did not collect this large and conspicuous species, in spite of the intensive collecting undertaken, may indicate that this is one of the species which only intermittently crosses the "Ekman Barrier" but is unable to become permanently established in the less favorable localities which it finds in the eastern Pacific.

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Museum of Comparative Zoology

CAMBRIDGE, MASS.

JANUARY 17, 1963

NUMBER 180

A NEW FRESH-WATER AMPHIPOD CRUSTACEAN FROM OREGON

By E. L. BOUSFIELD

National Museum of Canada

In a recent account of the fresh-water amphipod fauna of Oregon (Bousfield, 1961), the writer listed ten known species including two species of *Crangonyx*, *C. richmondensis occidentalis* Hubricht and Harrison and *C. pseudogracilis* Bousfield. During a further examination of *Crangonyx* material from small alpine lakes in southwestern Oregon, a third species was identified. It proved to be distinct from other North American species studied by the writer (Bousfield, 1958) and from other known species of the genus and is herewith described as *Crangonyx alpinus* sp. nov.

The present study is part of a general survey of gammaridean amphipods in the collection of the Museum of Comparative Zoology, Harvard University, conducted in May, 1962, with the aid of a grant from the National Science Foundation. The writer wishes to thank Dr. Elisabeth Deichmann for instigating the study and for her many kindnesses and co-operation during the undertaking.

In the list of specimens, MCZ refers to the Museum of Comparative Zoology, and NMC to the National Museum of Canada.

Family GAMMARIDAE

CRANGONYX ALPINUS n. sp.

(Figs. 1, 2)

Material examined: A total of 52 specimens, collected in alpine lakes of Lane and Douglas counties, Oregon, by F. Ziesenheim during the summer of 1937, as follows: Corner L. (alt. 4800 ft.), Lane Co., July 29, MCZ No. 10027 — 3 fem., 12 juv.; Ledge L.

(5350 ft.), Lane Co., Aug. 5, MCZ No. 10028 — 1 ovig. fem. (TYPE), 1 juv.; Pork L. (4820 ft.), Lane Co., Aug. 9, MCZ No. 10029 — 3 fem. imm.; Plumb L., Lane Co., Aug. 21, MCZ No. 10030 — 6 juv.; Opal L. (5480 ft.), Douglas Co., Sept. 7, MCZ No. 10031 — 8 imm.; Whig. L. (5270 ft.), Douglas Co. Sept. 24, MCZ No. 10032 — 2 imm.; Emma L. (5190 ft.), Lane Co., Sept. 25, MCZ No. 10033 — 6 fem. imm., 4 male imm.; Easter Brook L. (5050 ft.), Lane Co., Sept. 27, MCZ No. 10034 — 1 fem. (Br. 1), 3 juv.; Mud L. (4950 ft.), Lane Co., Sept. 29, NMC No. 10035 — 1 fem. imm.

Diagnosis: A small species of the *richmondensis* group having elongate antennae, peraeopods and uropods, reduced mouthparts, shallowly cleft telson, and powerful gnathopods, but distinguished by the acuminate abdominal side plates, sharply serrated basal segments of peraeopods 3-5, singly inserted posterior marginal setae of segment 6 of gnathopod 1, long marginal spines of uropod 3 and telson, and by the small eye.

Female (10.5 mm.). Eye small, black, irregularly oval, removed from anterior head margin. Antenna 1, flagellum of 25 segments; accessory flagellum shorter than 1st flagellar segment. Antenna 2, flagellum of 9 segments.

Lower lip, inner lobes, distinct, rather broad. Mandibular palp, terminal segment slender, with 3 outer marginal setae. Maxilla 1, inner plate with only two plumose marginal setae. Maxilla 2, plates relatively narrow; inner plate with only one elongate plumose facial seta. Maxilliped, inner plate short, truncate apex with 5 slender spine-teeth; outer plate small, outer margin convex; dactyl of palp stout.

Lower corners of coxal plates 1 and 2 rounded, each with 3-5 short marginal setae. Gnathopod 1, posterior margin of segment 2 with numerous slender setae, anterior margin nearly bare; posterior margin of segment 5 with 3-4 clusters of long, slender, distally flexed spines, some minutely pectinate; segment 6 (propodus) subquadrate, widest distally; palmar margin evenly convex, slightly oblique, armed with about 12 medium-small spine-teeth on each side, strongest and closely crowded near posterior angle; posterior margin with 6-7 slender setae appearing singly inserted; dactyl fairly heavy, closely fitting palm. Gnathopod 2, segment 2 distally broadening, margins with several long setae; posterior margin of segment 5 with 5 posterior groups of setae; segment 6 subrectangular, distally broadening;

palm smoothly convex, oblique, lined with widely-spaced medium-strong spine-teeth; posterior angle with one prominent spine and another smaller spine; posterior margin nearly two-thirds the anterior; inner face of propodus with 4 groups of superior lateral setae, 1-3 setae per cluster; dactyl rather slender.

Peraeopods 1 and 2 slender, subequal; posterior margins of segments 4-6 moderately spinose. Coxal plate of peraeopod 2 nearly as broad as deep, proximally emarginate behind. Peraeopods 3-5 long and slender, 4th longest. Basal segments of peraeopods are similar in size and shape; posterior margins gently convex, with about 7-9 rather deep serrations, distally sharpest; length of dactyls $\frac{1}{4}$ to $\frac{1}{3}$ the propods.

Brood plates moderately large; setae numerous, elongate, minutely cleft at tip. Coxal gills present on segments 2-7, paired sternal gills on segment 6, two pairs on segment 7.

Pleopods powerful, 1st strongest; rami about twice the length of the peduncle, inner ramus somewhat longer than outer. Peduncles of pleopods each with a few simple marginal setae and 3-4 coupling spines of at least two types. Proximal setae of inner ramus are non-plumose and bifid at the tip.

Abdominal side plates, posterior margin shallowly incurved distally, corners sharply acuminate and produced posteriorly, most strongly in side plate 2.

Uropods 1 and 2 rather long and slender, lateral margins of both rami armed with short spines. Uropod 3, outer ramus slender, about twice the peduncle, lateral margins armed with about 4 groups of longish spines; inner ramus with 1 sub-apical spine; peduncle with 1 or 2 lateral marginal spines. Telson about as broad as long, shallowly emarginate, each lobe terminated by 2 longish spines.

Remarks: Mature males were not present in material at hand. The principal breeding period is probably June and early July following which the adults die off.

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Abbreviations for the Figures

A1 — Antenna 1	P3 — peraeopod 3
A2 — Antenna 2	P4 — peraeopod 4
LL — lower lip	P5 — peraeopod 5
Lft Md — Left mandible	PL1 — pleopod 1
Rt Md — Right mandible	PL3 — pleopod 3
Mx1 — Maxilla 1	U1 — uropod 1
Mx2 — Maxilla 2	U2 — uropod 2
Mxpd — Maxilliped	U3 — uropod 3
Gn1 — Gnathopod 1	T — telson
Gn2 — Gnathopod 2	EP1 — abdominal side plate 1
P1 — peraeopod 1	EP2 — abdominal side plate 2
P2 — peraeopod 2	EP3 — abdominal side plate 3

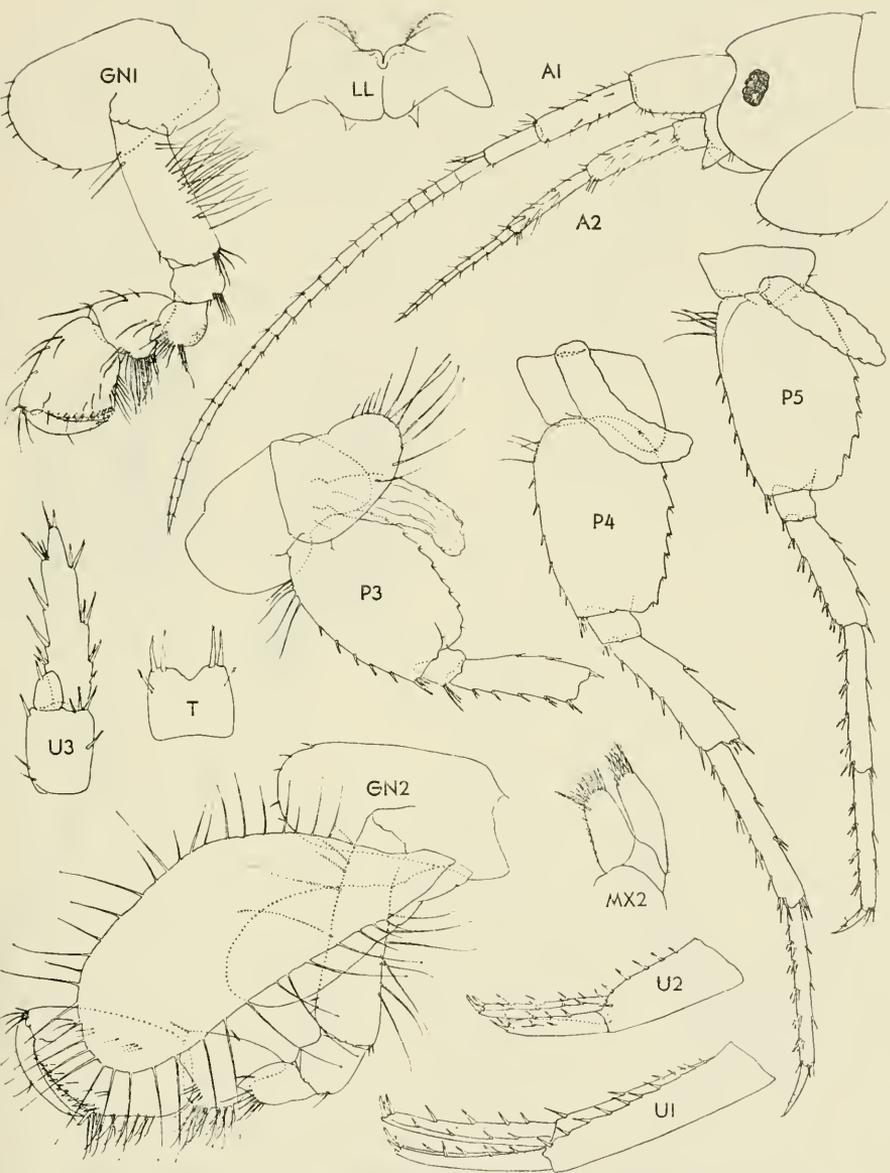


Figure 1. *Crangonyx alpinus* n. sp. Ledge L., Lane Co., Oregon, August 5, 1937, female (TYPE) 10.5 mm.

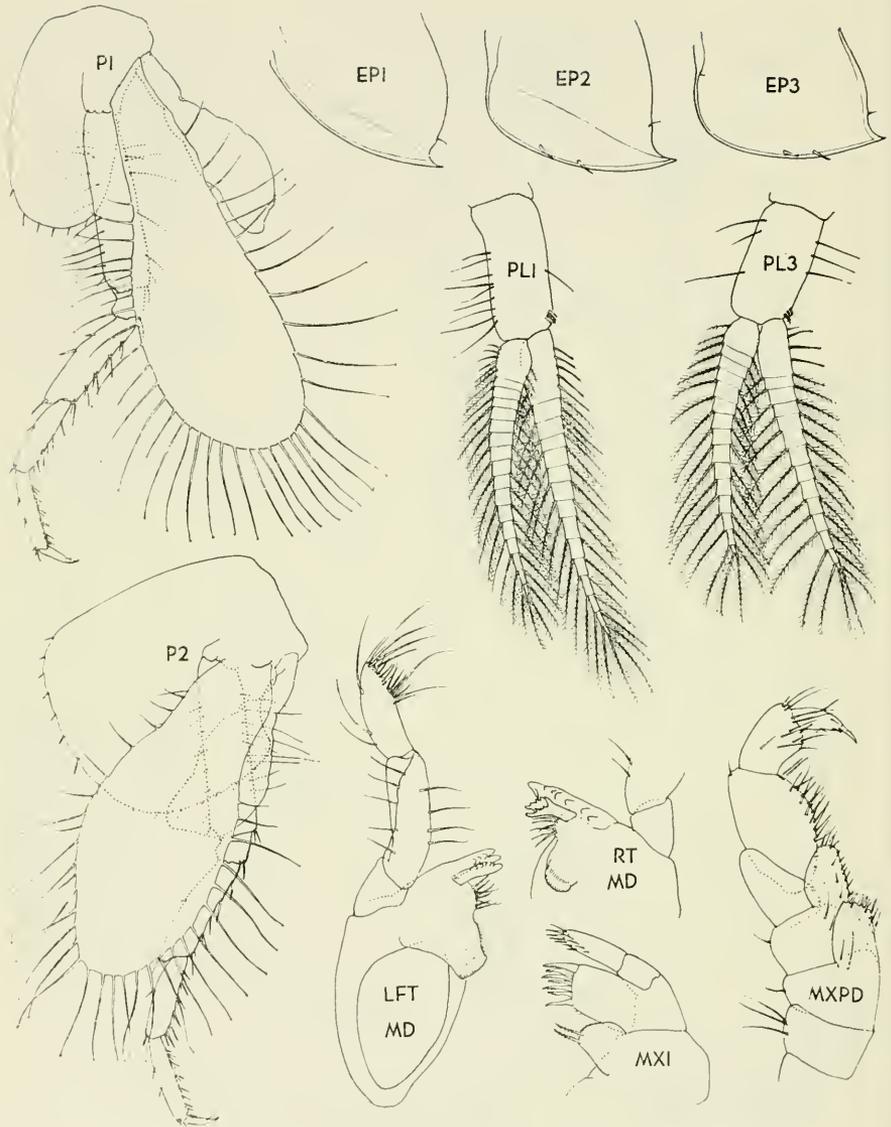


Figure 2. *Crangonyx alpinus* n. sp. Ledge L., Lane Co., Oregon, August 5, 1937, female (TYPE) 10.5 mm.

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Museum of Comparative Zoology

CAMBRIDGE, MASS.

FEBRUARY 1, 1963

NUMBER 181

SYSTEMATIC NOTES ON THE LAND SNAILS OF THE GENUS *TOMOCYCLUS* (CYCLOPHORIDAE)

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University of Miami

The genus *Tomocyclus* includes neotropical cyclophorid snails with a chondroid operculum, bearing a spiral lamella, an elongate-turrite shell and a double peristome. The outer peristome flares to produce a broad collar around the aperture. The parietal region of the outer peristome is bent anteriorly to pass under the preceding whorl. At this point a notch, the pseudosiphon, occurs in the reflected outer peristome.

Present knowledge of the anatomy of *Tomocyclus* is based on the account of Fischer and Crosse (1886). The verge is long, simple, tapering and unbranched. It originates on the right side of the neck, behind the tentacle, and possesses an open seminal groove. The jaw is typically cyclophorid, with a median projection. The radular formula is 3-3-3-3. Morrison (1955: 152) classified the American cyclophorid snails, and placed *Tomocyclus* in the subfamily Neopupinae, an allocation complying with most previous systems of classification. Torre and Bartsch (1942: 3) proposed the name Megalomastominae for this same subfamily, because the name Neopupinae was proposed five years prior to its assumed type genus, *Ncopupina* (Kobelt, 1902: 261), and because they recognized *Ncopupina* as a subgenus of *Megalomastoma*. Whether *Ncopupina* is or is not distinct from *Megalomastoma*, the name Megalomastominae should be retained for this subfamily.

The genus *Tomocyclus* is known from British Honduras, eastern Guatemala, and in Mexico from Chiapas and the isolated mountain region of San Andres Tuxtla, Vera Cruz.

MEASUREMENTS

For purposes of this study, measurements of height were made to include only the last four remaining whorls. Mature specimens of *Tomocyclus* are generally decollate, and shells in a single lot may have 4-8 whorls remaining. Therefore, measurements must be made from a point that is consistently present, and represents the same relative growth.

Measurements of length and diameter were made with vernier calipers, and are standard except for the special condition mentioned above. Measurements of the aperture and outer peristome were made with a calibrated Whipple disc. The diameter of the aperture was measured from the outside of the extended inner peristome. The width of the outer peristome (the collar) was measured at four places, and the readings were averaged.

ACKNOWLEDGEMENTS

I wish to express my gratitude to the following people for lending specimens in their charge and for other courtesies that have facilitated this study: Dr. Tucker Abbott, Academy of Natural Sciences of Philadelphia (ANSP); Dr. William J. Clench, Museum of Comparative Zoology, Harvard University (MCZ); Dr. Harold A. Rehder, United States National Museum (USNM); and Dr. Henry van der Schalie, Museum of Zoology, University of Michigan (UMMZ). The photographs for Plate I were taken by William L. Bruden, staff artist of the Museum of Zoology, University of Michigan.

Key to the Species of TOMOCYCLUS

- | | |
|----------------------------------------------------------------------------------------------------------|----------------------|
| 1. Basal carina present | 2 |
| 1a. Basal carina absent | 4 |
| 2. Axial sculpture consisting of well developed riblets | <i>gealei</i> |
| 2a. Axial sculpture consisting of fine striations | 3 |
| 3. Basal carina passing in front of reflected outer peristome; diameter of aperture 7.45-9.50 mm. | <i>fistulosus</i> |
| 3a. Basal carina passing beneath or behind reflected outer peristome; diameter of aperture 5.73-7.13 mm. | <i>simulacrum</i> |
| 4. Width-height ratio about 0.4 | <i>guatemalensis</i> |
| 4a. Width-height ratio about 0.5 | <i>lunae</i> |

TOMOCYCLUS GEALEI Crosse and Fischer

Tomocyclus gealei Crosse and Fischer, 1872, Jour. Conchyl., 20: 70; Fischer and Crosse, 1886, Miss. Sci. Mex. Amer. Cont., 2 (7): 118-120, pl. 40.

figs. 1-3; Bartsch and Morrison, 1942, Bull. U. S. Nat. Mus., 181: 143-144, pl. 19, fig. 1.

Megalomastoma (Tomocyclus) galei (Crosse and Fischer), von Martens, 1890, Biol. Cent. Amer., 9: 10.

Type locality: State of Chiapas, Mexico.

Records: GUATEMALA; *Alta Vera Paz*: woods between Tacic and Tamahu; Polochic Valley above Panzos and Senahu (von Martens, 1890: 10).

TOMOCYCLUS FISTULOSUS, new species

(Pl. I, figs. 1-3)

Description: Shell dull yellow, with early whorls and last quarter of last whorl becoming cinnamon, or rosy; translucent, large, elongate-turrite; decollate, 5 $\frac{1}{4}$ whorls remaining in the holotype; whorls gradually increasing in size, fourth from last whorl about 0.6 times diameter of last whorl, rate of increase in diameter of whorls nearly constant; spire slightly convex, nearly straight sided; whorls convex, suture moderately impressed; whorls crossed by fine, poorly developed, posteriorly arched growth wrinkles, which lie about 0.5 mm. apart; wrinkles faintly discernible, distinctness and spacing of wrinkles steadily increasing on last whorl; wrinkles continuing onto reflected outer peristome; whorls also with numerous fine spiral striations, which are frequently broken along their courses; base of last whorl with a strong carina, which passes in front of the aperture (Pl. I, fig. 3); carina originating on last half of penultimate whorl, and continuing nearly to reflected peristome; last half of last whorl lying just inside of crest of carina; peristome double; outer peristome dull white, forming a slight irregular collar, 0.97-2.06 mm. wide, 0.1-0.24 times the diameter of the aperture; face of collar with several annulations, which are crossed by numerous close, fine, irregular, granular ridges that occasionally anastomose; parietal region of collar indented by a nearly rectangular pseudosiphon notch, about 1 mm. deep and 2 mm. wide; aperture dull white, circular; columella tubular, continuing spirally through length of shell, open at first remaining whorl and umbilicus as a narrow slit; umbilicus nearly obscured by collar. Operculum dark brown, typically tomocyclid, consisting of a thin inner chondroid plate, and an external spiral lamella; inner surface of chondroid plate bearing a central knob; spiral lamella originating in center of operculum, and reflected to lie parallel to chondroid plate; edge of lamella frequently broken to produce a fringed appearance.

Measurements of holotype: total length, 32.5 mm.; length of last four whorls 30.0 mm.; diameter, 11.2 mm.; major height of aperture, 10.9 mm.; major width of aperture, 11.02 mm.; height of inner peristome, 7.56 mm.; width of inner peristome, 7.78 mm.

Measurements of paratypes:

Length	Diameter	Width of Collar	Inner Peristome
28.5 mm.	10.9 mm.	0.97 mm.	9.50 mm.
29.7	10.8	1.78	7.83
28.6	10.7	1.48	7.45
33.1	11.8	2.06	8.48

Major variations involve only size of the shell and width of the collar, and even these variations are relatively slight.

Holotype: UMMZ 194095, high rainforest at Vallentine Camp, 50 miles southwest of Cayo, British Honduras. Collected by C. L. Lundell and E. B. Mains in 1936 while conducting botanical investigations.

Paratypes: UMMZ 66226 (4 specimens): same data as the holotype.

T. fistulosus appears to be most closely related to *T. simulacrum*. Characters which separate these two species from the other species of the genus are the presence of a basal carina and fine axial sculpture.

T. fistulosus is separated from *T. simulacrum* on the basis of five characters: (1) the diameter of the fourth from the last whorl is about 0.60 times the diameter of the last whorl; (2) the aperture is 7.45-9.50 mm. in diameter; (3) the collar is relatively narrow, 0.10-0.24 times the diameter of the aperture; (4) the pseudosiphon is a rectangular indentation; (5) the basal carina is larger in circumference, passing in front of the reflected outer peristome, and continuing to the last quarter of the last whorl (Pl. I, fig. 3).

T. simulacrum may be recognized by the following characters: (1) the diameter of the fourth from the last whorl is about 0.75 times the diameter of the last whorl; (2) the aperture is 5.73-7.13 mm. in diameter; (3) the relative width of the collar is 0.24-0.38 times the diameter of the aperture; (4) the pseudosiphon is circular, and is open or closed; (5) the basal carina is smaller in circumference, passes beneath or behind the reflected outer peristome, and extends only a little beyond the last half of the last whorl.

TOMOCYCLUS SIMULACRUM (Morelet)

Cyclostoma simulacrum Morelet, 1849, Test. Nov. Insul. Cub. Amer. Cent.: 22 (Type locality: Petén, Guatemala).

Cyclostoma copanense Sowerby, 1850, Thes. Conchyl., 1 (Suppl.): 165, pl. 13B, figs. 310, 311 (Type locality: Coban, Guatemala).

Megalomastoma simulacrum var. *minus* von Martens, 1890, Biol. Cent. Amer., 9: 10.

Megalomastoma simulacrum var. *gracilis* von Martens, 1890, Biol. Cent. Amer., 9: 10 (Type locality: between Tactic and Tamahu, Guatemala).

Tomocyclus siphonis Bartsch and Morrison, 1942, Bull. U. S. Nat. Mus., 181: 145, pl. 19, fig. 5 (Type locality: Alta Vera Paz, Guatemala).

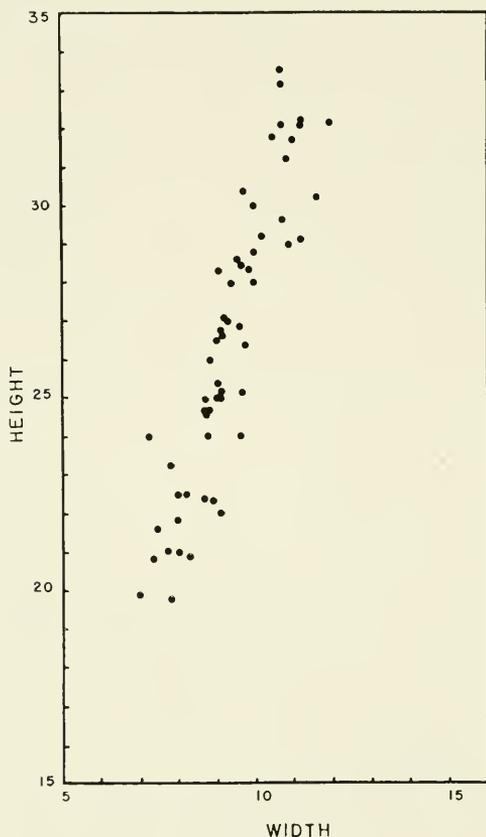
Tomocyclus constrictus Bartsch and Morrison, 1942, Bull. U. S. Nat. Mus., 181: 145-146, pl. 19, fig. 2 (Type locality: Coban, Guatemala).

Shell cinnamon or rosy, early whorls and last half of last whorl dull yellow brown; opaque or only slightly translucent; of moderate or large size (measurements of height and width, and their relationship, are expressed in Text-figure 1); pupiform to elongate-turrite; decollate, 4-8 whorls remaining; spire nearly straight sided or moderately convex (Bartsch and Morrison, 1942: pl. 19, figs. 2, 3, 5, 6); diameter of fourth whorl about 0.75 times the diameter of last whorl; whorls convex, depth of suture variable, usually moderately impressed; whorls crossed by numerous fine posteriorly arched axial striations, which continue onto reflected peristome; raised spiral sculpture only faintly evident at irregular intervals; base of last whorl with a distinct carina which passes below or behind the reflected outer peristome, carina usually evident only on earlier half of last whorl; peristome double; outer peristome usually forming a broad, irregular collar 1.55-2.89 mm. wide, 0.24-0.38 times the diameter of the aperture; face of collar dull white, with a few annulations which are usually distinguishable only near the inner peristome; parietal region of collar with a pseudosiphon which may vary from an open crescent to a round hole connected to the outside by a narrow slit; aperture dull white, circular, 5.73-7.13 mm. wide; columella tubular, spiral, open at first remaining whorl, and at umbilicus as a circular chink.

T. simulacrum is highly variable, as is indicated by its lengthy synonymy. The name proposed by Morelet has been properly applied by subsequent authors. *Cyclostoma copanense* Sowerby was described as being smaller than *simulacrum*. Later authors found that the two forms were not as distinct as Sowerby believed, and Fischer and Crosse (1886: 121), von Martens (1890: 10) and Kobelt (1902: 271) considered *copanense* as a variety

of *simulacrum*. Recently, Bartsch and Morrison (1942: 147-148) reallocated *copanense* to specific status. Specimens under 27 mm. in total length were assigned to *copanense*, and specimens over 35 mm. in total length were assigned to *simulacrum*.

As is demonstrated in the diagram (Text-figure 1) no significant difference in size will distinguish the two forms. Different specimens in various lots are represented near both extremes



Text-figure 1

This diagram demonstrates the relationship between height and width of the shell of *Tomocyclus simulacrum* (Morelet). Measurements of height were made to include the last four remaining whorls. Measurements of width are standard. All measurements are in millimeters.

of the same graph, and the remaining specimens in these same lots are represented at many intermediate loci. Since such variability of size commonly occurs within a single lot, *copanense* cannot be recognized even as a variety of *simulacrum*.

Megalomastoma simulacrum var. *minus* was proposed by von Martens as a synonym of *copanense*. This is clear by his use of the two names. *Megalomastoma simulacrum* var. *gracilis* is also indistinguishable from *simulacrum*, for the slight difference of shape used to separate the two forms is highly variable and lots containing only a few specimens cannot be satisfactorily sorted into two groups by use of this character.

Tomocyclus siphonis Bartsch and Morrison was distinguished from *simulacrum* by the presence of a closed pseudosiphon as opposed to an open one. Comparison of the type of *siphonis* (USNM 162511) with many specimens of *simulacrum* shows that this character varies from a completely enclosed hole connected to the outside by a narrow slit, to a broad open crescent. The distinction between a closed and an open pseudosiphon is obscured by many intermediate stages, thus preventing the differentiation between *siphonis* and *simulacrum*.

Tomocyclus constrictus Bartsch and Morrison was recognized on the basis of a closed pseudosiphon and a relatively deeply impressed suture. As shown above, the nature of the pseudosiphon is an unreliable character. The degree of impression of the suture is also variable. Several lots examined contain specimens that completely bridge the difference from a deep suture with strongly rounded whorls, to a shallow suture with slightly convex whorls. Occasional specimens have a deep suture between the early whorls, and a shallow suture between the later whorls. Thus, *constrictus* cannot be separated from *simulacrum*.

Specimens examined. MEXICO: no additional data, UMMZ 87073 (2). GUATEMALA: no additional data, ANSP 45643 (3), UMMZ 87075 (1), UMMZ 87076 (1). *Atta Vera Paz*: Chama, ANSP 13105 (1), ANSP 13107 (3), USNM 484861 (1); Coban, MCZ 10061 (6), MCZ ex Bland (4), MCZ ex Robson (2), MCZ ex Bequaert (6), USNM 250693 (4), USNM 516028 (1); Samac, USNM 515763 (2); Finca de Providencia, USNM 32070 (2), USNM 203656 (1), USNM 316385 (3), USNM 321005 (1), USNM 321030 (1), USNM 515764 (1); nr. Arroya Yalchaitla, 4 mi. sw of Seiba, UMMZ 64717 (2); 1 km. n of Hacienda Finca Samac, UMMZ 132317 (2); 55 mi. ne Coban, UMMZ 195169 (1); nr. Chinaja, UMMZ 208413 (1). *El Quiché*: 4-6

km. w of Hacienda Finca Pacala, UMMZ 132318 (5). NO DATA: MCZ 4592 (1), MCZ 6791 (4), MCZ 148330 (3), USNM 365365 (1).

TOMOICYCLUS LUNAE Bartsch

Tomocyclus guatemalensis (in part) Fischer and Crosse, 1886, Miss. Sci. Mex. Amer. Cent., 2: 124, pl. 40, fig. 11a.

Tomocyclus lunae Bartsch, 1945, Proc. Biol. Soc. Wash., 58: 63.

Type locality: Santecomapan, Veracruz, Mexico.

Specimens examined. MEXICO: Veracruz: south slope Volcan San Martin, 1040 ft. alt., UMMZ 195170 (1); Volcan San Martin, MCZ (1).

TOMOICYCLUS GUATEMALENSIS (Pfeiffer)

Cyclostoma guatemalensis Pfeiffer, 1851, Proc. Zool. Soc. Lond.: 245.

Megalomastoma guatemalensis Pfeiffer, 1852, Monog. Pneumon. Vivent., 1: 132.

Tomocyclus guatemalensis (Pfeiffer), Crosse and Fischer, 1872, Jour. Conchyl., 20: 76; Fischer and Crosse, 1886, Miss. Sci. Mex. Amer. Cent., 2: 124, pl. 40, fig. 11.

Type locality: Vera Paz, Guatemala.

Known only from the type locality.

T. guatemalensis is of doubtful status. I have seen only a single specimen identified as this species (UMMZ 87072, ex Bryant Walker). In most respects this form resembles *T. simulacrum*, but it lacks the basal carina that is present in that species. The distinction between *T. guatemalensis* and *T. lunae* is also uncertain, for the characters used by Bartsch (1945) to separate these two species are subject to variation.

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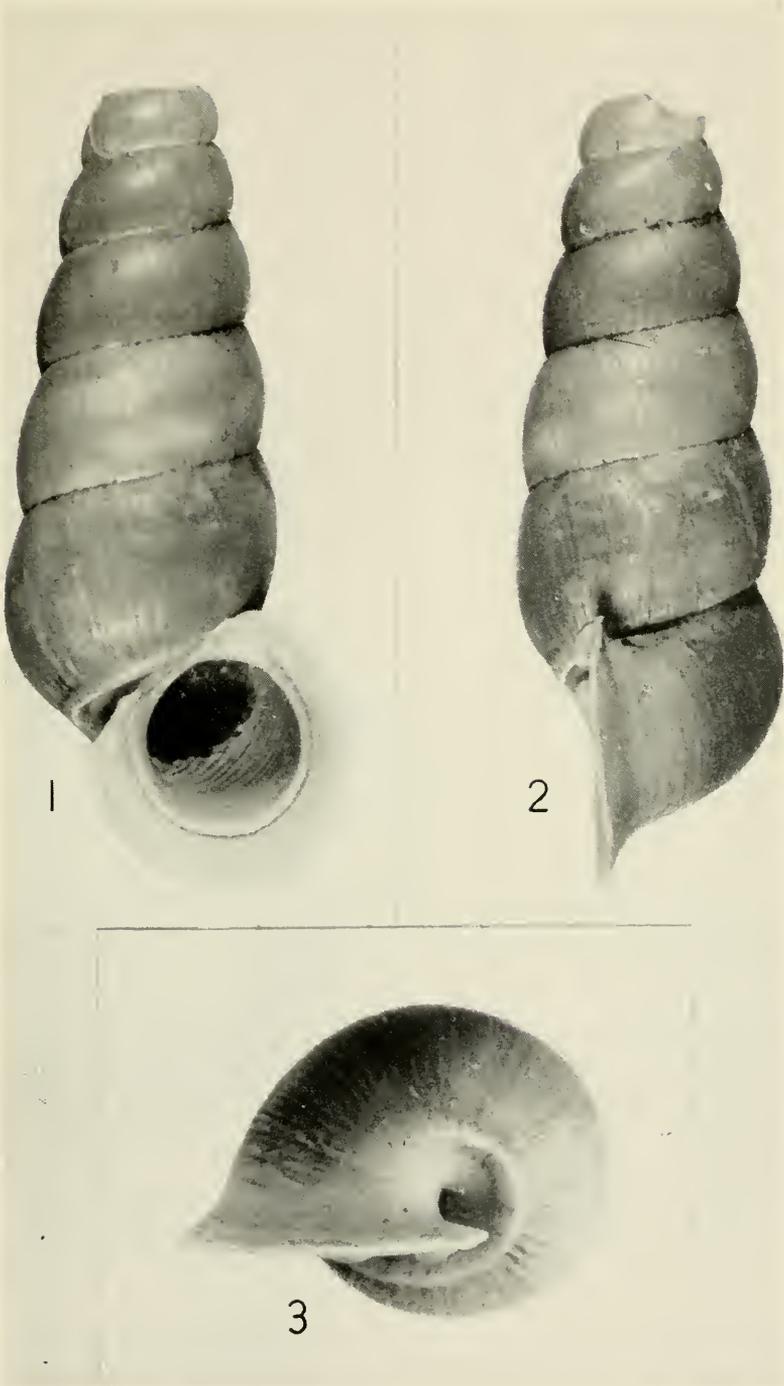
Plate I

Holotype of *Tomocyclus fistulosus*, new species (UMMZ 194095); high rainforest at Vallentine Camp, 50 miles Southwest of Cayo, British Honduras.

Fig. 1. Frontal view.

Fig. 2. Lateral view.

Fig. 3. Basal view.



B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS.

FEBRUARY 1, 1963

NUMBER 182

BIRDS FROM FLORES. LESSER SUNDA ISLANDS

By RAYMOND A. PAYNTER, JR.

During recent years the Museum of Comparative Zoology has received from the Rev. J. A. J. Verheijen, S.V.D., several collections of birds from the western part of Flores Island. Without using a gun, Father Verheijen and his local assistants have secured representatives of 70 species. Eleven of these have not been previously recorded from the island and several others are of taxonomic importance. It is the purpose of this paper to note briefly these more interesting species.

NYCTICORAX CALEDONICUS subsp.

A bird in partial adult plumage was snared at Tjantjar, Rahong, on 19 May 1957. Until 1940, when an example of *N. caledonicus* was found paired with one of *N. nycticorax* in western Java (Hoogerwerf, 1952), this night-heron was not known west of Timor. This is the only record from Flores.

DENDROCYGNA JAVANICA

A wing has been preserved of a bird collected in 1956. Sumbawa is the farthest east it had been recorded previously.

ELANUS CAERULEUS subsp.

The easternmost localities for this hawk were Sumba and Celebes. A nestling, just about to fledge, was taken near Ruteng, at about 1000 meters, in July, 1957.

RALLUS PECTORALIS EXSUL

Three birds, the first known since the type specimen was secured, were collected in 1958 and 1959. One is an adult; unfortunately it was not sexed. The other two are juvenals which

have little barring on the ventrum, lack the rufescent head, and have no bright olive margins to the feathers of the back.

I have examined two specimens of *Rallus mirificus* Parkes and Amadon (1959) from Luzon, Philippine Islands, and believe that this form is a race of *R. pectoralis*. From Australia through New Guinea to Flores, *R. pectoralis* exhibits a fairly orderly cline of decreasing dorsal streaking, darkening head color, and shortening of the dorsal feathers. The characters of *mirificus* are the culmination of these trends and are those one might have predicted at the end of a cline extending from Australia to the Philippines. The differences between the Philippine bird and the Australian races are marked, but the subspecies from Flores is almost perfectly intermediate. Additional races may well be discovered between Luzon and Flores, showing that the cline is less disjunctive than it now appears. Support for this prediction may be found in the knowledge that *R. p. mirificus* remained unknown until only four years ago, in spite of its presence within 50 miles of Manila, long a center of ornithological research.

PORZANA PUSILLA PUSILLA

Three specimens were collected: two at Tjara in late April and mid-May, 1957, and one at Wangjung in late April, 1956. One is a male, and two were not sexed, but on plumage characters these seem to be a male and a female. The species apparently breeds on Flores, although there are no prior records of its presence.

It may be that these specimens represent an undescribed race. However, our birds are too poorly preserved and few in number to be certain that the apparent racial characters are real. The specimens are close to nominate *pusilla* but are somewhat darker dorsally, with more extensive black centers to the feathers, particularly on the tail, and have heavier, but not longer, bills. The pale area on the chin and upper throat of the males seems whiter and more sharply demarcated than in the nominate form. The bills of two birds are black with very narrow yellowish markings on the anterior edges of both the maxilla and mandible. The third specimen is similar but also has a small pale area near the tip of the mandible. In a series of 26 specimens of *P. p. pusilla* one has a bill similarly colored to the third Flores bird, and none of the series resembles the other two birds.

The dried legs of the Flores specimens are considerably darker than any of *P. p. pusilla*.

The three birds from Flores are easily distinguished from *mayri* of New Guinea and from *palustris* of Australia by their larger size (wing 84-86 mm.). I have not seen an example of *mira*, from East Borneo, but the original description (Riley, 1938) notes that the bill is olive-yellow and bronze, which seems vastly different from the Flores birds.

POLIOLIMNAS CINEREUS CINEREUS

This widespread rail is new for Flores.

GALLICREX CINEREA

A specimen was collected at Tjantjar on 14 May 1957. The species apparently has not been found before on the Malay Archipelago east of Java, where it seems to be a winter visitor (Kuroda, 1936). Its presence on Flores in mid-May suggests that it may breed there but, unfortunately, the gonads of our specimen were not examined.

GALLINULA CHLOROPUS ORIENTALIS

Nine specimens were collected, one of which contained an egg in mid-May. No prior records from Flores exist.

ROSTRATULA BENGHALENSIS BENGHALENSIS

This is another bird not reported from the island before and which represents an eastward range extension. A specimen collected in July was breeding.

GALLINAGO STENURA

Three specimens establish this snipe as a winter visitor on Flores.

GALLINAGO MEGALA

A long series, collected over several winters, represents a new record for the island.

OTUS (BAKKAMOENA) SILVICOLA

This endemic owl is probably a giant geographical representative of *O. bakkamoena*. It is similar to *O. b. semitorques* of Japan, but it is considerably larger and lacks the buff crescent on the upper back. This was noted by Hartert (1897), who also

remarked on the similarity of *silvicola* to *O. b. whiteheadi* of Luzon. The Philippine form has a white hindneck and is darker below than *silvicola*, but in size more nearly approaches the Flores bird than any other race of *O. bakkamoena*. Compared to the geographically closer Javan and Bornean populations, *silvicola* is markedly larger. This is suggestive of the situation in the Philippines, where *whiteheadi* is considerably larger than any nearby races.

TYTO CAPENSIS subsp.

A specimen obtained in March, 1956, is the first record of the species from the Sunda Islands, thus confirming Hartert's suggestion (1929) that it might some day be found there.

I am following Amadon and Jewett (1946) in treating *longimembris* and *capensis* as conspecific.

In view of the variability of the species and the paucity of material, particularly from the southwest Pacific, I am reluctant to assign this specimen to any race. Amadon (1959) tentatively placed two individuals from Celebes and Kalidupa with *T. c. walleri* (type locality Queensland); the Flores bird may also belong here.

CORACINA DOHERTYI

An immature bird was collected in early March. Rensch (1931) recorded several specimens from the island, but Flores was inadvertently omitted from the range of the species as given in Volume 9 of the "Check-list of Birds of the World" (Mayr and Greenway, 1960).

ACKNOWLEDGEMENTS

I am grateful to James C. Greenway, Jr. and Ernst Mayr for assistance with several problems, and to Father Verheijen for depositing his collection in this museum. Dean Amadon generously lent specimens from the collections of the American Museum of Natural History.

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B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS.

MARCH 12, 1963

NUMBER 183

AUSTRALIAN CARABID BEETLES XIII. FURTHER NOTES ON AGONINI, AND A GENUS OF LICININI NEW TO AUSTRALIA

BY P. J. DARLINGTON, JR.

Museum of Comparative Zoology, Cambridge, Mass.

Since publication of my "Notes on the [Australian] Agonini" (1956) I have spent nineteen months in Australia (Dec. 1956-June 1958), mostly collecting in the eastern forested areas. My itinerary, with list of localities, is summarized in a recent paper (1961). The following additional notes on Agonini are based on material secured during this trip and borrowed from the Queensland Museum, and on examination of some of Sloane's types. The most exciting new discovery is an Australian species of the Indian genus *Dilonchus*, which is a licinine rather than an agonine but which is in some ways suitable to be ancestral to the supposedly agonine genus *Homothes*. The finding of dimorphism of "fixed" setae in *Notagonum macleayi* (Sloane) is noteworthy too.

Tribe AGONINI

Before considering the Agonini proper, I have to say that one supposed Australian agonine does not belong in this tribe. It is:

COPTOGLOSSUS CARTERI (Sloane) (new combination)

Platynus carteri Sloane 1915, p. 460.

The type of this species, from Dorrigo, New South Wales, is in the Sloane Collection at Canberra. I have compared one of my specimens with it. It is a broad, depressed, dull black carab that looks superficially as if it might be either an agonine or a lebiine. The elytra are broadly rounded apically, not obliquely

truncate as usual in Lebiini, but this is not an invariable tribal character. Two other characters show that the insect is a lebiine and that Sloane was wrong in assigning it to the Agonini ("Sphodrini"). One character is that the middle tibiae are sparsely pubescent rather than spinose externally. The other is that the basal bulb of the aedeagus is small and not much bent down, not large and strongly curved as in the Agonini. "*Platynus*" *carteri* Sloane should therefore be transferred to the tribe Lebiini, where it can be placed tentatively in the genus *Coproglossus*.

NOTAGONUM Darlington

Darlington 1952, p. 127.

In my recent collecting I found 4 species assignable to *Notagonum* in tropical North Queensland. However, this is a genus of convenience, and I am not sure that these species are all related to each other. They may represent 4 independent stocks, so far as the Australian fauna is concerned. The 4 species are distinguished in the key and briefly discussed thereafter. In addition, the following agonines were found in North Queensland: *Lorostenma* ("*Platynus*") *cooki* (Sloane), distinguished from *Notagonum* by sole of hind tarsus with a single, regular row of bristles on each side; *Dicranoneus queenslandicus* (Sloane), a slender brown agonine with toothed tarsal claws; *Violagonum* ("*Colpodes*") *violaceum* (Chaudoir), a blue or purple species with spined elytra; *Colpodes habilis* Sloane, larger, with bright green elytra; the well known *Homothes*; and *Odontagonum*, a convex, shining black, flightless agonine with dentate humeri.

Key to Species of NOTAGONUM of North Queensland

1. Slender; head more than .75 width prothorax; 4th segment hind tarsus broadly emarginate (Fig. 5); (length *c.* 9.5 mm.) *submetallicum*
- Less slender; head less than .75 width prothorax; 4th segment hind tarsus narrower, usually more lobed 2
2. Larger (9-10 mm); aeneous, elytral striae shallow, intervals flat *lafertei*
- Smaller (6-8 mm.); brown, sometimes slightly iridescent, but not aeneous; elytral striae deeper, intervals slightly convex 3
3. Apex of elytron not subtruncate, usually not distinctly denticulate (Fig. 9); 4th segment hind tarsus wider apically, with angle between lobes *c.* right (Fig. 4). *macleayi*

- Apex of elytron subtruncate, usually denticulate (Fig. 10); 4th segment hind tarsus oval, strongly narrowed apically, with angle between lobes acute (Fig. 3) *dentellum*

NOTAGONUM SUBMETALLICUM (White) (new combination)

Colpodes submetallicus White 1846, p. 2.

This is a very common species in south temperate Australia and Tasmania, and it occurs also in New Zealand. It lives in a variety of situations on the ground by water. It is apparently rare in tropical Australia but does occur there. I found 2 specimens by tramping down tall grass and thick herbage growing in sluggishly flowing water in open country near Atherton, North Queensland, in February, 1958. This is an example of a phenomenon which is probably zoogeographically significant: penetration of the tropics by a temperate carabid associated with water. Some other, north temperate Carabidae seem to have crossed the whole width of the tropics in waterside habitats. I have recently given examples in *Bembidion* and the Trechini (1959, esp. pp. 332, 342).

NOTAGONUM LAFERTEI (Montrouzier) (new combination)

Anchomenus lafertei Montrouzier 1860, p. 238.

Although *lafertei* has been placed in *Colpodes*, the 4th hind tarsal segment is only weakly lobed (Fig. 6). I tentatively assign the species to *Notagonum* because of absence of any obvious distinguishing characters. *N. lafertei* is common from the vicinity of Cooktown south through Queensland and part of New South Wales. I did not find it on the Cape York Peninsula north of Cooktown and it is unknown in New Guinea, but it occurs on New Caledonia. It is frequently found with the two following species in debris and among dead leaves on the ground by water, but it often occurs also away from water and in more arboreal habitats, especially in clumps of wilted leaves on fallen trees in rain forest.

NOTAGONUM MACLEAYI (Sloane) (new combination)

Platynus macleayi Sloane 1910, p. 454.

Sloane described *macleayi* from Kuranda, North Queensland. The type in the Sloane Collection is now reduced to one elytron

which, however, is identifiable. I have topotypes, one of which matches the type elytron almost exactly. (The form of the elytral apex is somewhat variable in both this and the following species but does serve to identify most individuals satisfactorily.)

This species is unknown in New Guinea and I did not find it near the tip of Cape York, but it occurs from the mid-peninsular forests (Iron Range, Rocky Scrub, etc.) south to the Atherton Tableland and the Kirrama Range, which is west of Cardwell. It lives beside brooks and rivers, often in masses of drift caught on obstructions above the water or in accumulations of dead leaves deposited on stream banks at bends or beside pools.

N. macleayi proves to be dimorphic in presence or absence of anterior lateral prothoracic and anterior discal elytral setae (Figs. 1, 1A). These particular setae are apparently inherited as a group: all 4 of them are present or all absent in most individuals. This dimorphism is presumably due to a single mutation inherited in Mendelian fashion. The only possible exception to strict dimorphism is a female from Shipton's Flat which lacks the setae in question except for an apparent trace of the anterior discal elytral puncture on the right elytron only. With this exception, my 48 specimens of the species divide as follows.

<i>Locality</i>	<i>With designated setae</i>	<i>Without designated setae</i>
Tozer Gap (W. of Iron Range)	3 ♀ ♀	1 ♀
Iron Range	16 ♂ ♂, 12 ♀ ♀	
Rocky River	3 ♂ ♂	

Shipton's Flat (S. of Cooktown)	1 ♂	3 ♀ ♀
Kuranda	2 ♂ ♂	2 ♂ ♂, 3 ♀ ♀
Kirrama Range	1 ♂	

These figures suggest that the population of *macleayi* in the base-of-peninsular forests (from the Atherton Tableland to near Cooktown, tabulated below the broken line) includes a considerable proportion of individuals without the setae in question, but that the population in the mid-peninsular forests of the Cape York peninsula (tabulated above the broken line) includes only an occasional individual that has lost setae.

In my paper on New Guinean Agonini (1952, pp. 89-252) I used presence or absence of the anterior lateral prothoracic setae

as a character to help distinguish genera, especially to distinguish the two "genera of convenience" *Notagonum* and *Allagonum*. However, I made it clear in that paper (bottom of p. 97) that the character was only a useful "tag" and not a character of generic value in itself. The setae in question are not known to vary in any species of agonine in New Guinea, and they do provide useful tags for dividing the New Guinean species into convenient groups.

NOTAGONUM DENTELLUM Darlington

Darlington 1952, p. 147.

In New Guinea, this species is common, widely distributed, and somewhat variable. In Australia, it occurs from the tip of the Cape York Peninsula (Loekerbie and Bamaga) south to the Atherton Tableland and the Kirrama Range. It lives in about the same situations as the preceding species.

COLPODES HABILIS Sloane

Sloane 1907, pp. 178, 179.

Darlington 1952, p. 164.

Colpodes habilis is black with green elytra and is 13-17 mm. long (in New Guinea). It has a wide range in the eastern Malay Archipelago, including Buru, New Guinea, New Britain, the Solomons, and the Santa Cruz Islands. It has not previously been reported from Australia, but I have seen specimens from Cairns District, Coen, and Port Douglas (near Mossman) (all in the Queensland Museum), and an individual flew into the lighted window of a house where I was staying in Cairns in February, 1958. The species' usual habitat (in New Guinea) is in foliage, including clumps of wilted leaves on fallen trees in rain forest.

ODONTAGONUM NIGRUM Darlington

Darlington 1956, p. 9.

This flightless species is the type of a very distinct monotypic genus of unknown relationships. It was described from three individuals from Millaa Millaa and Lake Barrine, on the Atherton Tableland, North Queensland. It proves to be fairly widely distributed on the Tableland but apparently does not reach either the Dividing Range west of Atherton or the vicinity of Kuranda, although apparently suitable rain forests exist in both these places. It lives on the ground in rain forest.

Tribe LICININI

DILONCHUS Andrewes

Andrewes 1936, p. 179.

This genus was proposed for one medium sized *Agonum*-like species from India. The Australian species described below seems congeneric. It combines characters of the tribe Licinini with color pattern suggesting *Homothec*. Generic characters are included in the following specific description, and the place of the genus among other Australian Licinini is discussed after the description.

DILONCIUS PICTUS n. sp.

Form (Fig. 2) like *Agonum* but with elytra more ample; color black; reflexed margins of prothorax testaceous; elytra with humeri, epipleuri, and outer margins testaceous, the pale color extending to the 9th intervals anteriorly and forming separated spots on these intervals posteriorly; a small testaceous spot at each dorsal seta; lower surface testaceous with episterna more or less darker; femora pale, tibiae, tarsi, antennae, and palpi browner; upper surface rather dull, with close reticulate micro-sculpture isodiametric on head and pronotum and slightly transverse on elytra.

Head short, .66 & .64 width prothorax (from measurement of ♂ type and ♀ paratype); mandibles slightly sinuate externally, then abruptly curved and bent down toward apex, each with very large triangular inner tooth and short terebra; eyes large and prominent; 2 supra-ocular setae each side; antennae slender, pubescent from near base 4th segment, with segment 1 c. 5 X long as wide, segments 3 and 4 slightly shorter and subequal, segment 2 much shorter; maxillary palpi with last segment somewhat thickened, labial palpi with last segment subsecuriform in both sexes (wider than in *bidens*); clypeus truncate or nearly so; labrum moderately emarginate, 4-setose; front nearly evenly convex, with neck impression and frontal impressions weak, clypeal suture finely impressed; mentum joining gula without distinct intervening sclerites, broadly emarginate, without tooth.

Prothorax: width/length 1.29 & 1.33; base/apex 1.39 & 1.41; base/head 1.31 & 1.33; apex broadly emarginate; anterior angles not otherwise advanced, moderately rounded; base very broadly

arcuate, almost truncate at middle; sides broadly rounded anteriorly, slightly so posteriorly, slightly sinuate before posterior angles; latter slightly obtuse, slightly blunted; lateral margins rather wide, moderately reflexed, each with usual 2 setae about $1/3$ from apex and at basal angle; disc moderately convex, depressed at sides, margined at base and apex; median line distinct, apical and basal transverse impressions weak; surface faintly sparsely transversely wrinkled at middle, more strongly longitudinally so at apex and base; basal foveae broad, not well defined, impunctate or nearly so. *Elytra* long-oval, about $2/3$ wider than prothorax (E/P — & 1.64); anterior margin entire, humeral margins vaguely angulate, lateral margins slightly sinuate before apex but not interrupted, apices simple; scutellar striae well developed; striae entire, impunctate; intervals nearly flat, not specially modified; no 10th interval; 3rd interval 2-punctate near 2nd stria behind basal $1/3$ and near apical $1/3$. Inner wings fully developed. Legs slender; tibiae spinescent; hind tibiae not specially grooved externally; hind tarsi with first 3 segments finely grooved each side above, 4th segment shallowly emarginate but not lobed, 5th segment with conspicuous accessory setae; claws simple; sole of hind tarsus with a single regular row of setae each side. Secondary sexual characters: ♂ with first 3 segments each front tarsus dilated, squamulose below, the squamae small and forming 4 longitudinal rows; ♂ with apparently only 1, ♀ with 4 or 5 (asymmetrical) setae near apex each side last ventral segment. Length *c.* 7.5-8.0; width *c.* 3.1-3.3 mm.

Holotype ♂ (M. C. Z. Type No. 30,394) from Longlands Gap, Atherton Tableland, North Queensland, about 3000 ft. altitude, Feb. 1958; and 1 ♀ paratype from Kirrama Range, W. of Cardwell, North Queensland, about 2000 ft. altitude, Dec. 1957. Both specimens taken by myself in accumulations of dead leaves on the ground under the heads of small fallen trees in partly felled rain forest. The ♂ type is teneral and warped, so that width of elytra cannot be measured and the genitalia cannot be dissected.

This species runs to *Microferonia* in Sloane's (1898, p. 488) key to Australian genera of Liciniini but has a more *Agonum*-like form, simpler clypeus (almost truncate, with only a narrow transverse membrane anteriorly), longer and less emarginate labrum, more distinct subapical sinuations of elytra, longer scutellar striae (these are characters of *Dilonchus*), and different color pattern. As compared with the genotype of *Dilonchus* (*bidens*

Andrewes, of which I have a cotype), the new Australian species has a relatively narrower prothorax with better defined posterior angles, more distinct elytral microsculpture, wider last segment of labial palpi, and more extensive elytral markings. However *bidens* has indications of the same pattern of markings, especially laterally, that *pictus* has. (Two apparent errors in Andrewes' description of *bidens* should be noted. The insect is not apterous. My "cotype" has fully developed inner wings. And the elypeus is probably not emarginate. It seems squarely truncate in front but semicircularly impressed, and the impressed area is pale and easily mistaken for an emargination — but dissection would be necessary to make sure of this detail.)

The rather *Agonum*-like form, untoothed mentum, and *Homothes*-like color pattern (and habitat) together suggest that the present new species may represent the ancestral stock of *Homothes*. If so, *Homothes* has lost some of the specializations (of mouth parts) that characterize most Licinini, while developing other specializations of its own, some of which suggest agonine rather than licinine affinities. To determine the inter-relationship (if any) and probable evolution of *Dilonehus* and *Homothes* would require both more material and more time than I now have.

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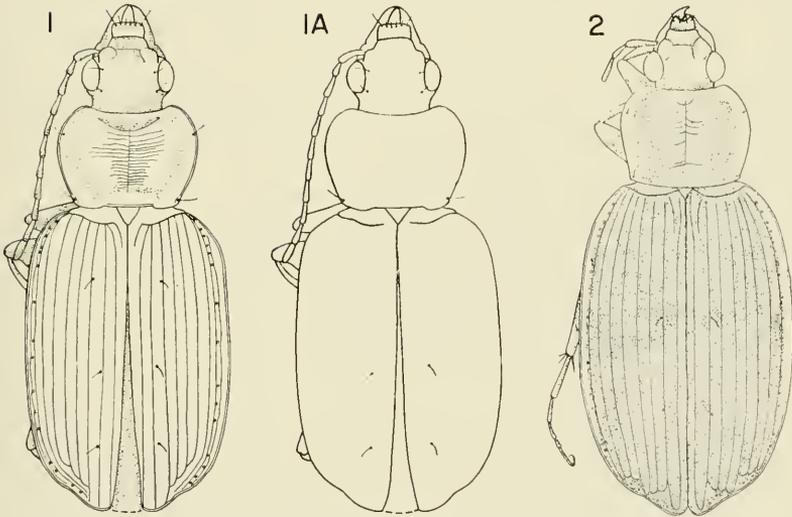


Fig. 1. *Notagonum macleayi* (Sl.), with full complement of setae.

Fig. 1A. Same, outline with anterior lateral pronotal and anterior discal elytral setae absent.

Fig. 2. *Dilonchus pictus* n. sp.

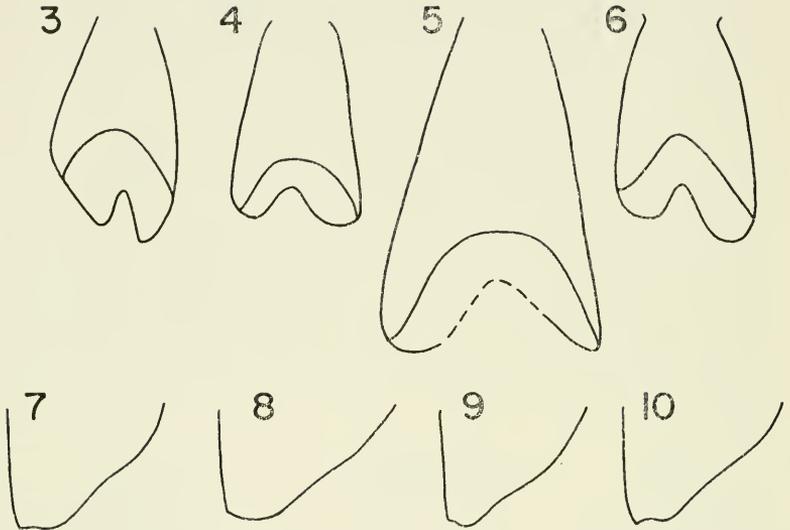


Fig. 3. Fourth segment right hind tarsus, outline from above with setae omitted, of *Notagonum dentellum* Darl.

Fig. 4. Same of *Notagonum macleayi* (Sl.).

Fig. 5. Same of *Notagonum submetallicum* (White).

Fig. 6. Same of *Notagonum lafertei* (Montr.).

Fig. 7. Apex right elytron of *Notagonum submetallicum* (White).

Fig. 8. Same of *Notagonum lafertei* (Montr.).

Fig. 9. Same of *Notagonum macleayi* (Sl.).

Fig. 10. Same of *Notagonum dentellum* Darl.

B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS.

APRIL 18, 1963

NUMBER 184

BEHAVIOR AS A TAXONOMIC CLUE: RELATIONSHIPS OF *LISSONYCTERIS* (CHIROPTERA)

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Re-examination of the generic status and relationships of *Rousettus*, *sensu stricto*, and *Lissonycteris*, a supposed subgenus of *Rousettus*, has been prompted by the great differences observed between live specimens of the two genera. In 1955 and 1956, Novick was able to make extensive observations of living bats not only of these two genera but of six other pteropids as well (Novick, 1958). Of these, according to Andersen (1912), *Eidolon helvum* and *Pteropus g. giganteus* as well as *Rousettus* belong in the *Rousettus* section of the Pteropinae, *Cynopterus brachyotis luzonicensis*, *Cynopterus sphinx cyclonensis*, and *Ptenochirus jagorii* belong in the *Cynopterus* section of the Pteropinae, while *Eonycteris spelaea glandifera*, *Eonycteris robusta*, and *Macroglossus l. lagochilus* are in the subfamily Macroglossinae.

BEHAVIORAL COMPARISONS

A single wild colony of about twenty *Lissonycteris angolensis* was observed in the Belgian Congo and various wild colonies of *Rousettus amplexicaudatus*, *R. seminudus*, and *R. acgyptiacus* were observed in the Philippines, Ceylon, and the Belgian Congo, respectively. Two *Lissonycteris angolensis* were captured

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and one, a mature female, lived in captivity for fifteen months. Many *R. aegyptiacus* were also taken alive and observed for a period of some weeks in the Belgian Congo. One, a mature male, was kept for over nine months concurrently with the *Lissonycteris* mentioned above. In addition, some six *R. seminudus* and a dozen *R. amplexicaudatus* were observed in captivity for periods of six weeks to more than three months.

From the very first, the differences in behavior of *Lissonycteris* and *Roussettus* were grossly apparent. These can best be described as differences in limb use and in orientation.

LIMB USE

Roussettus ordinarily occupy dimly lighted caves with large entrances and sheltered retreats. Here they commonly hang in large clusters along the walls or ceiling. On the wall, they hang by their hind feet with their legs so turned that their backs are to the wall, their wings folded at their sides. They take flight by swinging their body up and rotating around their feet which remain temporarily in position here though the legs are now crossed. This position is well illustrated by Kulzer (1958), in an excellent paper on the biology of *Roussettus*. *Roussettus* also roost in crevices. Here one cannot see their undisturbed resting position but they must use all four limbs in entering and leaving such crevices. *Roussettus* can fold their wings considerably and walk awkwardly on their wrists and hind feet or they can climb vertically, head first, or move along the irregular surface of a cave or crevice ceiling using the claws of their thumbs and hind feet. When *Roussettus* roost in trees, as they do when disturbed in their caves or at night when feeding, they almost always hang by both hind feet plus one or both thumbs in a sloth-like position, one foot and one thumb on each side of the branch and their wings folded. They frequently move along the underside of the branch in this position using all four limbs. Thus, wild *Roussettus* use their wrists for walking and their thumbs for climbing, roosting, and moving along the underside of branches or fruits.

Captive *Roussettus* would roost in all of the positions described above. When they were exposed to light, they would frequently crawl into a corner of the cage floor or into their feeding dish where they would press themselves as closely as possible against their surroundings, avoiding the light on their eyes. Crawling is a not uncommon mode of locomotion for *Roussettus*, whether

restricted to a cage or allowed to move freely about a room. While feeding, for example, they would crawl between the hands of a stem of bananas. In addition, they occasionally used their wrists and thumbs as pushers to readjust morsels of fruit in their mouths and *R. aegyptiacus* once was seen using the claws of one hind foot to manipulate the food in its mouth.

Lissonycteris never use their wings for locomotion other than flight. In the wild, and in captivity in a large flight room, *Lissonycteris* always roosted hanging free from the ceiling or a branch or, occasionally, hanging from an irregularity of the wall, their ventral surface out as with *Roussettus*, but never using their wrists or thumbs for support and never entering a crevice. *Lissonycteris* would hang from a branch or the ceiling by the claws of one or both hind feet. If they used both feet, characteristically both would be on the same side of the branch or irregularity. *Lissonycteris* seemed incapable of folding their wings tightly as *Roussettus* do; when roosting they hold their wings only slightly folded enveloping their ventral surface (see Fig. 5).

Lissonycteris were incapable of walking or climbing since both activities require that the wrists or thumbs be used. They moved along their roost only by releasing their hold with one foot, moving this foot along to a new hold and then following with the other foot. Such movements, always slow and inefficient, were suitable only for slightly changing their roosting position. *Lissonycteris* never landed on a horizontal surface by choice and, when forced to do so to take its fruit from a dish, its movements were awkward and incompetent. After picking up a piece of fruit, it would flap off without crawling.

Lissonycteris regularly use their hind feet, but rarely their wrists or thumbs, for handling their food. When one was handed a piece of banana, it would grasp this with its teeth. Then, having readjusted its roosting foothold, it would bring one foot down (either one with apparently equal facility) to its mouth and hold the piece of fruit with its widely spread toes while biting or breaking off a manageable fragment (see Fig. 1). Then, while chewing this fragment, it would hold the bulk of the piece of fruit, with its toes, against its chest or abdomen, frequently partly or completely covered by its wings (see Fig. 4). Rarely, when through carelessness or fragmentation it was about to drop the piece of fruit which it was chewing, the bat would regain its tooth-hold by using its wrists and thumbs as awkward pushers. Thus *Roussettus*, *sensu stricto*, differs from *Lissonycteris* in its

use of wrists, thumbs, and hind feet in roosting, climbing, moving along branches, walking, and handling its food.

Among the other pteropids, *Eidolon* and *Pteropus*, though they never enter caves, roost in trees in much the same posture as *Roussettus*, holding on with both hind feet as well as with one or both thumbs. *Eonycteris*, in caves and in captivity, roost and move in all ways like *Roussettus*. In all of these genera the wings can be considerably folded; some also commonly roost with their wings enveloping their ventral surface. Neither *Eidolon* nor *Pteropus* can walk well on horizontal surfaces and both would probably be incapable of entering cave crevices as do *Roussettus* and *Eonycteris*. *Pteropus*, at least, use their wrists and thumbs skillfully to handle fruit and to orient the morsels in their mouth.

Cynopterus, *Ptenochirus* and, to a certain extent, *Macroglossus* also use their limbs very much as does *Lissonycteris*. All three hang from above, by their hind feet only, though, unlike *Lissonycteris*, they appear to use their thumbs for climbing up walls or along branches. The wings of *Cynopterus* and *Macroglossus* do not seem to fold in life any more tightly than those of *Lissonycteris*. Judging from pictures of *Epomophorus* (Allen, Lang, and Chapin, 1917, pl. 46) and the position of *Myonycteris*' wings in alcoholic specimens, their posture in life is also like that of *Lissonycteris*.

Lissonycteris (as also *Cynopterus* and *Ptenochirus*) tended to hold large amounts of food in their cheeks and to carry food to their roost, there to chew very slowly. When required to fly while eating, they would sometimes drop a really large piece. If *Lissonycteris* was holding a piece of fruit with its hind foot, it would either transfer this to its mouth for flight or drop it. *Roussettus* never seemed to store fruit in its cheeks or to fly with any in its mouth but, like *Eonycteris*, *Eidolon*, and *Pteropus*, generally stayed at the food source, biting and worrying off fragments and chewing these at once.

Lissonycteris would chew and crush fruit, such as melon and pineapple, until all of the juice had been expressed and swallowed and then push the remaining small bolus of fiber out of its mouth with its tongue. Banana, being non-fibrous, was swallowed completely after chewing. *Roussettus* usually ate banana and, like *Lissonycteris*, swallowed the whole fruit but when *Roussettus* ate mango, papaya, or melon, unlike *Lissonycteris*, they seemed to swallow the whole substance.

ORIENTATION

Lissonycteris and *Rousettus* differ strikingly in their orientation. *Lissonycteris* orient entirely by vision (Novick, 1958). The captive bat was helpless in the dark and refused to fly in the dark or when blindfolded. When it was forced to fly without vision, by being thrown into the air, it always crashed into the first obstacle it met.

Rousettus amplexicaudatus, *R. seminudus*, and *R. aegyptiacus* all orient visually and acoustically (Möhres and Kulzer, 1956; Kulzer, 1956, 1958; Novick, 1958; Griffin, Novick, and Kornfield, 1958). The single *R. aegyptiacus* observed for over nine months in captivity oriented largely visually in strong light but oriented acoustically in the dark, in dim light, when avoiding intricate obstacles, and when landing or taking off. Such acoustic orientation obviously demands specializations for sound production, emission, reception, and interpretation. The brain, in particular, must be highly specialized for handling acoustic information.

In the pteropids, acoustic orientation has so far been found only in *Rousettus, sensu stricto*, and not in *Eidolon*, *Pteropus*, *Cynopterus*, *Ptenochirus*, *Eonycteris*, *Macroglossus*, or *Lissonycteris* (Novick, 1958). The orientation of *Stenonycteris*, a subgenus of *Rousettus*, has not been observed. The distinctness of *Rousettus*, not only from *Lissonycteris* but from a fair sample of other pteropids as well, is clearly established by its acoustic orientation and the behavioral, physiological, and anatomical features associated with it.

SUMMARY

To summarize, *Lissonycteris* differ from *Rousettus, sensu stricto*, in their roosting posture, in their non-flight locomotion, and in their inability to orient acoustically. Comparing the roosting and locomotory behavior of those bats observed alive, we find that *Rousettus* resembles *Eidolon*, *Pteropus*, and *Eonycteris*, while *Lissonycteris* resembles *Cynopterus* most closely. Brief observation of live epomophorine bats and examination of pictures and preserved specimens of epomophorine bats and of *Myonycteris* suggest that in behavior *Lissonycteris* resembles these bats as well.

MORPHOLOGICAL COMPARISONS

The behavioral differences between the live bats are reinforced by less spectacular, but equally definite, characters of the more conventional taxonomic sort. These make it clear that *Lissonycteris* is far closer to *Myonycteris*, a supposed intermediate genus between the rousettine and cynopterine groups, than to *Roussettus*. They also show that *Lissonycteris* and *Myonycteris* form a natural group probably intermediate between the rousettine and epomophorine groups, and one whose resemblances to the cynopterines are more apparent than real.

The rousettine and cynopterine sections of the Pteropinae are chiefly distinguished by the following characters possessed by the latter and not by the former: The rostrum is shortened and the facial axis is not deflected, M_3 and usually M^2 are lost, the eyes are larger, and there is a tendency to form tubular nostrils. The differences in the ridges of the soft palate described by Andersen (1912, pp. lx, 485, 591, figs. 29A, 50) are also characteristic.

On the basis, largely, of these characters, Andersen points out that *Myonycteris* is somewhat intermediate between the cynopterine and rousettine sections. He says (1912, pp. lvi-lvii): "*Myonycteris* . . . has in many respects remained on the Rousettine level of development, while in others it exhibits modifications approaching those of *Cynopterus*. The general appearance, the dental formula, and the palate ridges are quite or nearly as in *Roussettus*, but the rostrum is conspicuously shortened, the facial axis less deflected, m_3 and m^2 (last lower and upper molar) reduced almost to rudiments, the orbits larger, the nostrils more prominent and the calcar weaker," and later (p. lxi): "The fact is that this genus has retained many characters of *Roussettus*, while in practically all the features in which it differs from *Roussettus* it more or less closely approaches to *Cynopterus*. Whether a genus exhibiting characters of this description ought, in a linear arrangement, to be classed at or near the end of the Rousettine section or as the 'opening' genus of the Cynopterine section, must necessarily remain a matter of opinion."

The resemblance of *Lissonycteris* to *Myonycteris* in all the above traits, except the shortening of the rostrum and reduction of the dentition, was not noted by Andersen when he classified the former as an aberrant form related to but possibly generically distinct from *Roussettus* (*op. cit.*, 1912, p. 814). At the same time he does note (1912, p. xlix): "the brain case [*Lissonycteris*] is peculiarly flattened posteriorly and the facial axis even less

deflected than in *Roussettus*, both characters giving the skull, viewed in profile, a rather striking resemblance to *Epomops*.''

EXTERNAL CHARACTERS

Actually, in addition to the rather generalized myonycterine characters given above, both *Lissonycteris* and *Myonycteris* have a number of traits in common which the small size of *Myonycteris* and the superficial resemblance of *Lissonycteris* to *Roussettus* have tended to mask. Chief among these, externally, is the development of the wing in these two genera which greatly exceeds that of *Roussettus*. Though it is more similar in size to that in *Cynopterus*, it is different in proportions. The size difference shows most conspicuously in the greater length of the combined metacarpal and first phalanx of digits three to five as compared with length of forearm. The following comparison of finger lengths refers only to these two joints. In *Lissonycteris*, the fifth finger is conspicuously longer than the forearm; in *Myonycteris*, the slightly smaller wing has digit five subequal in length to the forearm. In *Roussettus*, the fingers are much shorter; usually only digit three has the upper joints as long as the forearm; occasionally three is somewhat longer and four is subequal to the forearm. In all three genera, these two joints of digit five are shortest though the relative lengths vary specifically. *Cynopterus*, while longer fingered than *Roussettus*, is less extreme than the other two genera and differently proportioned. The metacarpal and first phalanx of digits four and five are subequal in length, with four being slightly shorter than five which is about the same length as the forearm, while digit three is conspicuously longer.

Other differences in ratios of wing bones can be worked out, but the most significant fact is that in development of the wing *Lissonycteris* and *Myonycteris* are not intermediate between *Roussettus* and *Cynopterus* but differ equally from both. The same is true of the attachment of the wing which in the two former genera is near the middle of the first phalanx of the second toe, in *Cynopterus* is near the distal end of the first phalanx of the first toe, and in *Roussettus* is usually between metatarsals one and two, sometimes near the bases of the first phalanges, often well proximal to this.

Lissonycteris and *Myonycteris* are also equally distinct from the other two genera in shape and arrangement of the odontoid papillae. These papillae, which border the lips, inside, from the

angle of the mouth forward, are rather high and pointed and, in *Lissonycteris*, form a single row extending about to the canines. In *Myonycteris*, the shape and arrangement of the papillae are about the same, but in some instances on the upper lip toward the angle of the mouth there is a poorly defined second row. In *Roussettus*, the single row of small papillae is much reduced in extent and size. In *Cynopterus*, the more numerous, larger papillae are irregularly arranged in a broad band two or three rows wide and somewhat better developed on the upper than the lower lip.

The arrangement of the palatal ridges in *Lissonycteris* is very different from that in *Cynopterus* and, while more like that in *Roussettus*, differs in certain details which again point up *Lissonycteris*' close resemblance to *Myonycteris*. In the two latter, the three anteriormost ridges are not divided and scarcely, if at all, bowed forward; four and five are divided in the middle, slope forward (as in *Roussettus*), and have the inner ends recurved; six and seven, which lie behind the tooth row, are similarly shaped and these last four converge somewhat at their medial ends. Behind this, there are two or three other poorly defined ridges. *Roussettus* differs in general in having the anterior ridges more bowed forward, number four usually not divided, and the posterior ridges more nearly parallel with each other.

Other external characters which set *Lissonycteris* and *Myonycteris* apart from *Roussettus* are the shorter, less robust tail, the longer, denser fur on the notopatagium and on the proximal, dorsal surface of the tibia, the smaller foot with the basal quarter to third of the first phalanges webbed (see Fig. 1), the more slender claws, the more delicate calcar, and the extensive patch of glandular fur on the throat of adult males.

HAIR STRUCTURE

Additional evidence of the close relationship of *Lissonycteris* and *Myonycteris* comes from Benedict (1957) who says that they have essentially the same hair structure: the pigment distribution, absence of a medulla, and form, arrangement and dimensions of the scales being alike. The slight difference she describes in the more distal maximum diameter of the hair in *Myonycteris* seems scarcely important. The hairs of *Cynopterus* are so different as not to need comparison here. Those of *Roussettus* are less compellingly so, being similar in pigment distribution and

absence of a medulla. They apparently differ however in arrangement and size of scales and, to a certain extent in their form. In general, these differences seem more of degree than kind.

CRANIAL CHARACTERS

Cranially, as externally, *Lissonycteris* and *Myonycteris* possess a number of features in common which distinguish them equally from *Roussettus* and *Cyanopterus*. In addition to the proportions of the skull as a whole, the shape and spacing of the teeth, the occlusion pattern, and the structure of the inter-orbital region are particularly important. In general proportions, the dominant feature of the small *Myonycteris* skull, and one in which it agrees with the much larger *Lissonycteris*, is the relatively great length of the anterior part of the skull (measured from behind the postorbital processes to the tips of the premaxillaries) as compared with both length of the brain case (measured from behind the postorbital processes) and its bulk. Typically, also, the brain case in *Myonycteris* is elongated behind the temporal root of the zygomatic arch, and the rostrum is slender with the posterior ends of the nasals depressed giving the skull in profile a dish-faced appearance, an appearance that is accentuated by the great development of the lateral of the two pairs of frontal sinuses.

Compared with *Roussettus*, *Lissonycteris* and *Myonycteris* have a more slender rostrum. In the two latter, a projection of a line along the top of the nasals passes ventral to the top of the orbit and the brain case. In *Roussettus*, *sensu stricto*, such a line passes dorsal to both of these points. In the myonycterines, the brain case is elongated and flattened so that the distance from the bottom of the occipital condyles to the top of the occipital crest is less than the distance from the postglenoid process to the back of the condyle, whereas in *Roussettus* the first distance is equal to or greater than the second. The larger orbit, though difficult to measure, is easy to see. In *Lissonycteris* and *Myonycteris* the diameter of the orbit taken approximately parallel to its antero-rostral margin is equal to or greater than the lacrymal width; in *Roussettus* it is less. Further, the antero-ventral border of the orbit formed by the root of the zygomatic arch is a better developed, sharper edged rim; it is thin and plate-like where the infraorbital canal pierces it. The thicker root in *Roussettus* results in a noticeably longer canal.

When *Lissonycteris* and *Myonycteris* are compared with *Cynopterus*, the angle of the nasals, the elongation of the back of the skull, and the rather large orbit with a short infraorbital canal show no striking differences. That these similarities are indicative more of parallelism than relationship is suggested by the pronounced differences in overall proportions of the skull. The short, heavy rostrum and relatively large brain case of *Cynopterus* contrast sharply with the more slender nosed, less chunky skulls of *Lissonycteris* and *Myonycteris*. Such features are hard to measure, but in *Cynopterus* the distance from the postorbital foramen to the back of the occiput is much longer than the distance from this foramen to the premaxillary suture, while in *Lissonycteris* and *Myonycteris* these distances are almost equal; further, the height of the brain case vertically above the interpterygoid region is usually a third or more of the length of the skull in the former, while in the two latter it is usually considerably less than one-third of this length.

Certain features of the frontal sinuses are also very distinctive. Characteristically, those of *Lissonycteris* and *Myonycteris* have the lateral pair much more inflated than the medial. This, together with the tilting up of the orbital margin posteriorly, makes the interorbital region concave. In *Rousettus*, the reverse is true; the smaller, lateral pair of sinuses are relatively less inflated, the medial more, and the orbital margins are not tilted up, so the interorbital region is flattened or domed, sometimes with a median sulcus anteriorly. In all three of these genera, the lateral pair of sinuses end in front of the postorbital foramina. In *Cynopterus*, on the other hand, the well inflated lateral pair extend at least to the level of the postorbital foramina which are thus crowded outwards into the postorbital processes, and the much smaller, medial pair show scarcely any inflation.

DENTITION

In past classifications, the reduction of the last molars has been one of the most important reasons for grouping *Myonycteris* with *Cynopterus*, while the number of teeth has been used to relate the former to *Rousettus*. Actually, the shape of the anterior teeth is far more important than either of these in showing generic relationships and is one of the most clearcut characters relating *Lissonycteris* and *Myonycteris*. Variation at the end of the molar row is, on the other hand, an important differential character separating these latter two. Typically, the cynopterine

bats have lost the last upper and lower molars, while these teeth are retained and well developed in the rousettine group. Both *Lissonycteris* and *Myonycteris* have the rousettine formula but, in the latter, the last molars are tiny and clearly obsolescent, while in the former they are the opposite. Reduction of the molars in *Myonycteris* is no more reason than their stronger development in *Lissonycteris* for grouping the one with *Cyno-pteris* and the other with *Roussettus*.

The structure of the teeth, their spacing, and the occlusion pattern are remarkably similar in *Myonycteris* and *Lissonycteris* and differ equally from both *Cyno-pteris* and *Roussettus*. The most striking feature of the tooth rows of *Lissonycteris* and *Myonycteris* is the wide spacing of the short, broad teeth; in addition, the anterior teeth have the main external cusps placed well back on the outer margin so that in profile the teeth look more equilaterally triangular. The teeth in *Cyno-pteris* differ sharply in being larger and more crowded, and in the arrangement of the cusps, with the main external cusp more anterior and a deeper sulcus separating the inner and outer halves of the teeth. In the upper jaw of *Cyno-pteris*, P³ has a well marked ridge or internal cusp, whereas in *Lissonycteris* and *Myonycteris* this tooth, though thick, is simple. In the lower jaw of *Cyno-pteris*, P₁ is relatively large and P₃ compared to P₄ is conspicuously higher, almost as broad, but shorter with a less well developed heel. In *Lissonycteris* and *Myonycteris* P₁ is tiny and P₃ reduced, much narrower and only slightly higher than P₄, with no trace of a heel; P₄ is relatively large with a high, almost central, main cusp, bilobed in *Lissonycteris* and in *Myonycteris* with sometimes a suggestion of a heel. In general, these premolars are more similar to those of *Roussettus*; in the latter, P³, P₃, and P₄ are simple, high, and differ from *Lissonycteris* and *Myonycteris* chiefly in having the single cusp set farther forward with a trace of a heel posteriorly. P⁴ has the more usual pteropid elongated shape with the main cusps forward and the inner margin sometimes bilobed. In the lower jaw, neither of the first two premolars of *Roussettus* is reduced, as in the former genera, while the molars are longer and narrower.

The wide spacing and simple shape of the teeth in *Lissonycteris* and *Myonycteris* relate to a very characteristic occlusion pattern in which the P₃ and P³ alternate with each other, P₄ barely occludes with the posterior edge of P³, and there is scarcely any more contact between P⁴ and the posterior edge of P₄. In *Roussettus*, the overlapping of the teeth is more pronounced, correlated

with the beginning of a heel. In *Cynopterus*, it is even more so with the crowded teeth slanting forwards and P_3 reaching the back of the upper canine.

On the basis of the material at hand, *Myonycteris* and *Lissonycteris* differ sufficiently from each other to warrant generic distinction. However, it may be significant that *M.* (*Phygetis*) is distinguished from *M.* (*Myonycteris*) by its relatively larger teeth, especially M^2 and M_3 , and the bilobed main cusp of P_4 , characters which also help distinguish *Lissonycteris* from *Myonycteris, sensu stricto*. Further, two small species of *Lissonycteris*, *smithii* and *crypticola*, which are described as having reduced dentition, may prove to be somewhat intermediate between the two genera. Study of these possibly annectant forms may make it necessary to reconsider the generic status of *Lissonycteris*. For the present it seems best to retain both as full genera.

DISCUSSION

While the results of this study point up the distinctness of the myonycterine from both the cynopterine and the rousettine sections of the Pteropinae, they also suggest that the former may be more closely related to the epomophorine section than has previously been supposed. A casual inspection of the epomophorines and myonycterines shows such extreme external differences, such differences in structure of the palate, posterior bony nares, shape of the molars and tooth formula, and such a greatly elongated rostrum in many epomophorines that any close relationship might seem most unlikely. However, in the rather unspecialized genus *Epomops*, the little or not deflected skull, the relative size as well as shape of the brain case and rostrum, the details of the interorbital region, and the size of the orbits all show a strong resemblance to *Lissonycteris*. In similar ways, *Epomophorus labiatus*, except for its elongated rostrum, resembles *Myonycteris*. There are other resemblances. In the epomophorines, the wide spacing of the teeth and the consequent alternating more than overlapping occlusion pattern of the anterior ones as well as the more posterior position of the main cusps of both upper and lower third and fourth premolars and the small size of the first lower premolar all suggest the myonycterine group. The characteristic tooth formula of the epomophorines is foreshadowed by the great reduction in *Myonycteris* of those teeth which are lacking in the former. Externally, the long-fingered wing, in which the metacarpal and

first phalanx of digit five is a little longer than the forearm in *Epomops*, and the attachment of the wing membrane in this and most of the epomophorine bats to the first phalanx of the second toe are also characteristically myonycterine. Finally, though the arrangement of the palatal ridges is highly variable from species to species, in one form at least of *Epomops* the divided fourth and undivided, straight first three ridges are not unlike those in *Lissonycteris*.

The epomophorine affinities of *Lissonycteris* and *Myonycteris* are further indicated by Benedict (1957, p. 292): "Strikingly, the scale form of *R. angolensis* [*Lissonycteris angolensis*] is more similar to that of the *Epomophorus* section than to the *Roussettus* section to which Andersen assigns it." and "The scales of *Myonycteris* are virtually indistinguishable from those of the *Epomophorus* section."

Analyzing the differences between the epomophorines and myonycterines, we find that the most conspicuous ones usually are found in the regions of the skull where, within the epomophorine group, there is much generic variation, or that these differences are more extreme developments of traits which *Lissonycteris* and *Myonycteris* already show. This suggests that the epomophorine is a specialized branch of the myonycterine group which in turn is fairly close to an early *Roussettus*-like stock. These annectant forms, the myonycterines, help to confirm Andersen's (1912, liii-lvi) supposition that the origin of the epomophorine group was from a primitive and *Roussettus*-like stock.

The cynopterine bats are clearly quite different. Resemblances between these and *Myonycteris* such as tooth formula, shortening of the rostrum, slight elongation of the back of the skull, reduction of the tail, and development of the wing as well as roosting and locomotory behavior are probably parallel developments in groups which diverged early. Andersen also supposes that the cynopterine bats arose from early *Roussettus*-like ancestors, but, with *Myonycteris* eliminated as an intermediate form, the two groups are more sharply distinct than was previously supposed.

Geographically, the picture presented by the morphological evidence is a very logical one. The cynopterine bats become exclusively an Oriental and Austro-Malayan group, the epomophorines are restricted to Africa where they center in the western forested regions, and in this same general area we find the rather more primitive but fairly closely related myonycterine

group. Common to both regions is the rousettine group considered, on the basis of morphological characters, to be the most primitive and therefore probably the most direct descendant of the ancestral stock from which all arose. The occurrence of a highly developed sonar system in the otherwise not particularly specialized *Rousettus* suggests, however, that they are farther removed from the ancestral stock than was previously supposed.

ACKNOWLEDGMENTS

This work was supported in part by the Office of Naval Research¹, the United States Public Health Service, the Sigma Xi-RESA Fund, the Belgian American Educational Foundation, and Harvard University. During part of this period, Novick was a Fellow of the National Institute of Neurological Diseases and Blindness. For help in capturing and keeping these bats, we are grateful to the personnel of the Sangley Point Naval Air Station and Clark Air Base in the Philippines, to the Naval Attachés and other personnel of the American Embassies in the Philippines and Ceylon, to Mr. Pablo Tanciojo and the Negritos of the Zambales Mountains of Luzon, to Capt. J. A. Simon, USAF, to Major A. Weinman of the Dehiwela Zoo, Ceylon, and to Mr. and Mrs. W. W. A. Phillips formerly of Nammukula, Ceylon, to Dr. Louis van den Berghe, Messrs. J. Moureau, P. Pirlot, and G. Marlier of the *Institut pour la Recherche Scientifique en Afrique Centrale*, Lwiro, Belgian Congo, and to countless others who made these studies possible by giving of their time or experience. We are most deeply indebted to Dr. D. R. Griffin of Harvard University for help of every description.

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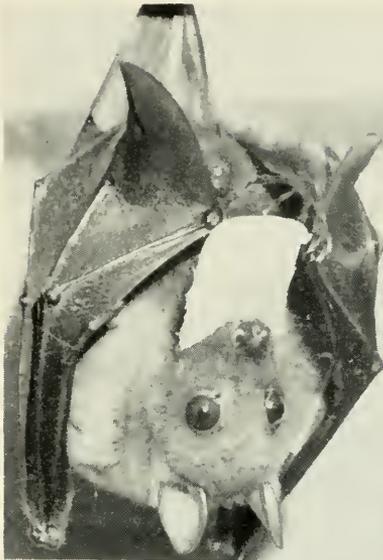
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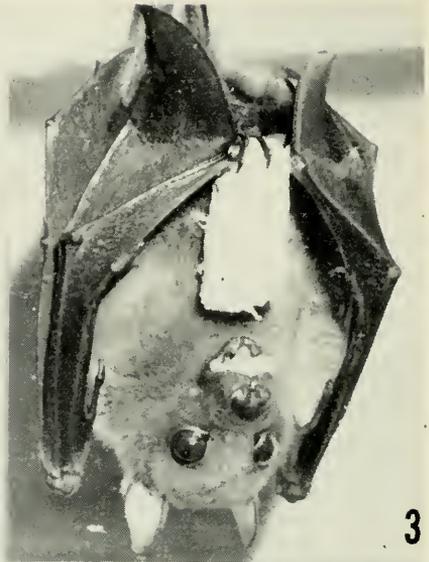
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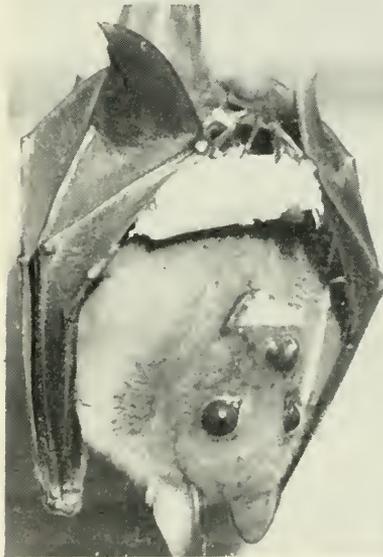
Figure 1. *Lissonycteris angolensis* hanging from slat by the left foot (not visible), holding a piece of banana with its right foot, while biting off a manageable portion.



2



3



4



5

Figures 2, 3, and 4. *Lissonycteris angolensis* handling pieces of banana. The use of the foot in handling food and the posture of the wings while doing so is clearly shown.

Figure 5. *Lissonycteris angolensis* resting, hanging on a canvas wall at its junction with the ceiling. Note the position of the feet which can hold onto a roost equally well in this or the opposite orientation. The wings are being held well overlapped, substantially enwrapping the body. If the bat had not been disturbed by the photographer, its chin would have been tucked against its chest and its eyes closed.

B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS.

APRIL 18, 1963

NUMBER 185

ELEUTHERODACTYLUS HEDRICKI, A NEW SPECIES OF FROG FROM PUERTO RICO (SALIENTIA, LEPTODACTYLIDAE)

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The finding of a new species of frog in Puerto Rico has seemed very improbable. The island has been thoroughly searched by a number of herpetologists, and since the calls of the described forms are well known, the recognition of a new voice is not difficult. Yet the author has traveled miles and miles in the island, at night, and no unfamiliar voice was ever heard in recent years. He was almost convinced that a new species was out of the question, but it appears that this conclusion may be premature in almost any country, no matter how well the fauna of the place is known. The reason is clear: there is a tendency to look for frogs in places where the known species occur, and hence many potential habitats remain uninvestigated.

Eleutherodactylus hedricki was heard while collecting *E. karlschmidti* in a mountain stream at El Yunque (El Verde). It was immediately evident that the voice heard was that of a new species, and the animal was desperately hunted, until at last collected. It is interesting to note that this frog was recognized as new before being seen—a proof of the usefulness of voice, especially where the fauna is well known, in the collecting of frogs new to science.

The name *hedricki* has been given in honor of Hedrick J. Rivero, aged 9, who has declared himself assistant to his father and who follows him through creeks, caves and mountains during any time of the day or night. The author also wishes to express his appreciation to his wife, Eneida, and to his son,

Juan Jr., 16, who always join him and Hedrick in the search for frogs. Horacio Mayorga, research assistant to the author, has also been extremely useful, not only in field work, but also in the tedious curatorial and laboratory work that usually follows. Dr. John Randall kindly took the photographs of *E. hedricki*, and the Galiñanes family of San Juan made their El Verde house available as a center of activities for the collecting party. To all these people, the author feels deeply indebted.

ELEUTHERODACTYLUS HEDRICKI sp. n.

Type. Museum of Comparative Zoology No. 36903, ♂ from El Verde, west flank of El Yunque, Puerto Rico, 1500 ft. Coll. J. A. Rivero, 11 Aug. 1962.

Paratypes. University of Puerto Rico (Mayagüez) Nos. 1132-1135, same data as type. UPRM Nos. 1136-1138, El Yunque, 10.9 km on road between Palmer and La Mina, elevation 1765 ft., September 1962. Coll. Rivero and Mayorga.

Diagnosis. A medium-sized *Eleutherodactylus* with short snout, the eye diameter more or less equal to the distance between eye and nostril; an indistinct tympanum, webless toes, and two, externally concave, light-colored markings on each side of the back, from behind the nape to the sacral region.

Description of type. Head much broader than long; snout short, sub-triangular, with a small vertical ridge at the tip; tongue large, free; vomerine odontoids distinct, almost transverse, separated, and well in back of the choanae, their exterior margin not quite reaching the inner borders of the latter; eye diameter almost as long as the snout; interorbital space much broader than an upper eyelid; tympanum indistinct, about $\frac{2}{3}$ the eye diameter; canthus indistinct; loreal region almost vertical; a slight supratympanic fold to the shoulder; first finger shorter than second, which is shorter than the fourth; disks large, fan shaped, the one on the first finger smaller than the others; two elongated metacarpal tubercles, and a third, smaller outside one; subarticular tubercles moderate; metatarsal tubercles small, the inner oval, the outer round and inconspicuous; heel of the adpressed hind limb extends to the posterior border of the eye; heels overlap when tibia and femur are placed perpendicular to the body. Skin above and on the sides of the head and upper flanks studded with small warts and granules. Below, the belly, lower flanks and buttocks granular; male with a large subgular vocal sac.

Color. Above, gray, with variegations and vermiculations of a lighter gray or whitish; snout dark gray, except for some lighter, indistinct markings below the eye; a dark supratympanic streak; a whitish interorbital bar followed posteriorly by a broader dark bar; two distinct, whitish, externally concave markings on the back from behind the nape to the sacrum; between these, on the anterior region, two shorter and more diffuse markings of the same color; a whitish transverse blotch with irregular margins posterior to the sacral region; seat blackish with a whitish blotch on each side; thighs cinnamon brown, with a longitudinal series of whitish blotches from base to knee; two whitish, irregularly margined, transverse bars on the tibiae, and two on the tarsi; throat of male intensely infuscated; chest and belly slightly infuscated.

Measurements. (δ , in mm) Snout-vent 34.8; head length 11.8; head breadth 13; femur 14.5; tibia 16; foot 21.

Description of paratypes. UPRM No. 1132 is a δ specimen with the same data as the type and with the following measurements: Snout-vent 34.1; head length 12; head breadth 13.1; femur 14.19; tibia 15; foot 20.8.

The snout has a more rounded appearance than in the type, because the ridge at the tip is more indistinct; the vomerine odontoids are rounded, set well apart and considerably behind the choanae; the tongue is indented behind, and the tympanum is fairly distinct.

The color above is blackish all over, with indistinct darker areas behind the nape and on the sacrum; the interorbital bars and externally concave dorsolateral lines are not evident, but there are three, small, light-colored areas that appear as if the skin had been eroded from those areas. The whitish thigh blotches are not too distinct and there is only one broad, dark band on the tibia and another on the tarsus. The venter is much darker than in the type, but still lighter than its own throat, which is deeply infuscated. This specimen (no. 1132) and the following were preserved during the daytime, while the type and paratype No. 1136 were preserved at night. This may account for the darker coloration of 1132 and 1133.

UPRM No. 1133 is also a δ with the same data and the following measurements: Snout-vent 33; head length 11; head breadth 12.3; femur 13.3; tibia 14; foot 20.

This animal is almost as dark above as UPRM 1132, but the dorsolateral lines are still evident and the light blotches on the

thighs are present, although not as distinctly as in the type. The axillae have colorless areas which appear like spots; there are two fine, light-colored lines margining a dark band on the tibia and the same situation is repeated on the tarsus. The belly is much lighter than in the specimen just described.

UPRM Nos. 1134 and 1135 are juvenile specimens just coming out of the eggs. The dorsolateral markings are present in both examples, but one is almost smooth above, while the other has a number of small warts and tubercles. The limb blotches are also more distinct in the warty example (UPRM 1134). They are 7 and 8 mm in snout-vent length.

UPRM No. 1136 is another ♂, from El Yunque, 10.9 km. between Palmer and La Mina, elevation 1765 ft., 2 Sept. 1962. Coll. Rivero and Mayorga. Its measurements are as follows: Snout-vent 35.3; head length 12.1; head breadth 14.8; femur 15.5; tibia 16; foot 22.2.

The snout in this specimen looks rounder and higher than in the type and the snout ridge is only shown by a small protuberance. In coloration it looks more like the type than any of the other examples, but it is more profusely reticulated and there is a ferruginous tinge on the dorsum, especially on the area of the dorsolateral lines. The colorless area of the axillae is very distinct, and the whitish thigh spots are transverse and well indicated, but the seat is not as dark as in the type. The venter is of a light color while the throat is as infuscated as in the other examples.

UPRM No. 1137 is a 7 mm juvenile from the egg clutch of the above paratype. It shows the dorsolateral markings (though much broader than in the adults) but the thighs are more or less marbled and the venter is pin-pointed with black.

UPRM No. 1138 is also from the egg clutch of 1136. It is 6.2 mm in length and has a small tail, 3.5 mm in length. Apparently it had just come out of the egg.

Distribution. Although *E. hedricki* has not been collected outside of El Yunque, its voice was recently heard at the Toro Negro Reserve Forest and it thus seems that the species ranges throughout the high elevations of the Cordillera Central. The female is thus far unknown.

Relationships. *Elutherodactylus hedricki* is not too closely related to any Puerto Rican frog and its habits are distinct from those of any of the known species. A comparative skeletal study of the Puerto Rican *Elutherodactylus* is under way and this

may reveal its true affinities. In the meantime, it is interesting to note that the two externally concave lines that are characteristic of this species are shared with diminutive *E. cochranæ*, *E. locustus* and *E. gryllus*. However, these seem to be basic in the genus and are shown here and there in various of the Antillean species.

Habits. *Eleutherodactylus hedricki* is a dense forest frog which breeds and apparently stays during the daytime in tree holes and cracks. The male guards the egg clutch, which in the case of the type consisted of 32, 4 to 4.5 mm eggs, while one of the paratypes had 14 eggs and 2 juveniles, and another had 15 eggs and 2 juveniles. In all cases where eggs were found, these were attached by gelatinous threads to the wood encircling the pith cavity. At the extreme ends of the cavity where the eggs were deposited, the pith was rotten and cracked and it does not appear improbable that juveniles wander through the pith for some time, eating the termites and small ants that abound in those areas.

The voice of the male *E. hedricki* is a sonorous "ping, ping, ping," quite distinct from anything known in Puerto Rico, but perhaps more similar to the call of *E. locustus*. The first specimen heard was calling from high up in a tree and could not be collected. One of the adult paratypes called from a dead tree trunk, three to four inches in diameter, about six feet from the ground and one inch from a hole that communicated with a small cavity inside. The third adult specimen was in a cavity inside the branch of a living tree about four feet from the ground. It was calling from the outside and retreated into the hole when collection was attempted.

The capture of the type and of paratype UPRM 1136 was interesting enough so that in both cases it will be related in detail. The call of the type was heard coming from a bushy area that included three, 10 to 12 ft. high young trees and a 4 to 5 in. diameter, rotten tree trunk with a hollowed upper end and one or two holes a few feet from the ground. Bending of the trees did not stop the animal from calling, so that it was suspected that it was hiding somewhere in the dead trunk. When this was broken at the base, the frog stopped calling, but a thorough search did not reveal its presence. However, one of the members of the party thought that something that appeared like eggs was deposited at the bottom of one of the cavities in the trunk. To the author, these appeared to be

fungous growths, and the search was abandoned and preference given to another call, coming from about 50 ft. away. This animal could not be found, but it was during this interval, which may have lasted one hour, that two of the adult paratypes were obtained. On returning to the original site, the frog was immediately located, calling from the entrance of the hole. A thorough search revealed the eggs that have already been mentioned. The collection of this specimen is described because, if the animal was not hiding deep inside the tree cavity when its search was abandoned, then it escaped to the outside and returned to the egg clutch in a trunk that was now in a completely different position, that is, lying down on the ground instead of standing erect.

In obtaining paratype No. 1136, a *Cecropia* tree had to be felled, since the animal was calling from a hole at about 25 ft. from the ground. The frog was seen to retreat further back into the hole when the tree hit the ground, but after that it managed to escape to the outside, perhaps because vigilance under the light of two flashlights whose batteries were almost dead, was not adequate. The cavity contained an egg clutch and two juveniles (paratypes 1137 and 1138). It was round and smooth inside and perhaps not larger than two inches in diameter. No possibility existed for the animal to escape into the pith cavity of the tree which, in *Cecropia*, is divided into compartments.

After the eggs and juveniles were obtained, the whole section of the tree containing the egg clutch was removed with a machete. Since a thorough search of the surrounding area did not reveal the presence of the adult animal, the place was abandoned and other voices traced. After about half an hour of unfruitful work, the call of *hedricki* led the party to the fallen *Cecropia*, from which the male was again calling, only two or three inches away from the place where the egg clutch had been removed. It thus appears that this frog has some way of guiding itself to the breeding site and that this ability may not depend exclusively, perhaps not at all, on visual cues.

Paratype UPRM 1136 had 5 yellowish eggs in an advanced state of development, 10 white eggs that were not as well developed, 5 empty egg cases and 2 juveniles. It appeared as if the two groups of eggs were laid at different times. It took 22 days for all the little frogs from the egg clutch of the type to hatch.



Left: Eleutherodactylus hedricki sp. nov. type, MCZ 36903. *Right: Egg clutch of Eleutherodactylus hedricki* inside a tree trunk. Some wood removed to expose the eggs.

B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS.

APRIL 18, 1963

NUMBER 186

NOTES ON HISPANIOLAN HERPETOLOGY

8. THE FORMS RELATED TO *ANOLIS HENDERSONI* COCHRAN.

BY ERNEST E. WILLIAMS

In 1923 Doris Cochran described *Anolis hendersoni* from Petionville, Haiti. This long-headed species with a reduced dewlap was represented by a single adult male collected by J. B. Henderson and Dr. Paul Bartsch in 1917.

Ten years later, without making any reference to *Anolis hendersoni*, Noble and Hassler (1933) described the very similar *Anolis baharucocensis* from the mountains of Barahona peninsula to the east of the type locality of *A. hendersoni*. This new species was represented by 76 specimens. The series demonstrated marked sexual dichromatism, and there was for the first time information on the habits and habitat of the species. Noble and Hassler (1933, p. 12) reported collecting it between the altitudes of 1500 and 3700 feet and stated: "It is believed that the lower mountain sides are not humid enough for the species. It is much more terrestrial in its habits than the other species of *Anolis* in the same locality, being found on the ground and on low brush in coffee groves and forested areas. Its favorite habitat, however, was on low plants, leaves and trash along mountain streams and in humid ravines."

Since these two descriptions the only additional published information is in Cochran's (1941) "Herpetology of Hispaniola." She reported six additional specimens of *hendersoni*: one (USNM 82566) is a misidentified young *coelestinus*; the others are a Fond des Negres specimen (USNM 72629) collected by A. Wetmore and four specimens (MCZ 13792, 13794, 13795, 13797) collected at Port-au-Prince by G. M. Allen. Cochran recognized the strong resemblance between *hendersoni* and *baharucocensis* but retained the latter as a full species. She said: "*A. hendersoni* has a close ally in *A. baharucocensis*, as they are

both distinguished by the same elongated head and body. Although at first glance the immaculate dorsum of *hendersoni* does not suggest alliance with the heavily banded *baharucoensis*, other details of coloration are more suggestive of the relationship. The lips are spotted in a nearly identical manner. The white lateral line, so striking a feature of *hendersoni*, is developed in a slighter degree in *baharucoensis*. The peculiarly crowded appearance of the scales just behind the mentals and their extreme convexity which makes them appear to be ridged without actually being keeled, is duplicated exactly in both species. Their differences are equally distinct and set them off in the same way that *chlorocyanus* and *coelestinus* are differentiated. The very fine body granules of *baharucoensis* and its rather square snout are not to be confused with the coarser scales and more rounded profile of *hendersoni*¹.” No additional material of *baharucoensis* was recorded.

Recent collections (1959-61) in Haiti have greatly increased our knowledge of *Anolis hendersoni* and have permitted recognition of a third member of the *hendersoni* complex from the western tip of the southwestern peninsula. This new form is recognizable on the color pattern and probably on head length of the adult male, but the wealth of new material appears to show that there are no consistent squamation differences between any of the members of the complex, and, therefore, despite the absence of any clear and positive instance of intergradation, I regard these three as subspecies of a single species. This problem is further discussed below.

We may now redefine *Anolis hendersoni* as a polytypic species of *Anolis* belonging to the Hispaniolan radiation of Etheridge's alpha section and *carolinensis* series² (i.e. an *Anolis* without caudal transverse processes, with the lateral processes of the interclavicle in close contact with the expanded proximal parts of the elavicles, and with three parasternal chevrons attached to the dorsal ribs followed by a single chevron not so attached) and with the following diagnostic external characters. Head and body slender (head *ca.* $\frac{1}{3}$ or more snout-vent length), dewlap very reduced, not extensible. Dorsal scales small, *ca.* four middorsal rows slightly enlarged and distinctly keeled but grading into

¹ Cochran (1941, p. 187) was able to examine only a single paratype of *baharucoensis*.

² These terms (for present purposes sufficiently defined by the data within the parentheses above) are derived from the doctoral thesis of Richard Etheridge at the University of Michigan (available on microfilm).

granular flank scales. Ventral scales smooth, polygonal, subimbricate. Digital dilations moderate. About 19-21 lamellae under phalanges ii and iii of fourth toe. Tail not compressed nor with crest. Verticils obscure. Sexually dimorphic in size and color pattern. Anterior head scales smooth. Supraorbital semicircles separated by one scale row. Interparietal scale separated from semicircles by 4-6 scales. Loreal rows 6-7, canthals 6-7, supralabials to center of eye 6-7, suboculars in contact with supralabials. Mentals much longer than wide, throat scales medially deeply inserted between them. Three populations conform to this definition but differ strongly in male color pattern (and in one instance in the relative head length of the adult male).

TAXONOMIC DESCRIPTION

ANOLIS HENDERSONI HENDERSONI Cochran¹

Anolis hendersoni Cochran 1923. Jour. Washington Acad. Sci. 13:25. (Type locality: Petionville, Haiti) — Cochran 1941, p. 181.

Specimen list. **Haiti.** Departement du Nord: *Citadelle* MCZ 25484, 25486, W. J. Eyerdam, 1927. Departement du Ouest: *Port-au-Prince* MCZ 13792, 13794, 13795, 13797, G. M. Allen, 1919. *Petionville* USNM 59210 (type), J. B. Henderson and P. Bartsch, 1917. *Boutillier Road* MCZ 59951-7, E. Williams and A. S. Rand, 1959; MCZ 62956-9, A. S. Rand and J. Lazell, 1960. *Morne Decayette* MCZ 62960-8, A. S. Rand and J. Lazell, 1960; MCZ 62969-75, 63443, L. Whiteman, 1960; MCZ 65635-46, L. Whiteman, 1961. *Diquini* MCZ 64824-40, L. Whiteman, 1961. *Below Kenskoff* MCZ 59950, L. Bonfil, 1959. *Penault* MCZ 63437-42, L. Whiteman, 1960. *Furcy* MCZ 64823, L. Whiteman, 1961. *Marbial, 21 km NE Jacmel* MCZ 65170-8, CM 3812-17, L. Whiteman, 1961. *Croix Joseph, Marbial, 21 km NE Jacmel* MCZ 65183-202, CM 37818 (16), L. Whiteman, 1961. *Source Fleury, Mayerre, 8 km E Jacmel* MCZ 65179-82, CM 37819-22, L. Whiteman, 1961. Departement du Sud: *Butete near Miragoane* MCZ 66029-62, CM 37919 (32), L. Whiteman coll. 13-viii-61. *Mingrette near Miragoane* MCZ 66063-79, CM 37920 (15), L. Whiteman coll.

¹The following abbreviations have been used for the museums or collections from which specimens of anoles of this complex have been examined: AMNH, American Museum of Natural History; CM, Carnegie Museum; MCZ, Museum of Comparative Zoology; UMMZ, University of Michigan Museum of Zoology; USNM, United States National Museum; YPM, Yale Peabody Museum; AS-X, Albert Schwartz, personal collection.

1961. *Risque near Miragoane* MCZ 66080-85, L. Whiteman coll. 1961.

Diagnosis. Head length in adult male about 33 per cent of snout-vent length. Male coloration distinctive. (Head brown. Nape vermiculate, lighter on darker brown. Dorsum brown anteriorly, greenish posteriorly, without transverse saddles or other markings. Flank stripe extending to groin bordered above by intense black and below at sides of belly by black vermiculation. Belly bluish.)

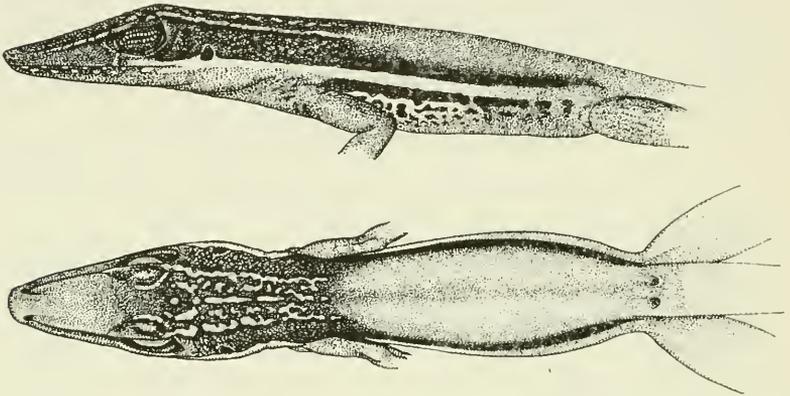


Figure 1. *Anolis hendersoni hendersoni*, MCZ 59949. Lateral and dorsal views. N. Strekalovsky del.

Color in life. Alive, *hendersoni* is quite spectacularly beautiful — especially the male. The differences between the two sexes are best shown by a tabular comparison of the descriptions of two specimens. I add a few remarks on color variation.

♂ from below Kenskoff

Head brown and anterior back brown merging into green at sacral region.

Nape with vermiculation behind interparietal which is white.

♀ from Boutillier Road

Head, nape and center of back dark brown, head somewhat mottled. The central dorsal area bordered by a cream line with an irregular boundary.

Nape without vermiculation. Interparietal white.

Blue spots on upper and lower labials. Limbs red brown. Tail with greenish tinge, becoming black posteriorly.

Upper and lower labials obscurely marked with darker. Limbs and tail brown, obscurely mottled.

A broad blue-black band from behind eye over shoulder, becoming less well defined posteriorly.

A broad brown band from snout through eye along flanks, lighter in center, dark edged above and below.

Below this a light line from upper labials to groin, white below eye, yellow from shoulder $\frac{3}{4}$ of way to hind leg, beyond this with greenish tinge.

A light line from upper labials above shoulder to groin, nearly white below eye, yellow green in front of shoulder, purplish and indistinct on flanks.

Flanks below light line boldly mottled with black.

Flanks below light line darker, not mottled.

Throat yellow green.

Throat yellow green with two narrow dark longitudinal lines.

Belly blue green, some orange under base of tail.

Belly and underside of tail pale greenish.

Comments. The female, as the table indicates, is basically similar to the male in pattern but with duller colors and with frequently a light dorsal longitudinal band. The light flank stripe of the male is very brightly colored and brought into bold relief by the black mottling below it and the blue-black of the dark band above it. The same stripe is always obscure or absent posteriorly in females and may be very little evident anteriorly. The green of the hind quarters of the male is absent in the female and so also is the vermiculation on the nape. On the other hand, the two narrow black lines on the sides of the throat may be present or absent regardless of sex.

There is a striking consistency in pattern in the animals from well-separated localities (i.e. Diquini and Mayerre). Such variation as exists seems to be individual only. In the males this appears to be a matter of clarity of expression of various elements of the pattern; this has undoubtedly been influenced by vagaries of preservation. In the females, along with this same variability in the boldness or obscurity of pattern, there seems to be also real pattern variation in the dorsal zone from interparietal to sacral region. In the live specimen described above the impression is of a wide dark middorsal stripe bordered by a narrow light area on

each side. In numerous other females, however, the middorsal dark stripe is narrow, broken or irregular with usually a narrow light center and bordered on each side by a wide light area. This appears to be the more frequent of the two conditions.

This long-headed and slender form has until now been considered very rare. While nowhere as abundant as the ubiquitous species *cybotes* and *distichus* or even the two common green anoles, it is, as is often true of "rare" species, not really uncommon in certain restricted situations. It seems to be a bush anole of middle elevations and associated especially with certain bushy thickets. Its habits are thus similar to those which Noble and Hassler (1933, p. 14) reported for *baharucoensis*. *Hendersoni* is, however, apparently less restricted to humid situations than Noble and Hassler believed *baharucoensis* to be.

A. S. Rand made field notes (July 30, 1961) for this species at Morne de Cayette. "*A. hendersoni* were on stems and branches close to the ground, three or four feet up at most. They were crawling about in the bushes, jumping from branch to branch, seldom coming to the ground, though one did do so to catch an insect. They are very shy and escape by dodging away through the stems, neither climbing nor hiding. Relatively slow moving normally."

James Lazell, Jr. provides in Figure 4 sketches from life of female *hendersoni* from Boutillier Road (August 9, 1961). These show in excellent fashion the characteristic postures and attitudes of the species.

ANOLIS HENDERSONI BAHARUCOENSIS Noble and Hassler

Anolis baharucoensis Noble and Hassler 1933. Amer. Mus. Novitates No. 652: 12. (Type locality: "Valley of Polo, Barahona Province, D. R.") — Cochran 1941: 184.

Specimen list. **Haiti.** Departement de Ouest: *Road to Sal Trou, on south side of range of Mt. La Selle* AMNH 50096, W. G. Hassler, 1935. *Caroyé near Sal Trou* MCZ 68693-714, USNM 146616-8, YPM 3704-13, UMMZ 123372-81, CM 38497 (11), G. Whiteman, 1962.¹ **Dominican Republic.** Barahona Province: *Vicinity of Polo* AMNH 49516. *Valle de Polo* AMNH 51081-106, 51108-19, 51123-27, 51128 (type), 51129-52, 51154-56, MCZ 43822, 45952-53, 56138. *Polo* AMNH 50317, 50322-23. *Palomino*

¹The records listed above for the vicinity of Sal Trou are the first for Haiti. At Caroyé, in addition to *A. baharucoensis*, George Whiteman obtained also the rare form, *Chamaetnorops wetmorei*.

Springs near Barahona AMNH 49840-42, 49884-85, MCZ 43827, 56137. *Barahona* AMNH 50263.¹

Diagnosis. Head not more than 33 per cent of snout-vent length. Coloration of male distinctive. (Head green. Nape green spotted with brown. Dorsum with broad brown saddles on a green ground. Flank stripe extending to groin, not sharply defined, sometimes broken, bordered irregularly above and below. No black vermiculations on sides of belly. Belly cream tinged with brown and green.)

Color in life. Noble and Hassler (1933, p. 13): "In life the male is an extremely beautiful lizard. In its usual and brightest phase the dorsal surface of the head is an olive green; the neck a lighter green, spotted with brown. The back is a bluer green,

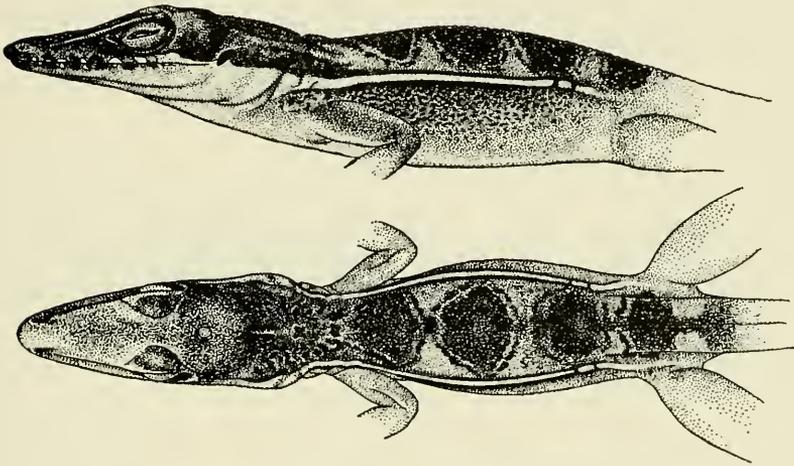


Figure 2. *Anolis hendersoni baharucensis*, MCZ 68917. Lateral and dorsal views. N. Strekalovsky del.

¹ Some confusion exists regarding the labelling of American Museum of Natural History specimens. Seventy-three paratypes of *baharucensis* — AMNH 51081-127, 51129-56, all apparently from Valle de Polo, are listed above. (The specimens missing from the series are all presumably exchanged.) However, Noble and Hassler's text mentions specimens from five additional localities, only two of which are now accounted for by specimens so labelled in the American Museum collections. Thus, unrepresented in the extant collections, though mentioned by Noble and Hassler, is material from Maniel Viejo, from the coffee finca of Senor Luis E. Del Monte near Barahona, and from the property of Mr. G. Hermann near Paradis. In addition, some of the specimens now catalogued in the American Museum as *baharucensis* from Polo are *pulchellus*, presumably from Puerto Rico or the Virgin Islands. Doubtless, as is known to have occurred with Hassler's and other material at this period, some of the lizards were kept alive for a period and only later and rather randomly catalogued.

Certain of the MCZ material (MCZ 43822, 43827) at present catalogued as paratypes, is listed as received in exchange from J. C. Armstrong and presumably was never at the American Museum and thus is not, in fact, paratype.

while the four broad saddles or cross bars are a tone of burnt umber. The dorsal surface of the tail, for the anterior two-thirds, is a yellowish green with several dark brown bars. The posterior end of the tail is brown. The side of the head is greenish brown back to the eye. The upper eyelid may be vivid golden yellow. The posterior corner of the lower lid may be blue or purplish. Just posterior to the eye is a narrow patch of dark brown, followed by a crescent of light blue or white. Posterior to this the side of the head is a brownish green merging into the lighter green of the side of the body which is peppered and veined with brown. Extending from a point on the upper labials anterior to the eye along the sides of the body nearly to the hind leg is a slightly broken white or cream-colored line edged with brown and suffused in the region above the front leg with yellowish green. The legs are light brown above with slightly darker bars. They are nearly white beneath. The ventral surface of the abdomen is cream-colored, faintly tinged with brown and green. The throat is the same color with several rows of very faint brown spots along the side.

“This species changes color rapidly and to a marked degree. When the lizard is caught or frightened, these colors almost instantly become darker, the green changing to gray or dark brown with the brown cross bars growing darker and almost black-edged. The head becomes dark brown and the labials greenish. The pineal region becomes white and very conspicuous. The ventral surfaces turn greenish or yellowish and the spots become more distinct.”

ANOLIS HENDERSONI DOLICHOCEPHALUS subsp. n.

Type: MCZ 64510, adult male, Place Negre near Jeremie, Departement du Sud, Haiti. Luc and George Whiteman coll. 12-xii-60.

Paratypes: **Haiti**. Departement du Sud. *Place Negre near Jeremie* MCZ 64507-9, 64511-36, Luc and George Whiteman coll. 12-xii-60. *Les Platons above Carrefour Canon near Ducis* MCZ 62976-82, A. S. Rand and J. Lazell coll. 4-viii-60. *Carrefour Canon near Ducis* MCZ 62983-92, A. S. Rand and J. Lazell coll. 4-5-viii-60. *Tombeau Cheval* MCZ 62993-7, A. S. Rand and J. Lazell coll. 7-viii-60. *Mountains on road to Jeremie* MCZ 56145, AMNH 49504, W. G. Hassler coll. 1935. *About 8 miles from Camp Perrin* AMNH 50098, W. G. Hassler, 1935. *Five miles from Camp Perrin on Jeremie Road* AMNH 50127, W.G. Hassler,

1935. *Camp Perrin* AS-X 2664, 2800-2802, 2923-25, A. Schwartz coll. 1962. *13 km N Cavillon* AS-X 3646, A. Schwartz coll. 1962.

Diagnosis. A subspecies of *Anolis hendersoni* differing in the greater elongation of the head in large males (more than 33 per cent snout-vent length) and in coloration. (Head brown, nape vermiculate lighter brown on darker. On dorsum of male a few small middorsal light-edged transverse bars at intervals, the widest just behind nape. Flank stripe extending only to mid-body, narrowing and terminating rather abruptly. A narrow black border above the stripe and black vermiculations below it, both disappearing abruptly along with the stripe itself. The posterior flanks unpatterned. Belly yellowish.)

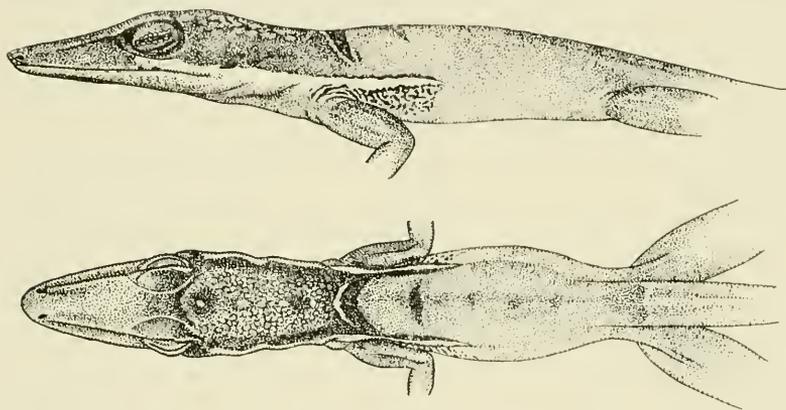


Figure 3. *Anolis hendersoni dolichocephalus* subsp. nov. Type, MCZ 64510. Lateral and dorsal views. N. Strekalovsky del.

Color in life. Description by W. G. Hassler of AMNH 50098 ♀ from mountains on Jeremie road about 8 miles from Camp Perrin, 2000-3000 ft.: "Dark brown, striped with lighter brown or yellowish lines. Belly and throat yellowish. Belly spotted. No green."

A. S. Rand for specimens from Les Platons: "♂ Uniform light brown above, grayer on head and neck. Darker brown on side of neck. A yellow stripe, black bordered above and below from below eye to midbody. Below pale yellowish. Faint dark striping on throat. Dewlap area with greenish tint. Eye brown.

"♀ A middorsal stripe edged with light gray. Sides brown with white, black bordered stripe from below eye to mid body. Belly yellow. Throat and chin white."

A. Schwartz for specimens from Camp Perrin: "♀ Dorsal ground color yellow-tan with a fine pale hairline with brown suffusions on each side. Sides dark brown with a light lower line on sides. Upper labials cream, occipital creamy. Ventral ground color pale greenish yellow."

Comments. Again the color pattern is remarkably consistent in the several populations sampled. Males from the south side of the Massif de La Hotte (Les Platons etc.) differ from those from the vicinity of Jeremie only in the weaker expression of certain features, i.e. the vermiculation of the nape and the small mid-dorsal transverse markings. The striking way, however, in which the flank stripe, the black line above it, and the vermiculation below stop abruptly at the same place is exactly repeated in all

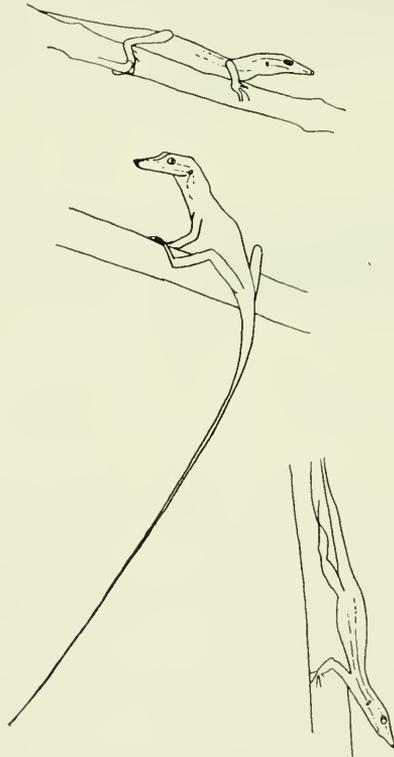


Figure 4. *Anolis hendersoni hendersoni*. A Boutillier Road female at the height of one foot above the ground. Characteristic poses. J. Lazell, Jr. del.

male specimens. The extreme long-headedness of fully adult males is again characteristic of all samples.

Female coloration is very like that of typical *hendersoni* except that in topotypic specimens from the vicinity of Jeremie the lateral light stripe fades rather abruptly at midbody, while in females from south of the Massif de La Hotte the stripe tends to continue very faintly to the groin as is usual in typical *hendersoni*.

Dolichocephalus at Tombeau Cheval (3000 ft. elevation) was captured along with *Anolis monticola*, *A. distichus* subsp., *A. cybotes* subsp. and *A. coelestinus* in the vicinity of a great heap of jagged limestone boulders overgrown with bushes and with much leaf litter — cool and shady. A. S. Rand reports that here while the *monticola* were found “around the cliffs on the rocks, roots, twigs, small branches and leaves close to the ground,” *dolichocephalus* was “. . . up on small branches, vertical stems one to four feet up and to a less extent among the rocks. *A. distichus* was common on the larger trees and less frequently on big rocks. *A. coelestinus* was seen and a few *A. cybotes* on rocks, trees, and bush stems. These last were much more common along the open trail and in coffee.”

SPECIES OR SUBSPECIES

The three members of the *hendersoni* complex are allopatric and in most respects extraordinarily similar. Despite Cochran's statement quoted above, I do not find the structural differences between these three taxa at all clear. Abundance of material has reduced rather than strengthened any suggestion of shape or squamation difference.

The color differences, on the other hand, are very marked. What is the biological significance of such differences in anoles without a functional dewlap? There is no objective evidence. I have reduced *baharucoensis* to a subspecies and have described *dolichocephalus* at this level for the following reasons: While color is very important in *Anolis* and while the importance of pattern and color may be expected to be still more important in forms which lack a functional dewlap, anoles which do differ strongly in color and pattern (and even in structure) may intergrade (e.g. Lazell, 1962). Further, every sibling *Anolis* species of which I am aware is discovered to show at least average structural differences once the sample is adequate. The apparently contradictory case of *A. alter* newly described by me (Williams,

1962b) I believe to be an instance of inadequate sample size. The material of the *hendersoni* complex is now quite sufficient to demonstrate average differences, were they in fact present. It is true that the largest males of *dolichocephalus* are slightly but distinctly longer headed than any other members of the complex, but this is quite obviously not the sort of evidence that suggests species status.

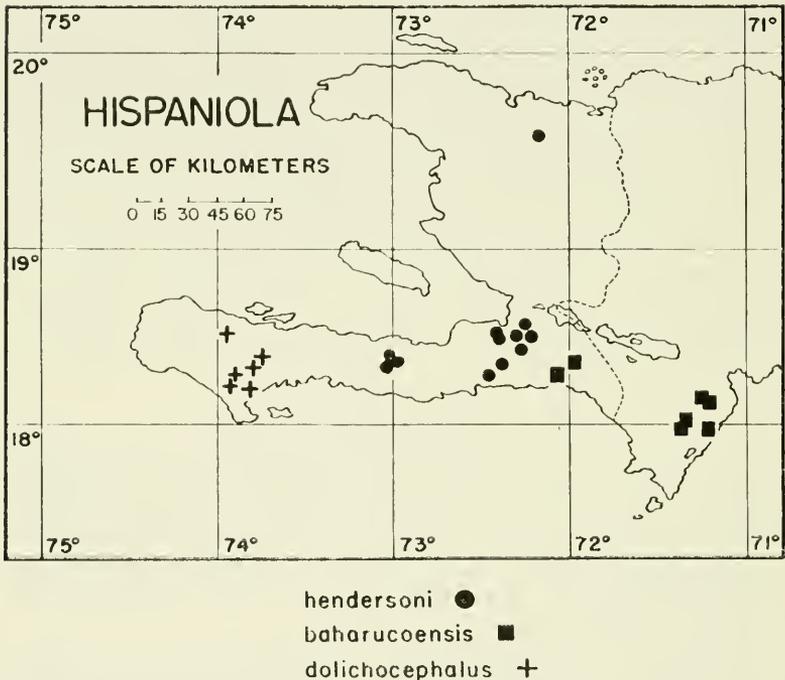


Figure 5. Map of the distribution of the races of *A. hendersoni*.

ZOOGEOGRAPHY

The two specimens from the Citadelle indicate that much is still to be found out about this group in Hispaniola. Rare as these forms have been in previous collections, they are abundant in some of the most recent. It is therefore impossible to reason on the basis of negative evidence that *A. hendersoni* is really absent in any part of Hispaniola north of the Cul de Sac—whether in Haiti or in the Dominican Republic.

It is thus too early to discuss the origin or history of the *hendersoni* complex. It is, however, worth calling attention to the tripartite division within what I have called (1961, 1962a) the "southern island"—Hispaniola south of the Cul de Sac. This singular pattern occurs in several other instances and will be discussed further in later papers of this series.

ACKNOWLEDGMENTS

I am indebted to A. S. Rand and J. D. Lazell, Jr. who first collected the new subspecies of *hendersoni* described herein and to Luc and George Whiteman of Port-au-Prince, Haiti, who obtained most of the other material reported here. I am grateful also to Dr. Doris M. Cochran and Mr. C. M. Bogert who permitted me to examine material in their charge and to Dr. Albert Schwartz who has allowed me to study material he has very recently collected. A grant from the American Philosophical Society and National Foundation Grant NSF G5634 have supported part of the collecting reported here. Work on these and other Haitian anoles has continued under NSF G16066.

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B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS.

JULY 10, 1963

NUMBER 187

THE LABYRINTHODONT DENTITION¹

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Because of the phylogenetic importance of the Labyrinthodontia, numerous studies have been made of the cranial anatomy of members of this great amphibian group. Little, however, has been written regarding their dentition. My attention was called to this subject because of the unusual nature of the dentition of a newly discovered trimerorhachoid rhachitome from the Texas Permian, which is to be described in a forthcoming paper as *Neldasaurus wrightae*.² In the present paper I shall review our current knowledge of the dentition of the Labyrinthodontia as a whole. The data on which this review is based, summarized in Table 1, were drawn directly from specimens in a few instances but most were obtained from the literature; measurements recorded are those quoted by authors or determined from scale drawings of original or reconstructed specimens. Fifty-one genera, including temnospondyls, anthracosaurs and a crossopterygian were reviewed. The arrangement of labyrinthodont genera in the table is essentially as in Romer's 1947 classification (pp. 310-319).

Characteristic of labyrinthodonts generally is a dentition which includes, in addition to marginal tooth rows, palatal tusks and often, at least, a shagreen of denticles on the palate and the coronoid region of the lower jaw. The primitive condition, it would seem, was one in which a relatively small number of marginal teeth were present and the palatal dentition consisted

¹This paper is part of a thesis submitted to the Department of Biology of Harvard University as partial fulfillment of the requirements for the degree of Doctor of Philosophy, August, 1962.

²This is a *nomen nudum* here, and will enter scientific nomenclature with the publication of my projected description of this new form.

of a single stout tusk-pair on each of the three lateral palatal elements. There is, however, wide variation in the number of marginal teeth, and in various instances a trend toward reduction in size and concomitant increase in numbers of palatal tusks.

In this paper I have confined attention to the dentition of the upper jaw and palate, since, apart from the occasional presence of symphyisial tusks, the lower dentition in great measure mirrors the marginal dentition of the upper jaw. Further, no attempt is made to ascertain how widely a shagreen of tiny denticles is present on the palate, since, even if present, such a shagreen is often destroyed in preparation and consequently unrecorded.

The data presented in the tabulation include:

- (1) A formula representing the palatal dentition, recorded in terms of the numbers of tusks (or tusk pits) and small teeth on the vomer, the palatine and the ectopterygoid of one side. For example, the formula for the palatal dentition of *Lyrocephalus* is 2—2(3)—(13), which means there are two tusks on the vomer, two tusks and three smaller teeth on the palatine, and thirteen small teeth on the ectopterygoid.
- (2) Information concerning the marginal upper jaw dentition such as (a) the number of premaxillary and maxillary teeth, (b) the presence of regionally enlarged teeth forming "canine peaks" whenever it could be determined, indicated on the table by a plus sign.
- (3) Skull length taken as the distance from the tip of the snout to the end of the occipital condyle. (This, taken together with the figure on the number of teeth, will give an indication of relative tooth spacing.)
- (4) Sources, placed here to avoid repetition in the text.

It is generally and reasonably assumed that labyrinthodonts are descended from rhipidistian crossopterygians. The dentition is known in only a few crossopterygians, such as *Eusthenopteron*, *Megalichthys* and *Ectosteorhachis*. In *Eusthenopteron* of the Upper Devonian we find: (1) a series of very numerous small marginal teeth, (2) a row of numerous small teeth along the outer margins of the vomer, palatine and ectopterygoid, (3) larger tusks, few in number, placed more medially on these three elements, with some indication of tusk and pit pairing; as far as known the vomer bears only one pair of tusks.

In the following discussion we will consider marginal and palatal dentitions separately.

MARGINAL TEETH

The oldest known labyrinthodont, *Ichthyostega* from East Greenland beds near the Devonian-Carboniferous boundary, is somewhat off the main line of labyrinthodont evolution but shows a modest number of well spaced teeth — 8-9 premaxillary, 16-18 maxillary — of fairly good size, most about the same length but with the posterior premaxillary teeth somewhat enlarged. *Acanthostega*, an ichthyostegalian of comparable age, appears to have had more maxillary teeth — about 30. Romer (1947) provisionally associated the Colosteidae of Linton with the ichthyostegals. The marginal dentition of the colosteid *Erpctosaurus*, however, does not agree with that of the ichthyostegals, for here, in contrast, there is a reduced number of rather large premaxillary teeth and very numerous small maxillary teeth.

All further well-known labyrinthodonts can be clearly divided into temnospondyls and antracosaur. The marginal dentition of temnospondyls will be dealt with first.

The most primitive temnospondyls (apart from their peculiar "keyhole orbit") are clearly the loxommids, such as *Baphetes* and *Megaloccephalus*. In the number of premaxillary teeth both appear primitive, but the maxillary series — 21 in *Baphetes*, 40 in *Megaloccephalus* — are in contrast, the larger number being perhaps proportional to skull elongation in *Megaloccephalus*.

Exemplifying the next higher stage are the edopsoids, *Edops* and *Eugyrinus* (the last was considered a trimerorhachoid by Romer, but recent studies by Carroll indicate that *Eugyrinus* is more primitive and generalized than the trimerorhachoids). Here the premaxillary teeth are primitive in number (9, ?7) and the number of maxillary teeth (24, 29) is fairly low.

Among trimerorhachoids, some agree fairly well with the primitive edopsoid pattern (the maxillary count of 19 in *Saurcrpton* is lower) but within the group there is a notable tendency toward an increase in the number of marginal teeth. The premaxillary count increases from 9 in *Saurcrpton* to 12 in *Trimerorhachis* and *Eobrachyops* and to 15 in *Neldasaurus* and *Drinosaurus*. The number of maxillary teeth is somewhat increased in *Eobrachyops*, *Drinosaurus* and *Trimerorhachis* and increased to the spectacularly high number of approximately 93 in *Neldasaurus*.

Certain forms which Romer grouped as the Micropholoidea show characters more or less intermediate between primitive edopsoids and the "typical" rhachitomes of the Lower Permian.

Three members of the group — *Archegosaurus*, *Chenoprosopus* and *Lysipterygium* — show a “normal” rhachitomous tooth count with 8-11 premaxillary and 27-29 maxillary teeth; *Micropholis*, however, has a reduced dentition with 5 premaxillary and 16 maxillary teeth, while *Platyops*, in correlation with an extremely elongate skull, has a total of about 65 marginal teeth in the upper jaw.

The “typical” rhachitomes, the Eryopsoidea, include a wide variety of Permian labyrinthodonts and a few Carboniferous predecessors. Dental formulas are given for nine members of this group (nos. 20-28, Table 1) and show some variation within the group. Premaxillary teeth range from a maximum of 15 in the broad-snouted *Zatrachys* and its Carboniferous relative *Acanthostoma*, through 13 in *Eryops* to a low figure of 5-8 for *Actinodon*, *Cacops* and trematopsids. Some eryopsoids have a reduced maxillary count with a low of 12 in *Cacops*; *Eryops*, on the other hand, has an increased count of 38.

The trematosaur, a persistently rhachitomous, early Triassic, fish-eating group, reflect accompanying snout elongation in tooth numbers. Although the premaxillary teeth retain a count of 10-12, in the long-snouted forms the number of maxillary teeth increases, reaching a figure of 50 in *Trematosuchus*.

The neorhachitomes of the late Permian are presumed to have been derived from eryopsoids. Such a typical form as *Rhincosuchus* has a marginal dentition almost exactly like that of its morphological ancestor *Eryops*; *Lydekkerina*, however, has a reduced formula, with only 20 maxillary teeth. Still more advanced neorhachitomes of the early Triassic, those apparently leading to the capitosaur, are such forms as *Wetlugasaurus*, *Volgasaurus* and *Benthosuchus*. Here, facial elongation is accompanied by an increase in the number of maxillary teeth to 52, 56 and 61 in these genera, respectively. A high number of maxillary teeth occurs in capitosaur, reaching a peak in *Mastodonsaurus*, which has 23 premaxillary and about 75 maxillary teeth. Parallel in development to the capitosaur are those forms grouped as the metoposaur. *Metoposaurus* itself has a “generalized” count of 10 premaxillary and 34 maxillary teeth, but in the American species *Eupclor browni* and the European *Eupclor fraasi* the count increases to about 60 maxillary teeth in the former and to 90 in the latter. Certain short-faced Triassic forms tend to have reduced counts; the brachyopid *Batrachosuchus* having but 17 maxillary teeth and the plagiosaur *Gerrothorar* having somewhat over 26.

A group by group account of variations of marginal tooth count in temnospondyls has been presented above. As can be seen, no consistent pattern emerges. One gains the general impression of a probable early temnospondyl condition of 9 or so premaxillary teeth and a maxillary count in the 20's, with a modest increase, on the average, in typical rhaehitomes. Occasionally there are reductions to lower figures (as, for example, in *Sclerocephalus*, *Actinodon*, or the dissorophid *Cacops*). On the whole, however, variations are toward higher figures in later forms. In some cases increases in tooth count are definitely associated either with notable snout elongation, as in *Platyops* and the trematosaur, or, as in capitosaur and metoposaur, with a combination of moderate skull elongation and absolute increase in size, the teeth failing to increase in proportion to the total size of the animal. Most exceptional of all are the trimerorhachoids, particularly *Neldasaurus*, where an exceedingly high tooth count may be found in a skull of modest proportions. No consistent correlation between tooth number and skull size can be demonstrated.

Anthracosaurian dentition is known in only a few, mainly Carboniferous forms. Here the premaxillary teeth are low in number, related to the usually narrow snout and the fairly large size of the individual teeth. Marginal teeth are essentially of two types: either large and few in number, as in *Anthracosaurus* and *Pteroplax*, or small and more numerous, as in *Pholiderpeton*, *Neopteroplx* and, especially, *Archeria*, where the exact count is indeterminate although the teeth are certainly very numerous. Marginal tooth counts in the premaxilla and maxilla of *Seymouria* are low; *Kotlassia* shows a slight increase over the primitive number.

Regionally enlarged teeth forming "canine peaks" occur sporadically in different labyrinthodont groups but appear to have been fairly common in primitive forms.

PALATAL TEETH

Known rhipidistian crossopterygians have, as mentioned above, (1) a very large number of small teeth in a row along the margins of the vomer, the palatine and the ectopterygoid, (2) larger tusks more medially placed on these three bones. As is well known, in all typical labyrinthodonts the larger teeth are retained while the lateral row of smaller teeth is lost. But, surprisingly, in *Ichthyostega* there is no trace at all of the "tusk" row;

instead it appears that the lateral row of numerous, essentially even-sized teeth has been retained. In this regard *Ichthyostega* is very far removed from the condition expected in the ancestor of later labyrinthodonts.

Primitive temnospondyls proper almost always have one pair of tusks on each of the three bones, the vomer, palatine and ectopterygoid. This is true almost without exception in loxommids, edopsoids and most eryopsoids. Occasionally, a replacement pit may be absent (? or indeterminate) but exceptions are rare. In palatal dentition, colosteids (e.g. *Erpetosaurus*) are typically temnospondyl in character, thus arguing strongly against Romer's suggestion of ichthyostegal relationships for these animals.

In numerous more specialized or advanced labyrinthodonts there is an increase in the number of smaller palatal teeth and a tendency toward reduction of the more prominent tusks, usually those on the ectopterygoid. The presence of this pattern in different groups indicates that this trend has occurred several times in parallel fashion. It is, for example, seen in trimerorhachoids (except *Eobrachyops*), micropholoids and trematosaurus. In *Rhinesuchus*, which appears closely related to typical eryopsoids, this trend is seen again, leading to conditions in capitosaurus where, as in metoposaurus, the increase in the number of small teeth is very prominent. In some short-faced Triassic forms the increase in smaller palatal teeth is not so pronounced — a condition no doubt correlated with the short palate in these animals.

Distinctive of the anthracosaurs is the absence of vomerine teeth — apparently related to the narrow palatal exposure of the vomers in these forms. In the few palates known, there are generally a pair of large palatine tusks and a modest number of ectopterygoid teeth, the front ones tusk-like. In *Pholidogaster*, with six tusk-like teeth on the ectopterygoid, and in *Anthracosaurus*, where a tusk pair is accompanied by a pair of fairly large teeth, we encounter conditions reminiscent of the crossopterygians, in which the palatine had a row of large teeth.

Seymouriamorphs are unusual among anthracosaurs. *Scymouria*, in contrast to other anthracosaurs, has a pair of vomerine tusks and — in parallel fashion to some temnospondyl groups — has lost the ectopterygoid teeth. *Kottassia* resembles other anthracosaurs in lacking vomerine teeth but has a close-set row of small teeth on the palatine and ectopterygoid, decreasing gradually in

size from front to back. These differences between known anthracosaurians suggest much variation within the group, but the extent of this variation is at present incompletely known.

I wish to express my appreciation to Dr. Alfred S. Romer of the Museum of Comparative Zoology for his generous aid and many helpful suggestions during the preparation of this paper. I am also indebted to Professor Bryan Patterson and Dr. Ernest E. Williams of the Museum of Comparative Zoology for constructive criticism of the manuscript.

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TABLE I
Labyrinthodont Dentition

Form	Palatal Dentition v - p - ee	Marginal Dentition		“Canine Peaks”	Skull Length (in mm.)	Source
		pmx	mx			
1. Eusthenopteron (Crossopterygian)	2 - 3 - 4 (12)-(15)-(28)	20±	60-61		80±	Jarvik (1954)
2. Ichthyostega	(6)-(8-10)-(6)	8-9	16-18	+	150	Jarvik (1952)
3. Epetosauros	(2)-2-2	4	49	+	85	Romer (1930; 1947) Steen (1931)
4. Baphetes	2 - 2 - 2	8	21	+	270	Watson (1929)
5. Megalocephalus	2 - 2 - 2	7	40	+	330	Watson (1929)
6. Denderpeton	0 - 2 - 2	—	—	?	70	Steen (1934)
7. Cochleosaurus	2 - 2 - 2	5?	7?	+	70	Steen (1931; 1938)
8. Edops	2 - 2 - 2	9	24	+	510	Romer and Witter (1942)
9. Eugyrinus	1 - 1 - 0?	7?	29		18	Watson (1940)
10. Saurepeton	2 - 2 - 2	9	19		60	Romer (1930)
11. Neldasaurus	2-2(8)-2(21)	15	93		158	M.C.Z. 2200
12. Trimerorhachis	2(6)-2(8)-(6)	12	38		100±	Case (1935)
13. Eobraehyops	1 - 2 - 1	12?	30		79	Watson (1956)
14. Dvinosaurus	2(12)-2-1(5)	15	30		180	Sushkin (1936) Bystrow (1938)
15. Archeosaurus	4 - 2(4) - (6)	8	27	+	350	Watson (1919) Whittard (1928)
16. Chenoprosopus	2 - 2 - 2	11	29	+	224	Langston (1953) Romer (1947) Watson (1919)

TABLE 1 (Cont.)
Labyrinthodont Dentition

Form	Palatal Dentition v - p - ec		Marginal Dentition pmx mix		"Canine Peaks"	Skull Length (in mm.)	Source
	v	p - ec	pmx	mix			
17. <i>Lysipterygiium</i>	0	(9) - (4)	8	29		58	Branson (1935)
18. <i>Platyops</i>	2	(15)-2(6)-(22)	—	-65-		278	Efremov (1933) Bystrow (1935) Watson (1913)
19. <i>Micropholis</i>	2	(2) - (3) - 0	5	16		34	Broili, Schroeder (1937)
20. <i>Eryops</i>	2	- 2 - 2	13	38	+	356	Sawin (1941)
21. <i>Sclerocephalus</i>	2	- 2 - 4	10	14		156	Broili (1926) Romer (1947)
22. <i>Actinolon</i>	1	- 2 - 2	7	16	+	170	Gandry (1887) Thevenin (1910) Williston (1910)
23. <i>Cacops</i>	1	- 2 - 0	8	12		127	Williston (1910)
24. <i>Acheloma</i>	2	- 2 - 2	5	25	+	63	M.C.Z. 1419
25. <i>Trematops</i>	2	- 2 - 2	7	23	+	63	Olson (1941) Williston (1909)
26. <i>Parioxys</i>	2	- 2 - 2	6	30	+	142	M.C.Z. 1162
27. <i>Zatrachys</i>	2	- 2 - 2	15	15-17	+	104	Langston (1953)
28. <i>Acanthostoma</i>	2	- 2 - 2	15	34		40	Steen (1937)
29. <i>Lyrocephalus</i>	2	- 2(3)-(13)	10	32	+	166	Säve-Söderbergh (1936)
30. <i>Trematosuchus</i>	2	(10)-1(4)-1(12)	12	50	+	411	Haughton (1915; 1925)
31. <i>Trematosaurus</i>	2	(4)-2(2)-(19)	6	40	+	157	Watson (1919)
32. <i>Platystega</i>	2	(6)-2(2)-(18)	12	32	+	335	Säve-Söderbergh (1936)
33. <i>Rhinesuchus</i>	2	(5)-2(21)-(9)	13	39	+	90	Watson (1919) Haughton (1925)

34. Lydekkerina	2(3)-1(5)-0	10	20	76	Watson (1912)
35. Wetlugasaurus	2(14)-2(11)-(14)	15	52	160	Broili and Schroeder (1937)
36. Volgasauros	1(18)-2(14)-2(19)	14	56	123	Bystrow and Efremov (1940)
37. Benthosuchus	2(27)-2(10)-(19)	13	61	123	Efremov (1940)
38. Mastodonsaurus	2(34)-2(10)-(30)	23	75	666	Efremov (1940)
39. Metoposaurus	2(16)-2(8)-(14)	10	34	294	Fraas (1889)
40. Eupelor (Anaschisma)	2(6) 2(9)-0	22	48-60	476	Watson (1919)
41. Eupelor	2(18)-2(9)-(30)	13	90	380	Watson (1919)
42. Batrachosuchus (Buetneria)	(7)-1(3)-(4)	12	17	156	Watson (1919)
43. Gerrothorax	(11)-(6)-(5)	8	26±	132	Branson and Mehl (1929)
44. Pholidogaster	0-2(2)-6		-29-	—	Case (1922)
45. Anthracosaurus	0-2-2(2)	4	17	288	Sawin (1945)
46. Anthracosaurus (Linton)	0 - 2 - 2(+?)	3	25±	+	Romer (1947)
47. Pholiderpeton	0 - 2 - 2(3)	3	40	+	Watson (1956)
48. Pteroplax	0 - 2 - 2(8)	6	27	400±	Nilsson (1934, 1937)
49. Neopteroplx	0 - 2 - 2(4)	3	37	+	Watson (1929)
50. Seymouria	2 - 2 - 0	5	17	+	Watson (1912, 1926)
51. Kotlassia	0 - (7)-(10-13)	8-9	29-32	190	Attthey (1876)
					Romer (1963)
					White (1939)
					Williston (1911)
					Bystrow (1944)

B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS.

JULY 29, 1963

NUMBER 188

REDESCRIPTION OF SOME CAVERNICOLOUS
PSEUDOSCORPIONS (ARACHNIDA, CHELONETHIDA)
IN THE COLLECTION OF THE
MUSEUM OF COMPARATIVE ZOOLOGY

By

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Through the courtesy of Dr. H. W. Levi, the author was able to examine the collections of pseudoscorpions in the Museum of Comparative Zoology at Harvard College. The material considered in this paper was discovered among undetermined collections and recognized as type material by the characteristics mentioned in the treatment of the individual species. Included here are the types of three little-known, cavernicolous forms, *Blothrus packardi* Hagen, 1879, *Chthonius coccus* Packard, 1884, and *Obisium cavicola* Packard, 1884. Detailed redescriptions of these species based on mounted specimens are presented. In addition, the specimens from Mammoth Cave, Kentucky, considered conspecific with *B. packardi* (from Wyandotte Cave, Indiana) by Hagen, Packard and others, are separated from that species and made the basis of a new species.

Suborder HETEROSPHEIRONIDA Chamberlin

Family CHTHONIIDAE Hansen

Subfamily CHTHONINAE Daday

Tribe CHTHONINI Chamberlin

Genus KLEPTOCHTHONIUS Chamberlin

Subgenus CHAMBERLINOCHTHONIUS Vachon

KLEPTOCHTHONIUS (CHAMBERLINOCHTHONIUS) PACKARDI
(Hagen), new combination

Blotrus packardi Hagen, 1879, Zool. Anz., vol. 2, p. 399.

Chthonius packardi [pro parte]: Hubbard, 1880, Amer. Ent., vol. 3, p. 83.

Chthonius packardii [pro parte]: Packard, 1888, Mem. Natl. Acad. Sci. Washington, vol. 4, p. 43.

Chthonius packardi [pro parte]: Banks, 1895, Jour. New York Ent. Soc., vol. 3, p. 13.

Chthonius? packardi: Beier, 1932, Das Tierreich, vol. 57, p. 61.

Genus? packardi: Hoff, 1949, Bull. Illinois Nat. Hist. Surv., vol. 24, p. 443.

Chthonius? packardi: Hoff, 1958, Amer. Mus. Novitates, no. 1875, p. 4.

Material: The type collection, consisting of 5 males and 1 female, was identified by a label reading "Wyandotte Cave, Ind." in the presumed handwriting of H. Hagen. Another female specimen with the label "Wyandotte New Cave, Packard" is taken to be that specimen mentioned by Packard (1888, p. 44). All of these specimens, with the exception of one male from the type collection, were mounted on slides for study. One of the mounted males has been designated the lectotype. Although Packard and Hubbard have given fairly accurate general descriptions (cf. Packard, 1888, p. 43-45), a redescription based on the mounted specimens is desirable.

Diagnosis: Male: (Measurements are given first for the lectotype, while in parentheses are given the ranges for the three paratypes.) Body and appendages generally of chthoniid facies but more slender than in epigeian species (see Packard, 1888, fig. 12, p. 45); lightly sclerotized and very light brown in color, the chelicerae and palps a little darker than other parts. Carapace nearly square in dorsal outline, the lateral margins usually a little convex; surface lightly sculptured; no epistome; no eyes or eye spots; total setae 16 (15-18), of which 3 (2-4) are on the anterior margin and 2 (2-3) near the posterior margin. Abdomen elongate; tergal and sternal scuta entire and smooth; pleural membranes very finely granulate; tergites of lectotype with 2:2:2:2:4:4:6:6:6:2 long, acuminate setae, paratypes with 2-3:2-3:2-3:2-4:4:4:5-6:6:6:2-5 setae; sternites 4-8 with 7-10 acuminate setae, shorter and more slender than those of the tergites.

Chelicerae generally of chthoniid size and proportions; hand with 7 setae; fixed finger with a row of 6-9 teeth, the movable finger with a row of 4-7 teeth, the teeth of each finger being heavy and triangular and becoming progressively lower and

smaller toward the proximal end of the finger; no isolated sub-distal tooth on either finger; the galea represented by a small, but distinct, elevation; galeal seta distal to the midpoint of the finger; serrula exterior with about 18 teeth; flagellum of 8 unilaterally branched setae.

Palps long and slender; surfaces smooth; setae long and acuminate; general proportions of podomeres shown in Figure 1; chelal hand rather long and narrow, fingers long and gently curved; tactile setae as shown in Figure 2; fixed finger with a marginal row of alternating large and small teeth — 28 (28-29) widely-spaced large, acutely triangular teeth and 20 (20-22) small, low, triangular teeth between; movable finger distally with teeth similar to those on fixed finger, 17 (16-21) large and 16 (14-18) small, while proximally the teeth abruptly become low, rounded and contiguous, 11 (9-11) in number; proximal end of the movable finger with a long cylindrical process from its dorso-median border, parallel with the long axis of the finger and extending well beyond the proximo-ventral margin (this projection apparently serves for broader attachment of the museles which move the finger and provides increased leverage). Trochanter 1.9 (1.7-2.0), femur 7.2 (7.1-7.2), tibia 2.5 (2.4-2.7), chela 7.6 (7.6-8.0) and hand 3.0 (2.8-3.1) times as long as broad; movable finger 1.69 (1.61-1.69) times as long as hand.

Legs generally of chthoniid form but elongate and slender. First leg with coxa bearing spines as characteristic of the genus, 5 (7) on the right coxa and 6 (6-8) on the left; fourth leg with tactile setae on tibia 0.40 (0.39-0.41), on metatarsus 0.24 (0.23-0.28), and on telotarsus 0.16 (0.21-0.26) the length of the segment from the proximal end.

Genitalia essentially as figured by Chamberlin (1931, fig. 50E) for *K. crosbyi*, and Vachon (1952, fig. 2) for *K. henroti*; about 15 setae on the anterior operculum; 10-12 setae on each side of the aperture; 7-8 setae on the posterior operculum between the spiracles.

Female: (The first measurements given are those for the female from Hagen's type series, which is designated the allotype, while in parentheses are given those for the specimen from "Wyandotte New Cave.") The female is essentially similar to the male except for slightly larger size. Carapace with a total of 16 (17) setae, of which 4 are on the anterior margin and 2 (3) at the posterior margin; no eyes or eye spots. Abdominal

tergites with 2:2:2:3:4:4:5:6:6:2 (2:2:3:4:4:6:4:6:6:4) setae; sternites with 6-10 setae.

Chelicera slightly larger than in the male; galea somewhat larger and more distinct than in the male, though not so sharply set off from the finger as indicated by Packard (1888, fig. 12d).

Palps like those of the male but slightly larger; fixed finger with 29 (29) large and 21 (20) small teeth; movable finger with 20 (18) large and 16 (14) small teeth distally and 10 (11) low, rounded teeth proximally; trochanter 1.8 (1.9), femur 7.0 (6.7), tibia 2.6 (2.5), chela 7.6 (7.1) and hand 2.9 (2.7) times as long as broad; movable finger 1.67 (1.64) times as long as hand.

Legs as in the male but slightly larger. Coxal spines 7 (6) on the right coxa and 7 (6) on the left. Leg IV with tactile setae on tibia 0.42 (0.40), on metatarsus 0.22 (0.24) and on telotarsus 0.20 the length of the segment from the proximal margin.

Genitalia essentially as figured by Chamberlin (1931, fig. 52A) for *Chthonius ischnochles* but with setae of anterior operculum grouped more toward the midline and the row of setae on the posterior operculum extending farther lateral on each side; anterior operculum with 10 irregularly grouped setae; posterior operculum with a row of 6 (8) setae between the spiracles.

Measurements (in mm.): Male lectotype and paratypes (range of latter in parentheses): Body length 1.97 (1.79-1.89); carapace 0.60 (0.55-0.58) long, greatest width 0.57 (0.55-0.57); abdomen 0.73 (0.80-0.88) broad. Chelicera 0.45 (0.45-0.47) by 0.22 (0.20-0.23). Palpal trochanter 0.26 (0.23-0.27) by 0.14 (0.13-0.14); femur 0.90 (0.90-0.93) by 0.12 (0.12-0.13); tibia 0.34 (0.33-0.34) by 0.14 (0.12-0.14); chela 1.32 (1.29-1.33) by 0.18 (0.16-0.18); hand 0.50 (0.50-0.51) by 0.17 (0.16-0.18); movable finger 0.84 (0.83-0.84) long; proximal process of movable finger 0.033 (0.039-0.043) long. Leg I: basifemur 0.56 (0.55-0.57) by 0.08 (0.08); telofemur 0.23 (0.23-0.25) by 0.07 (0.07); tibia 0.28 (0.29-0.31) by 0.06 (0.06); tarsus 0.59 (0.58-0.60) by 0.05 (0.05-0.06). Leg IV: entire femur 0.77 (0.76-0.80) long; basifemur 0.28 (0.30-0.31) by 0.21 (0.18-0.23); telofemur 0.55 (0.53-0.57) by 0.19 (0.16-0.20); tibia 0.51 (0.51-0.54) by 0.10 (0.09-0.10); metatarsus 0.25 (0.25-0.26) by 0.07 (0.07); telotarsus 0.66 (0.64-0.66) by 0.06 (0.05-0.06).

Female allotype and paratype (latter in parentheses): Body length 1.94 (1.89); carapace 0.59 (0.61) long, greatest width 0.61 (0.60); abdomen 0.88 (0.84) broad; chelicera 0.50 (0.48) by 0.23 (0.22). Palpal femur 0.96 (0.98) by 0.14 (0.15); tibia

0.36 (0.37) by 0.14 (0.15); chela 1.39 (1.40) by 0.18 (0.20); hand 0.53 (0.54) by 0.18 (0.20). Movable finger 0.88 (0.88) long; proximal process of movable finger 0.045 (0.043) long. Leg I: basifemur 0.57 (0.57) by 0.08 (0.09); telofemur 0.24 (0.24) by 0.07 (0.08); tibia 0.31 (0.31) by 0.07 (0.07) and tarsus 0.58 (0.61). Leg IV: entire femur 0.81 (0.82) long; basifemur 0.30 (0.32) by 0.22 (0.23); telofemur 0.58 (0.58) by 0.20 (0.21); tibia 0.54 (0.56) by 0.10 (0.10); metatarsus 0.26 (0.25) by 0.07 (0.08); telotarsus 0.66 by 0.06.

Remarks: This species is restricted to the type locality as far as is known at present. The specimens from Mammoth Cave, Ky., and vicinity recorded as *Chthonius packardi* by Hagen, Packard, and others, actually belong to *Kleptochthonius cerberus* Malcolm and Chamberlin or to *K. hageni* n. sp. (see below). This species and *K. gertschi* Malcolm and Chamberlin are unique in the genus in the complete absence of eyes or eye spots. These two species may be differentiated readily by the number of setae of the cheliceral hand (7 in *packardi*, 9 in *gertschi*) and the number of setae at the posterior border of the carapace (2 in *packardi*, 6 in *gertschi*).

KLEPTOCHTHONIUS (CHAMBERLINOCHTHONIUS) HAGENI
new species

Material: Holotype male and allotype "with a dead bat" at bottom of Mammoth Dome, Edmonson Co., Ky., collected Sept. 11, 1874 by F. W. Putnam. Male paratype from Mammoth Cave, Edmonson Co., Ky. (no other data). Female paratypes from Mammoth Cave collected by A. S. Packard (?), Apr. 30, 1874, and by L. Hubricht, Dec. 15, 1956, and from Long Cave, Glasgow Junction, Ky., collected by F. G. Sanborn, Nov. 5, 1874.

Diagnosis: Male: (Measurements are given first for the holotype, while in parentheses are given those for the male paratype.) Body and appendages generally of chthoniid facies but more slender than in epigean species; lightly sclerotized and pale brown in color, the chelicerae and palps somewhat darker than the body and legs. Carapace nearly square in dorsal outline, the lateral margins a little convex; no epistome; 2 eyes present in the anterior position with moderately well-developed corneas; no trace of posterior eyes or eye spots; total setae 20, of which 6 are on the anterior margin and 4 are situated near the posterior margin; surface generally smooth, but lightly sculptured on the sides. Abdomen elongate; tergal and sternal scuta entire and

smooth; pleural membranes weakly marked with fine granulations. Tergites of holotype with 2:2:2:3:5:4:6:6:7:7 long acuminate setae, paratype with 2:3:4:4:5:5:6:6:8:6 setae; sternites 4-8 with 8-11 acuminate setae, shorter and more slender than those of the dorsum.

Chelicera of chthoniid facies; hand with 7 setae; fixed finger with a row of 8-10 teeth, the movable finger with a row of 5-6 teeth, the teeth of each finger being generally heavy and triangular but becoming progressively smaller toward the proximal end of the row; no isolated sub-distal tooth on either finger; the galea represented by a low elevation on the movable finger; galeal seta distal to the midpoint of the finger; serrula exterior with about 18 teeth; flagellum consisting of 8 unilaterally branched setae.

Palps long and slender; surfaces smooth; setae long and acuminate; general proportions of podomeres shown in Figure 3; tactile setae of chela as shown in Figure 4; fixed finger of chela with a marginal row of alternating large and small teeth: 44 (39) large, acutely-pointed, widely-spaced teeth with 20 (18) tiny, rounded teeth between. Movable finger distally with teeth similar to those on the fixed finger, 30 (29) large teeth and 20 (10) tiny teeth between, while proximally the teeth abruptly become low, rounded and contiguous, 7 (7) in number; proximal end of the movable finger with only a short, broad projection from the dorso-median border, not extending beyond the proximo-ventral margin. Trochanter 2.0 (2.2), femur 6.9 (6.4), tibia 2.3 (2.1), chela 7.1 (6.8), and hand 2.8 (2.6) times as long as broad; movable finger 1.62 (1.66) times as long as the hand.

Legs generally of chthoniid facies but elongate and slender. First leg with coxa bearing spines as characteristic of the genus, 7 (8) on the right and 8 (8) on the left coxa; fourth leg with tactile setae on tibia 0.38 (0.38), on metatarsus 0.24 (0.23) and on telotarsus 0.26 (0.20) the length of the segment from the proximal end.

Genitalia essentially as in other species of the genus; with 12-15 setae on the anterior operculum; 7-12 setae on each side of the aperture; and 6-9 setae on the posterior margin of the 4th sternite between the spiracles.

Female: (The first measurements given are those for the allotype, while in parentheses are given the ranges for the three paratype females.) The female is essentially similar to the male. Carapace with a total of 20 (19-20) setae, of which 6 (5-6) are at the anterior margin and 4 (3-4) near the posterior margin;

2 eyes in the anterior position with moderately well developed corneas; no trace of eyes or eye spots at the posterior position. Abdominal tergites with 2:2:3:4:4:6:6:6:?:?:(2:2:2:4:3:4:4:5:6:6:6:7:6:7:4:6) setae; sternites with 8-12 setae.

Chelicera similar to that of the male; 7 (7) setae on the hand; galeal tubercle somewhat larger and more distinct than that of the male. Palps as in the male but somewhat larger and heavier. Fixed finger with 40 (37-39) large and 19 (15-17) small teeth; movable finger with 28 (25-27) large and 15 (15-17) small teeth distally and 7 (7-9) low, rounded teeth proximally. Trochanter 2.0 (1.9-2.0), femur 6.7 (6.3-6.6), tibia 2.3 (2.3), chela 6.7 (6.2-6.7) and hand 2.7 (2.4-2.7) times as long as broad; movable finger 1.63 (1.59-1.64) times as long as hand.

Legs as in the male; coxal spines 6 (7-9) on the right coxa and 7 (6-9) on the left. Leg IV with tactile setae on tibia 0.37 (0.29-0.36), on metatarsus 0.27 (0.26-0.29) and on telotarsus 0.28 (0.23-0.27) the length of the segment from the proximal margin.

Genitalia essentially as in *K. packardi*; anterior operculum with 9 (8-9) grouped setae; posterior operculum with a marginal row of 8 (7-8) setae between the spiracles.

Measurements (in mm.): Male holotype and paratype (latter in parentheses): Body length 2.14 (2.08); carapace 0.65 (0.62) long, greatest width 0.64; abdomen 0.84 (0.95) broad. Chelicera 0.56 (0.53) by 0.26 (0.25). Palpal trochanter 0.31 (0.31) by 0.16 (0.15); femur 1.06 (0.99) by 0.15 (0.15); tibia 0.41 (0.37) by 0.18 (0.18); chela 1.50 (1.45) by 0.21 (0.21); movable finger 0.96 (0.92) long; proximal process of movable finger 0.020 (0.016) long. Leg I: basifemur 0.63 (0.60) by 0.09 (0.09); telofemur 0.25 (0.25) by 0.08 (0.08); tibia 0.32 (0.33) by 0.07 (0.07); tarsus 0.64 (0.62) by 0.06 (0.06). Leg IV: entire femur 0.93 (0.86) long; basifemur 0.36 (0.34) by 0.28 (0.25); telofemur 0.66 (0.64) by 0.25 (0.23); tibia 0.60 (0.58) by 0.11 (0.11); metatarsus 0.31 (0.29) by 0.09 (0.09); telotarsus 0.74 (0.69) by 0.06 (0.06).

Female allotype and three paratypes (ranges of latter in parentheses): Body length 2.20 (2.30-2.55); carapace 0.60 (0.62-0.67) long, greatest width 0.60 (0.58-0.71); abdomen 0.95 (0.80-1.09) broad. Chelicera 0.56 (0.58-0.64) by 0.26 (0.27-0.29). Palpal femur 1.03 (1.05-1.18) by 0.15 (0.17-0.18); tibia 0.40 (0.42-0.46) by 0.18 (0.18-0.20); chela 1.48 (1.53-1.72) by 0.22 (0.23-0.28); hand 0.58 (0.58-0.67) by 0.21 (0.22-0.28); movable finger 0.94 (0.94-1.07) long; proximal process of movable finger 0.019

(0.017-0.025). Leg I: basifemur 0.60 (0.64-0.72) by 0.09 (0.09-0.10); telofemur 0.26 (0.26-0.31) by 0.08 (0.08-0.09); tibia 0.31 (0.31-0.36) by 0.07 (0.07); tarsus 0.62 (0.64-0.72) by 0.06 (0.06-0.07). Leg IV: entire femur 0.87 (0.94-1.00) long; basifemur 0.34 (0.36-0.37) by 0.25 (0.26-0.34); telofemur 0.62 (0.66-0.75) by 0.23 (0.23-0.30); tibia 0.57 (0.62-0.69) by 0.11 (0.11-0.13); metatarsus 0.30 (0.31-0.37) by 0.08 (0.09-0.10); telotarsus 0.72 (0.71-0.83) by 0.06 (0.06-0.07).

A deutonymph is at hand which probably pertains to this species. It was collected in Audubon Avenue, Mammoth Cave, Kentucky, by L. Hubricht on Dec. 15, 1956. It is of interest to note some points of difference evidently associated with immaturity. The appendages are all considerably stouter than those of the adults. Only 18 setae are present on the carapace, with 6 at the anterior edge and 2 at the posterior. Two coxal spines are present on each coxa I and the discal seta is wanting. The galeal tubercle is small but distinct (as in the adult). There are only 6 blades in the flagellum and only 5 setae on the cheliceral hand. The movable finger of the chela has only two setae (probably *st* and *sb*), while the fixed finger is lacking *ist* and one seta from the dorsum of the hand.

Remarks: This material from Mammoth Cave was considered by Hagen, Packard, and other early workers to be conspecific with *K. packardi* from Wyandotte Cave, Indiana, although they remarked the presence of eyes in the former and their absence in the latter. Later workers have been sceptical of this relationship (cf. Hoff, 1958, p. 4; Chamberlin and Malcolm, 1960, p. 111), but only recently has material become available to clarify the situation. Restudy of the type material has made obvious the differences between the Indiana specimens and those described here as *K. hageni*. *K. hageni* can be distinguished from *K. cerberus* Malcolm and Chamberlin, which it closely resembles, by the possession of small, but distinct, microdenticles between the macrodenticles of both fixed and movable chelal fingers, by the possession of a small but distinct galeal tubercle, and by the smooth inner edge of the movable cheliceral finger distal to the row of teeth.

In addition there are a number of other specimens from Mammoth Cave and vicinity, collected by Packard and others, and more recently by T. C. Barr, Jr., L. Hubricht, and C. Kreckler, which differ from the described forms in certain details, particularly number of eyes, chaetotaxy, and proportions of the proximal

process of the movable chelal finger. The relations of these forms to *K. hageni* and to the cave species recently described by Malcolm and Chamberlin (1961) will be treated in a later paper.

This species is named in honor of H. A. Hagen who initiated the study of cave pseudoscorpions in the United States.

Genus APOCHTHONIUS Chamberlin

APOCHTHONIUS COECUS (Packard), new combination

Chthonius coecus Packard, 1884, Amer. Nat., vol. 18, p. 203; 1888, Mem. Natl. Acad. Sci. Washington, vol. 4, p. 46.

Chthonius? coecus: Beier, 1932, Das Tierreich, vol. 57, p. 61.

Chthonius? coecus: Hoff, 1958, Amer. Mus. Novitates, no. 1875, p. 4.

Material: The two type specimens in the collection of the M.C.Z. have been mounted on slides for study. They are a male, which has been designated the lectotype, and a female, the allotype. Both were collected by Packard in Weyer's Cave (Grand Caverns), Augusta Co., Virginia, in 1874. The descriptions of the species by Packard (1884, 1888) are generally accurate, but a detailed description based on the mounted specimens is desirable. It is obvious that the species belongs in *Apochthonius*.

Diagnosis: Male lectotype: Body and appendages typical of the genus; very lightly sclerotized and pale brownish in color, the chelicerae and palps being slightly darker than the body and legs. Carapace slightly broader than long, being slightly narrower toward the posterior end; no epistome; no eyes or eye spots; total setae 22, of which 8 are at the anterior margin and 4 near the posterior margin; surface smooth. Abdomen longer than broad and smoothly rounded in outline; tergal and sternal scuta entire and smooth; pleural membranes very faintly, longitudinally striate. Tergal chaetotaxy 4:4:5:6:6:7:7:8:8:6; sternites with 8-10 setae.

Chelicera large and heavy, typical of the genus; hand with 7 setae; fixed finger with a row of 7 triangular teeth which become progressively smaller toward the base; movable finger with a row of 7-8 similar teeth and an additional tooth situated half way between the distal end of the row and the tip of the finger; galea represented by a low but distinct elevation.

Left palp of typical facies (right palp missing); general proportions of podomeres shown in Figure 5; tactile setae of chela as shown in Figure 6; fixed finger with a marginal row of 72 nearly contiguous teeth, which are tall and rectangular at the

distal end of the row, becoming low and broadly rounded toward the proximal end; movable finger with 71 similar teeth. Trochanter 1.8, femur 4.5, tibia 1.9, chela 5.5, and hand 1.7 times as long as broad; movable finger 2.27 times as long as the hand.

Legs of typical facies. First leg with coxa bearing spines as characteristic of the genus, with 2 spines on the right coxa and 3 on the left. Fourth leg with tactile setae on tibia 0.46, on metatarsus 0.25, and on telotarsus 0.20 the length of the segment from the proximal margin.

Genitalia as in other members of the genus; anterior operculum with an irregular group of 6 setae anteriorly and a row of 9 setae along the posterior margin; posterior operculum with 7 setae on each side of the aperture and a marginal row of 8 setae between the spiracles.

Female allotype: Essentially similar to the male. Carapace with a total of 22 setae of which 8 are at the anterior margin and 4 near the posterior border; no eyes or eye spots. Abdominal tergites with 4:4:6:6:6:7:7:8:?:?: setae.

Right chelicera missing; left apparently similar to that of male.

Right palp missing; left palp similar to that of male. Fixed chelal finger with 72 teeth and movable finger with 70 teeth. Trochanter 1.9; femur 4.8; tibia 1.8; chela 4.9 and hand 1.6 times as long as broad; movable finger 2.12 times as long as hand. Legs as in the male. Leg I with 3 spines on each coxa. Leg IV with tactile setae on tibia 0.46, on metatarsus 0.31, and on telotarsus 0.24 the length of the segment from the proximal margin.

Genitalia essentially the same as for *K. packardi*; anterior operculum with 8 grouped setae; posterior operculum with 7 setae in a row between the spiracles.

Measurements (in mm.): Male lectotype and female allotype (latter in parentheses): Body length 1.13 (1.07); carapace 0.40 (0.41) long, greatest width 0.44 (0.44); abdomen 0.51 (0.51) broad. Chelicera 0.36 (0.38) by 0.18 (0.18). Palpal trochanter 0.18 (0.20) by 0.10 (0.10); femur 0.43 (0.46) by 0.10 (0.10); tibia 0.22 (0.23) by 0.12 (0.12); chela 0.68 (0.72) by 0.12 (0.15); hand 0.21 (0.23) by 0.12 (0.15); movable finger 0.48 (0.50) long. Leg I (missing in female): basifemur 0.24 by 0.05; telofemur 0.12 by 0.05; tibia 0.14 by 0.04; tarsus 0.26 by 0.04. Leg IV: entire femur 0.35 (0.36) long; basifemur 0.17 (0.17) by 0.15 (0.15); telofemur 0.23 (0.23) by 0.12 (0.13); tibia 0.26

(0.27) by 0.07 (0.07); metatarsus 0.12 (0.12) by 0.05 (0.05); telotarsus 0.26 (0.25) by 0.04 (0.04).

Remarks: This is the first species of *Apochthonius* known to be cavernicolous. Unlike the troglobious species of *Kleptochthonius* it is not markedly modified for life in caves. It is generally similar to the epigean species, *A. moestus*. From this it differs in the following respects: no trace of eyes; derm less heavily sclerotized and lighter in color; slightly more slender palpal podomeres; slightly reduced chaetotaxy of the carapace and the abdominal tergites.

It is pertinent at this point to mention that we have at hand a tritonymph collected in Madison Cave, Augusta Co., Virginia, Aug. 23, 1958 by T. C. Barr, Jr. This specimen is perhaps referable to *A. coccus*, since Madison Cave is close to Weyer's cave. It is similar in most details to the type adults, but with numbers and measurements somewhat reduced as would be expected of a tritonymph. Unexpectedly, however, this individual clearly possesses two eyes in the anterior position, weakly but definitely corneate. The explanation of this situation is not certain. It may be that this nymph belongs to a separate, new species. Or it may be that the species, *A. coccus*, may contain individuals both with and without eyes. A third possibility is that nymphs of *A. coccus* possess eyes which are then lost at the adult molt (as is suggested for *Chitrella archeri* below). Only study of larger, as yet uncollected, series of specimens can throw further light on this problem.

Suborder DIPLOSPHYRONIDA Chamberlin

Family SYARINIDAE Chamberlin

Subfamily CHITRELLINAE Beier

Genus CHITRELLA Beier

CHITRELLA CAVICOLA (Packard), new combination.

Obisium cavicola Packard, 1884, Amer. Nat., vol. 18, p. 202.

Obisium cavicola: Packard, 1888, Mem. Natl. Acad. Sci. Washington, vol. 4, p. 42.

Microcreagris? cavicola: Beier, 1932, Das Tierreich, vol. 57, p. 157.

Microcreagris? cavicola: Hoff, 1958, Amer. Mus. Novitates, No. 1875, p. 12.

The specimen upon which Packard based the species *Obisium cavicola* was preserved in the M.C.Z. with a label bearing only the notation "New Market Cave, Packard." There can be no

doubt that it is the specimen in question, inasmuch as it retained the peculiar pose of the appendages and outline of body as depicted in Paekard's illustrations (1884, fig. 1, and 1888, fig. 11). The figure and description are, however, at variance with the specimen in two major respects: 1) there is no cleft in the carapace, which is, indeed, perfectly normal; and 2) there are actually four eyes present with distinct, albeit weak, corneas. In the alcoholic specimen the illusion of a cleft carapace was given at first glance, due to the transparency of the carapace and the converging medial borders of the rather opaque cheliceral muscles. It is difficult to understand how the eyes could have been overlooked since they were readily visible in the alcoholic specimen. The specimen was mounted on a slide for detailed study. It was revealed to be a tritonymph of a species belonging in the genus *Chitrella* Beier. It is regrettable but necessary to base the description of the species upon this single, immature specimen.

Diagnosis: Tritonymph holotype: Body and appendages of typical chitrelline facies (cf. Malcolm and Chamberlin, 1960, fig. 4); very lightly sclerotized and pale in color; carapace slightly longer than broad, with its greatest breadth at about the middle; no epistome; four eyes weakly but definitely corneate; total setae 28, of which 6 are on the anterior margin and 6 at the posterior margin. Abdomen elongate; tergal and sternal scuta entire; pleural membranes longitudinally striate. Tergal chaetotaxy: 9:11:11:11:12:13:13:11:8:?. Sternal chaetotaxy 3:(3)8(3):(3)8(3):12: $\frac{2m}{13}$: 15:14:12:12:?, the two microsetae of sternite 6 lying side by side at the center of the scutum.

Chelicera typical, about twice as long as broad; chaetotaxy normal, with 5 setae on hand and a galcal seta; flagellum apparently consisting of 6 or 7 blades; fixed finger with 16-18 triangular teeth, largest in the middle of the row; movable finger with 8-10 irregular teeth, very heavy distally but smaller toward the base of the finger; galea absent.

Palps typical, showing no special adaptation to subterranean life; general proportions of podomeres as shown in Figure 7. Tactile setae of chela as shown in Figure 8; seta *isb* absent from the fixed finger and *sb* from the movable finger; fixed finger with a marginal row of 42 contiguous teeth, quadrangular in the distal third but low and rounded in the basal two-thirds of the row;

movable finger with 49 contiguous teeth, all low, broad and somewhat rounded. Trochanter 2.1; femur 3.8; tibia 2.4; chela 3.6, and hand 1.5 times as long as broad; movable finger 1.52 times as long as hand.

Legs generally typical of the genus but with the telotarsus of each leg swollen subbasally so that its depth is equal to or greater than that of the metatarsus. Leg IV with a tactile seta on the tibia 0.67 the length of the segment from the proximal margin; apparently no tactile seta present on the metatarsus.

Measurements (in mm.): Tritonymph holotype: Body length 1.90; carapace 0.48 long, greatest width 0.45; abdomen 0.81 broad. Chelicera 0.29 by 0.15. Palps: trochanter 0.26 by 0.12; femur 0.44 by 0.12; tibia 0.37 by 0.15; chela 0.72 (0.77 with pedicel) by 0.20; hand 0.30 by 0.19; movable finger 0.45 long. Leg I: basifemur 0.22 by 0.07; telofemur 0.15 by 0.07; tibia 0.20 by 0.05; metatarsus 0.11 by 0.044; telotarsus 0.15 by 0.047. Leg IV: entire femur 0.38 long; basifemur 0.15 by 0.13; telofemur 0.23 by 0.14; tibia 0.31 by 0.07; metatarsus 0.13 by 0.058; telotarsus 0.19 by 0.058.

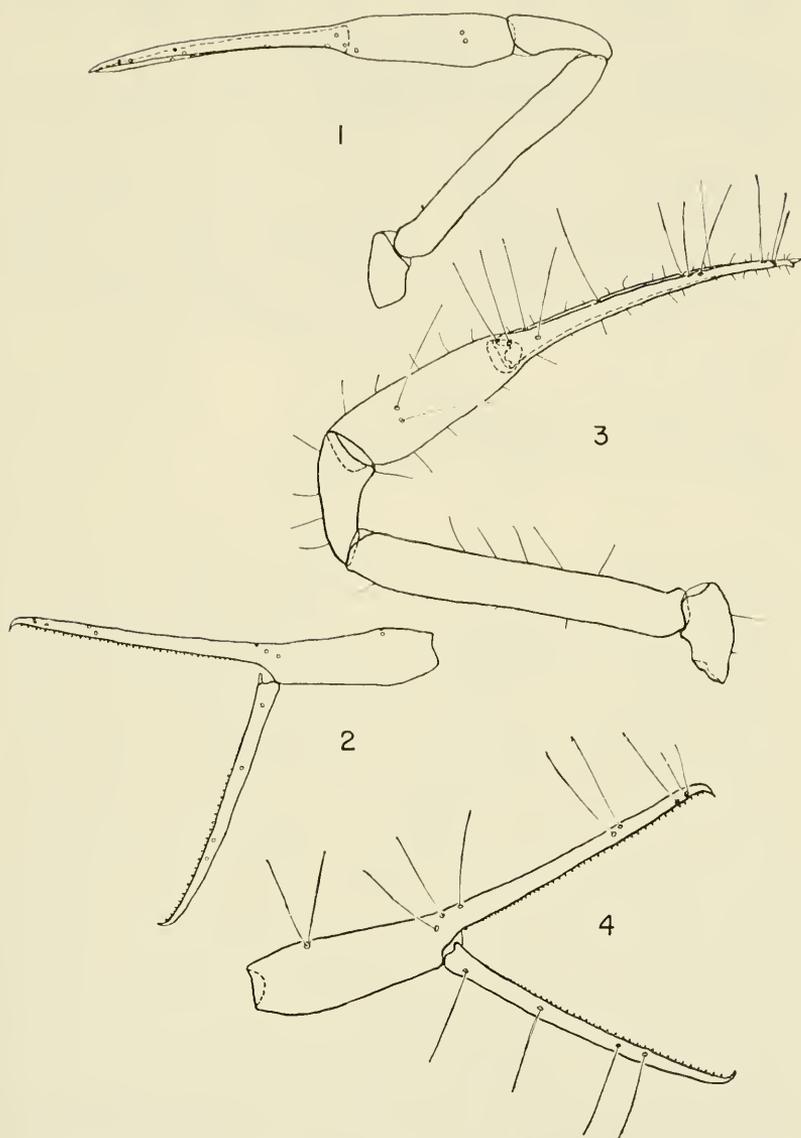
Remarks: Though this species is presently known only from a single tritonymph some idea of the adult form may be surmised from a comparison with *C. archeri* Malcolm and Chamberlin, of which 3 tritonymphs have been studied (unpublished). In most respects the tritonymph of *C. cavicola* is similar to those of *C. archeri*, but it is a little smaller and slightly less slender both in body and in the appendages. It has fewer teeth on the chelal fingers (fixed finger 42 and movable finger 49 as compared with 49-54 and 56-58, respectively); it has 9 setae on the first tergal scutum as compared with 4-6; and tactile seta *t* of the movable chelal finger is slightly closer to the tip of the finger (index 0.328 as compared with 0.361-0.370). On the other hand, it shares with *C. archeri* tritonymphs the possession of two microsetae on the sixth sternite; the subbasal swelling of the telotarsi (unpublished observation; cf. also Vachon, 1954, p. 219); and (with one specimen) the lack of a tactile seta on metatarsus IV. Furthermore, it should be mentioned here that, while the adults of *C. archeri* are without demonstrable eyes, the tritonymphs possess definite, though weakly developed, corneas corresponding to, but weaker than, the anterior eyes of *C. cavicola*.

From the foregoing it seems warranted to assume that the adult of *C. cavicola* is similar to that of *C. archeri*, but slightly smaller and more robust and differing in details of chaetotaxy,

etc., and perhaps very close to the adult of *C. muscbecki* Malcolm and Chamberlin.

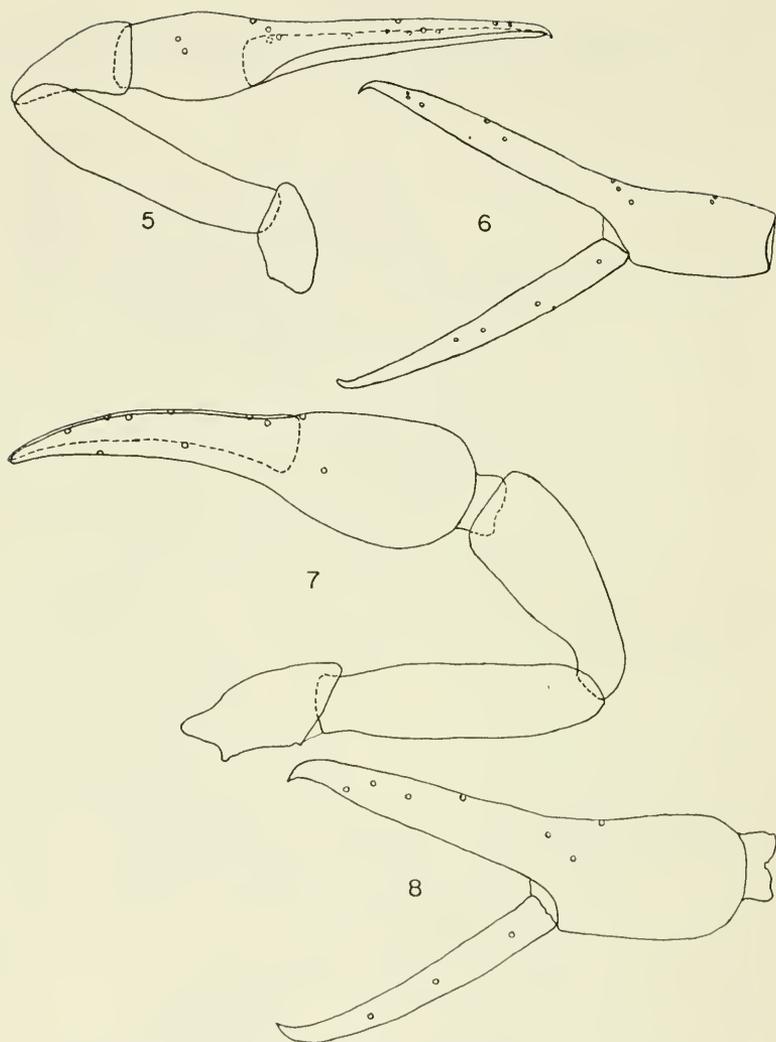
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Figures 1 and 2. *Kleptochthonius* (*Chamberlinochthonius*) *packardi* (Hagen), allotype female. 1. Dorsal view of right palp. 2. Lateral view of left chela (setae missing from specimen).

Figures 3 and 4. *Kleptochthonius* (*Chamberlinochthonius*) *hagani*, new species, holotype male. 3. Dorsal view of left palp. 4. Lateral view of right chela.



Figures 5 and 6. *Apochthonius coccus* (Packard), lectotype male. 5. Dorsal view of left palp. 6. Lateral view of left chela (setae missing from specimen and teeth omitted).

Figures 7 and 8. *Chitrella cavicola* (Packard), holotype tritonymph. 7. Dorsal view of right palp. 8. Lateral view of left chela (setae missing from specimen and teeth omitted).

B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS.

AUGUST 29, 1963

NUMBER 189

NOTES ON AMPHISBAENIDS (AMPHISBAENIA; REPTILIA). 10. REDESCRIPTION AND REDEFINITION OF *AMPHISBAENA PERICENSIS* NOBLE FROM THE MOUNTAINS OF NORTHWESTERN PERU.

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In 1921 Noble described the new species *Amphisbaena pericensis*, basing his description upon a single specimen (M.C.Z. No. 14631) collected by him, while a member of the "Harvard Peruvian Expedition of 1916." The holotype came from "Perico, Peru," but Noble added that the species was represented in the collection by a "large series of specimens." He neither listed, nor otherwise commented upon these, except to state the range of the form as the "arid valleys of the Chinchipe and Marañon, from Perico on the north to Bellavista on the south."

The series of specimens referred to has never been discussed in the subsequent literature. The only reference to additional specimens was made in error. S.U. 8314-8315 (Burt and Myers, 1942, p. 48) actually were *A. occidentalis townsendi* from the Pariñas Valley. Our concept of *A. pericensis* thus still rests upon the description of the holotype. Half of the remaining specimens, referred to as paratypes with but faint justification, have been traded to at least eight other museums. The form has had repeated mention in catalogs and specimen lists (Barbour and Loveridge, 1929; Burt and Burt, 1930, 1931; Cochran, 1961; Marx, 1958).

The present notes are based upon the re-assembly of a significant fraction of the original series. They include a redefinition and standardized redescription (cf. Gans and Alexander, 1962), coupled with the first illustration of the form.

I am indebted to the following curators of institutions (identified throughout by the abbreviations given in parentheses) for permission to borrow or examine material in their care: Mr. Charles M. Bogert of the American Museum of Natural History

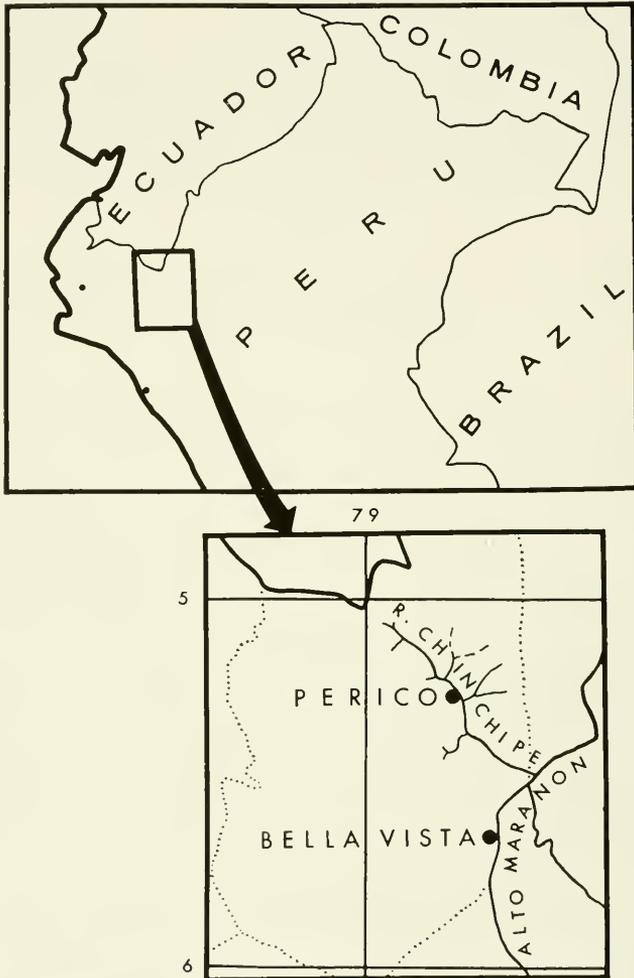


FIG. 1. *Amphisbaena pericensis*. Map showing localities mentioned in the text. The two small dots in the small scale map indicate the type localities of *Amphisbaena o. occidentalis* Cope [bottom or south], and *A. o. townsendi* Stejneger [top or north]. The dotted line on the large scale [detail] map indicates the Province of Jaen of the Department of Cajamarca, Peru.

(A.M.N.H.), Miss Alice G. C. Grandison of the British Museum (Natural History) (B.M.), Dr. Alan Leviton of the California Academy of Sciences at San Francisco (C.A.S.), Mr. Hymen Marx and Dr. Robert F. Inger of the Chicago Natural History Museum (C.N.H.M.), Dr. Ernest E. Williams of the Museum of Comparative Zoology (M.C.Z.), Dr. Konrad Klemmer of the Senckenbergische Naturforschende Gesellschaft of Frankfurt a. M., Germany (S.M.F.), Dr. George S. Myers of Stanford University, Museum of Natural History (S.U.), Dr. Hobart M. Smith of the University of Illinois Museum of Natural History (U.I.M.N.H.), Dr. Doris M. Cochran of the United States National Museum (U.S.N.M.), and Dr. Heinz Wermuth [formerly] of the Zoologisches Institut der Universität in Berlin (Z.M.U.). Dr. Virginia Cummings figured the specimen and Miss Charlyn Rhodes furnished technical assistance. The overall project has been supported by grants NSF G-9054 and G-21819 from the National Science Foundation.

AMPHISBAENA PERICENSIS Noble, 1921

Amphisbaena pericensis Noble, 1921, p. 141. Terra typica: "Perico, Peru." HOLOTYPE: M.C.Z. 14631. PARATYPES: A.M.N.H. 28501-03; B.M. 1929.6.1, 85-RR 1946.8.31.83; C.A.S. 54614; C.N.H.M. 16106-07, 73371; D.Z. [?]; M.C.Z. 14764-65, 14767-68, 14770, 14772-75; S.M.F. 11826, 11887-88; U.I.M.N.H. 41494; U.S.N.M. 75970; Z.M.U. 29659 [Perico], M.C.Z. 14789-90 [Bellavista], U.S.N.M. 59926 [Chimilpe River], U.S.N.M. 60057-58 [Marañon River].

Status of the types: The status of the various specimens collected by G. K. Noble is thoroughly confused, possibly because the collection does not appear to have been catalogued at the M.C.Z. in its entirety, and certainly because Noble neither gave the total number of specimens examined, nor otherwise identified the "paratypes." (See table on p. 13.)

There does not seem to be any difficulty about the holotype, M.C.Z. 14631. It was listed both by Noble and by Barbour and Loveridge (1929, p. 215).

The latter authors also listed M.C.Z. 14764-68, 14770, 14772-80 and 14789-90 as paratypes then remaining in the Museum of Comparative Zoology. A check of the catalog disclosed that the series originally ran from 14764 to 14790. Of these I have been able to identify 14764-65, 14767-80 and 14786-90 in various collections, relying always on the presence of one of the original parchment labels. Since 14766 is marked "Amaral" in the

M.C.Z. catalog (hence presumably in the Departamento de Zoologia, São Paulo collection = D. Z.), only 14781-85 remain in question.

All of the questionable specimens have their catalog entry marked "*Anomalepis aspinosus* Taylor" in A. Loveridge's handwriting. The astonishing thing is that Dunn's first report (1923, p. 185) on the collection mentions only three specimens of *Anomalepis*, while Taylor's original description (1939, p. 92) refers to six including 14781-85. Taylor apparently omitted mention of two other M.C.Z. specimens of this form, and the total of eight once in the M.C.Z. then suggests (1) that Dunn never saw M.C.Z. 14781-85, and (2) by implication that Noble did not check his "paratype" series very carefully. Nevertheless, the remaining 17 specimens may well be considered to be paratypes.

An even more complex problem is posed by seven specimens also supposedly from the Noble collections; four of these are labelled paratype, stem from Perico, and are respectively in the American Museum (A.M.N.H. 28501-03) and California Academy (C.A.S. 54614) collections. Since Noble was curator of the American Museum collection at the time they were catalogued, it remains possible that these are indeed part of his material. Less probability attaches to three specimens from the "Chinchi River" (U.S.N.M. 59926) and the "Rio Marañon" (U.S.N.M. 60057-58). Stejneger marked the catalog "topoparatype" and these specimens were received from the M.C.Z., but were never catalogued there. Yet even they may be considered to have been included as paratypes by Noble's statement of species range.¹

Diagnosis: A form of *Amphisbaena* without major fusions of head shields; with pairs of very large first and slightly reduced second parietals; with the head relatively blunt and not particularly set off from the neck; with a cylindrical blunt-tipped tail; with a faint autotomy constriction at the sixth to eighth caudal annulus where autotomy takes place. The form has 198 to 218 body annuli; generally 18 or 19, occasionally 16 or 17 caudal annuli; 12 to 16 (generally 14) dorsal and 16 to 20 (generally 18) ventral segments to a midbody annulus; and 4 small

¹Two specimens (U.M.M.Z. 55767 A & B) just discovered in the collection of the University of Michigan Museum of Zoology confirm that Noble apparently distributed "paratypes" without first giving them M.C.Z. numbers. Their jar contains an M.C.Z. label reading (apparently in Noble's hand) "*Amphisbaena* sp. nov. in ms. — Perico, N. W. Peru. — Harv. Peru. Exp." Their counts and measurements fall within the range of the present description.

round preloacal pores. The color of preserved specimens is a uniform dark brown, much darker dorsally than ventrally, lightened on the tip of tail and snout and produced by a dense pigmentation of the segments (contrasted by lighter intersegmental sutures).

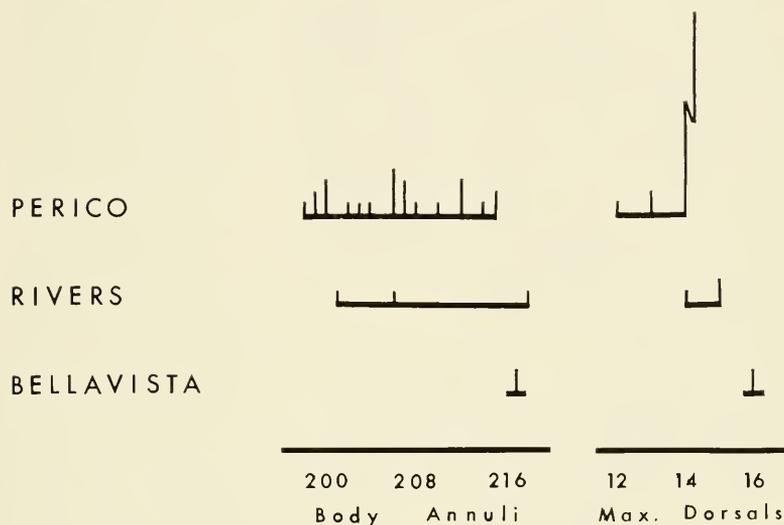


FIG. 2. *Amphisbaena pericensis*. Diagram showing distribution of counts of body annuli and maximum dorsal counts of the three groupings collected respectively at Perico, along the "rivers" of Chinchipe and Marañon, and at Bellavista.

Geographic variation: The entire sample comes from a relatively restricted area and 24 out of the 29 available specimens from the single locality, Perico. Two other specimens bear the definite indication Bellavista, while the other three are marked only with the names of the river courses traversing the area.

Number of segments to the dorsal portion of the midbody annulus differs clearly between the Perico sample (12 to 14) and the Bellavista sample (15 to 16). Two of the river course specimens also range to 15. It may also be significant that the two Bellavista specimens and one of the river course individuals show a slightly higher number of body annuli than does the Perico sample (Fig. 2). Here, as in so many other instances, we are handicapped by the markedly inadequate samples.

Description: Figure 3 shows views of the head, Figure 4 the ventral surface of the cloaca and tail, and 6, 7 and 8 are photographs showing coloration and other aspects of the specimens. Figure 5 gives a scatter diagram of tail versus snout-vent lengths. Meristic data are listed in the table.

This is a small species of *Amphisbaena*, of a dark brownish color and without pattern, but with marked dorsoventral counter shading. The lightened ventral color continues anteriorly onto the rostral, and caudally to the cloaca and occasionally to the distal tip of the tail. The color is clearly restricted to the segments, as the intersegmental sutures and the lateral grooves are significantly lighter. The specimens thus present the impression of a checkerboard under magnification.

The coloration appears to result from two levels of pigmentation and two degrees of expression. There is a general darkening of the entire segmental surface, plus an additional intensification of pigmentation on the rectangular segmental centers. The dorsal segments of some well preserved specimens barely show this midsegmental pigment dichotomy; other, possibly more faded, specimens show it more clearly though never as markedly as in *Amphisbaena silvestrii* (Gaus, 1962) in which the margins are quite distinct from the centers. The dorsoventral fading occurs both by a general weakening of the coloration and by a complete dropping out of the main pigmentation by segments. (The absence of living specimens does not permit decision as to whether these ventral segments are truly unpigmented, or whether the phenomenon here discussed applies only to those pigments least affected by methods of preservation.) The general weakening of the pigmentation may result in disappearance or reduction to flecking of the darkening of the entire surface, as well as a reduction of pigment density and size of the rectangular segmental centers. The complete depigmentation varies in extent from a blanching of most midventral rows to that of scattered groups of ventral segments. Such areas as the tail are ventrally countershaded by the first phenomenon alone and all of their segments retain (more or less faint) dark centers.

The head segmentation is characterized by lack of major fusions, and by pairs of very large first and slightly reduced second parietals. The head is slightly flattened dorsoventrally particularly on the posterior half. The rostral region projects slightly across the tip of the recessed lower jaw. The entire body shows some dorsoventral flattening. The temporal muscles are

scarcely noticeable in juveniles, but are definitely swollen in adults in which they change the shape of the head.

The rostral is slightly smaller than are the first supralabials and only its dorsal tip is visible from above. Pairs of medium-

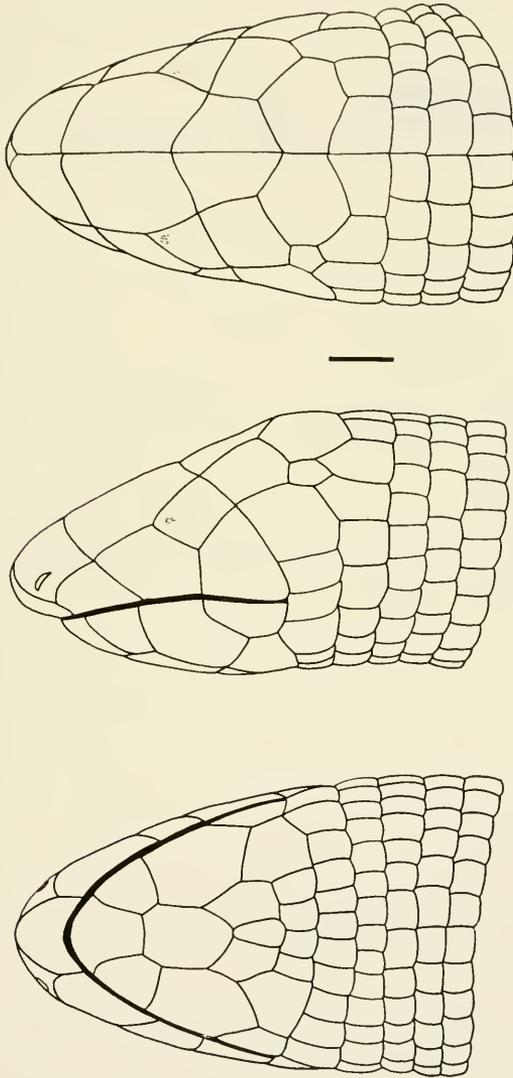


FIG. 3. *Amphisbaena pericensis*. Dorsal, lateral and ventral views of the head of the holotype, M.C.Z. 14631, from Perico. The line equals 1 mm to scale. (V. Cummings del.)

sized nasals, large prefrontals, smaller frontals and wide first and narrower second parietals follow in sequence along the dorsal midline of the head. The middle of the parietal lies on the level of the angulus oris. There are three supralabials of which the second is generally the largest. The position of the angulus oris lies at the posterior edge of this segment and is generally quite easy to determine as the intersegmental sutures of the first body annulus do not tend to align with the slit of the mouth. The suture between the first and second supralabials runs at an angle of 45° to the edge of the mouth, while that between the second and third runs directly rostrad or only very slightly anteriorly. The ocular is quadrangular, contacting the prefrontals and frontals anterodorsally, and the second and third supralabials anteroventrally. Its posterior margins adjoin the segments of the first body annulus.

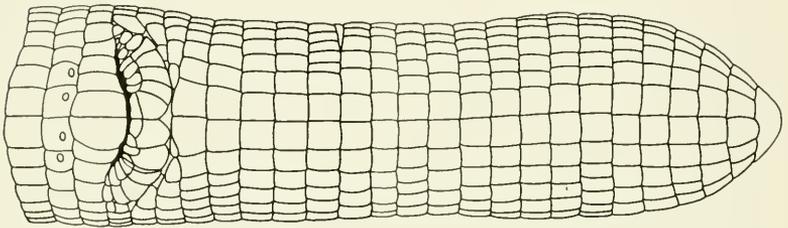


FIG. 4. *Amphisbaena pericensis*. Ventral view of cloaca and tail of the holotype. The line equals 1 mm to scale. (V. Cummings, del.)

The mental is medium sized and slightly larger than the first infralabials which are followed by the very large second infralabials (the largest segments of the lower jaw), and these in turn by the narrow third infralabials. The oval to pentagonal postmental is somewhat larger than the mental and is in contact with it, with the first and second pairs of infralabials, and with a row of postgenials that clearly exclude it from contact with the malars. The malars are small and fill the spaces between the wide second and narrow third infralabials. The anterior row of postgenials generally consists of two tear-drop shaped segments, occasionally separated by a small intermediate segment (indicated in the table under chin segments by a figure one in parenthesis). This segment occasionally contacts the postmental so that a first row of three postgenials is counted. The second postgenial row contains three to four segments. There are no postmalars.

Dorsally, the two pairs of very much enlarged segments of the first body annulus curve anteriorly and the topmost pair contacts the lateral edges of the frontals. A dorsal half-annulus of one to two segments on each side intercalates behind this, including the first parietals. The second parietals are the mid-

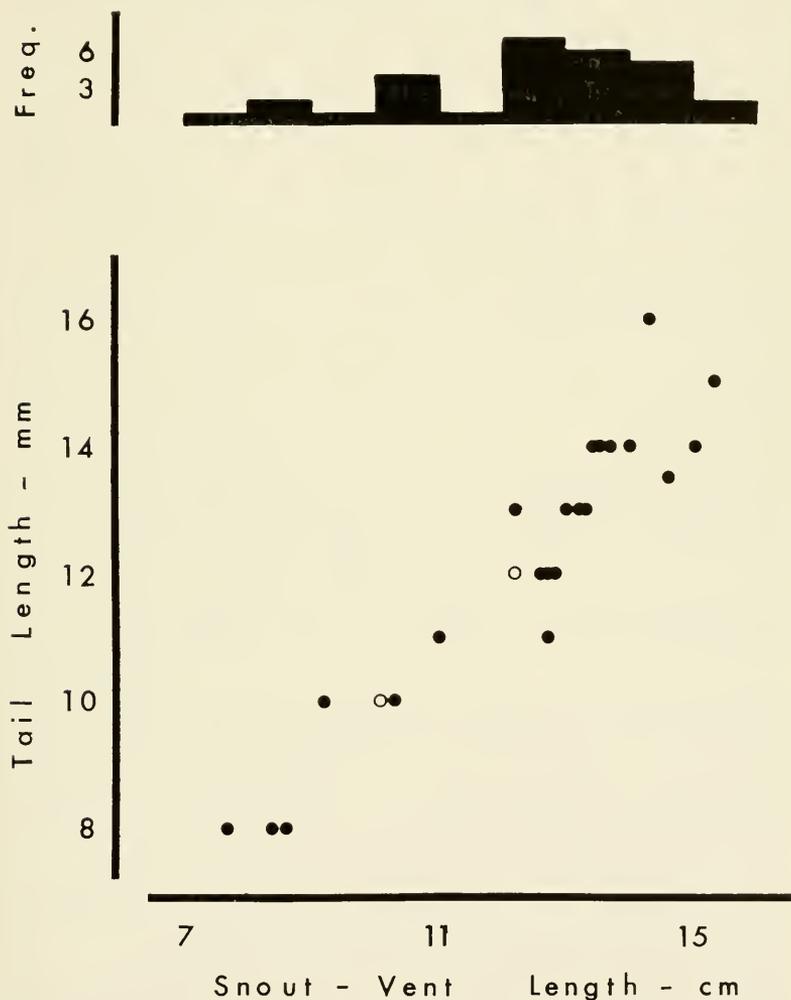


FIG. 5. *Amphisbaena pericensis*. Combined frequency histogram to show distribution of size classes of snout-vent length (summed in units of 1 cm, from 7.0 to 7.9, 8.0 to 8.9, etc.), and scatter diagram of tail versus snout-vent length (the hollow dots indicate two coincident points each).

dorsal segments of the second body annulus. The posterior edge of this annulus shows no forward curvature, though several of its segments are anteriorly elongate, particularly in the temporal region.

There are 198 to 218 body annuli from the back of the third infralabial, up to and including the pore-bearing precloacals. The fourth through sixth or eighth anterior annuli are modified. The anterior ones are shorter, and the posterior ones longer than the succeeding annuli on the trunk. There is generally no complexing of the segments in the "pectoral" region, nor are there intercalated dorsal half-annuli. There are 12 to 16 (generally 14) dorsal and 16 to 20 (generally 18) ventral segments to a midbody annulus, while the normal pattern appears to be 14/18 (see comments on geographical variation).

The cloacal region is characterized by 4 round precloacal pores, which are much less noticeable in juveniles and females. There are 6 to 8 precloacal and 11 to 14 postcloacal segments and three to five (generally four) lateral rows. The not particularly apparent autotomy annulus falls on the sixth to eighth postcloacal annulus and autotomy takes place here. Specimens have 16 to 19 (generally 18 to 19) caudal annuli. The cross section of the tail changes from a dorsoventrally flattened ellipse in the immediate postcloacal region, to a circle at the autotomy annulus, to an enlarged vertical ellipse behind this. The enlarged distal tip terminates in a blunt vertical keel.

The lateral sulci are clearly marked, starting between the twentieth and fortieth body annuli and continuing up to the level of the cloaca. At midbody, each of them is represented by little more than an elaboration of the normal intersegmental suture, which is made more complex by having the extreme corners of the adjacent segments diagonally cut off. The dorsal and ventral intersegmental sutures are aligned along the middorsal and midventral region, but there is no other indication of dorsal and ventral sulci.

The dorsal segments of a midbody annulus are approximately one and one-half times as long as wide, while the ventral ones are one and three-quarter times as wide as long.

Range: Peru, Department of Cajamarca, "arid valleys of the Chinchipe and Marañon, from Perico on the north to Bellavista on the south."

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Data for specimens of Amphisbaena pericensis Noble

Collection and number	A N N U L I Body/Lat/Tail	SEGMENTS Dors/Vent	Chin Segments	Cloaca	Length
AMNH 28501	204+5+ (6) 18	14/18	2-4	4-6-13	132+13
AMNH 28502	200+4+ (6) 16	13-4/18	2(1)-4	4-6-13	146+13.5
AMNH 28503	212+4+ (7) 18	14/18-20	2-3	4-6-12	128+12
BM 1929.6.1.85 -					
RR 1946.8.31.83	202+4+ (7) 18	14/18	irreg.	4-7-13	140+14
CAS 54614	214+4+ (7) 18	14/18	2-3	4-8-12	150+14
CNHM 16106	198+4+ (7) 19	14/18-19	2(1)-4	4-8-12	134+14
CNHM 16107	207+4+ (7) 18	13-4/18	2(1)-4	4-6-11	101+10
CNHM 73371	203+4+ (7) 18	12-3/18	2(1)-4	4-8-12	110+11
MCZ 14631	208+4+ (7) 19	14/20	3-4	4-8-12	137+14
MCZ 14764	212+5+ (6) 18	12/18	2-3	4-8-12	153+15
MCZ 14765	200+4+ (6)x	14/18	3-4	4-7-12	104+(3)
MCZ 14767	206+4+ (7) 18	14/18	2-4	4-8-14	77+8
MCZ 14768	199+4+ (6) 18	12-14/18	2-4	4-7-12	103+10
MCZ 14770	200+4+ (6) 17	14/16-8	2-4	4-8-13	122+12
MCZ 14772	206+ $\frac{3}{4}$ + (7) 19	12-3/17-8	2-3	4-7-12	127+12
MCZ 14773	207+ $\frac{3}{4}$ + (7) 19	13-4/18	2-3	4-8-15	135+14
MCZ 14774	212+4+ (7) 18	12-4/18	2-4	4-8-12	86+8
MCZ 14775	215+4+ (6)x	14/18	2-4	4-7-12	142+6
SMF 11826	215+4+ (7) 19	14/16-8	2(1)-4	4-7-13	122+13
SMF 11887	206+ $\frac{3}{4}$ + (7) 18	14/18	2-3	4-8-11	92+10
SMF 11888	206+4+ (—)-	13-4/18	2(2)-5	4-8-13	127+11
UIMNH 41494	210+4+ (7) 18	13-4/17-8	2-4	4-8-12	84+8
USNM 75970	207+4+ (7) 18	12-4/18	2(1)-4	4-7-13	101+10
ZMU 29659	199+4+ (6) 18	13-4/18	2(1)-3	4-6-12	122+12
MCZ 14789	217+3+ (6) 17	16/18	2(1)-4	4-8-13	133+13
MCZ 14790	217+3+ (7) 19	15-6/18-20	2(1)-4	4-7-12	130+13
USNM 59926	201+ $\frac{4}{3}$ + (8) 19	13-5/18	2-3	4-8-12	143+16
USNM 60057	218+4+ (7)x	14-5/20	2(1)-4	4-8-14	142+(5)
USNM 60058	206+ $\frac{3}{4}$ + (7) 18	12-4/18	2-3	4-8-11	126+12

Present status of the M.C.Z. paratypes of *A. pericensis*.

<i>Original number</i>	<i>Present number</i>
14764-65	Same
14766	“Amaral” = D.Z. ?
14767-68	Same
14769	Z.M.U. 29659
14770	Same
14771	S.M.F. 11826
14772-75	Same
14776	U.I.M.N.H. 41494
14777-79	C.N.H.M. 16106-07, 73371
14780	B.M. 1929.6.1.85-RR 1946. 8.31.83
14781-85 = <i>Anomalepis</i>	M.C.Z. and U.S.N.M.
14786	U.S.N.M. 75970
14787-88	S.M.F. 11887-88
14789-90	Same

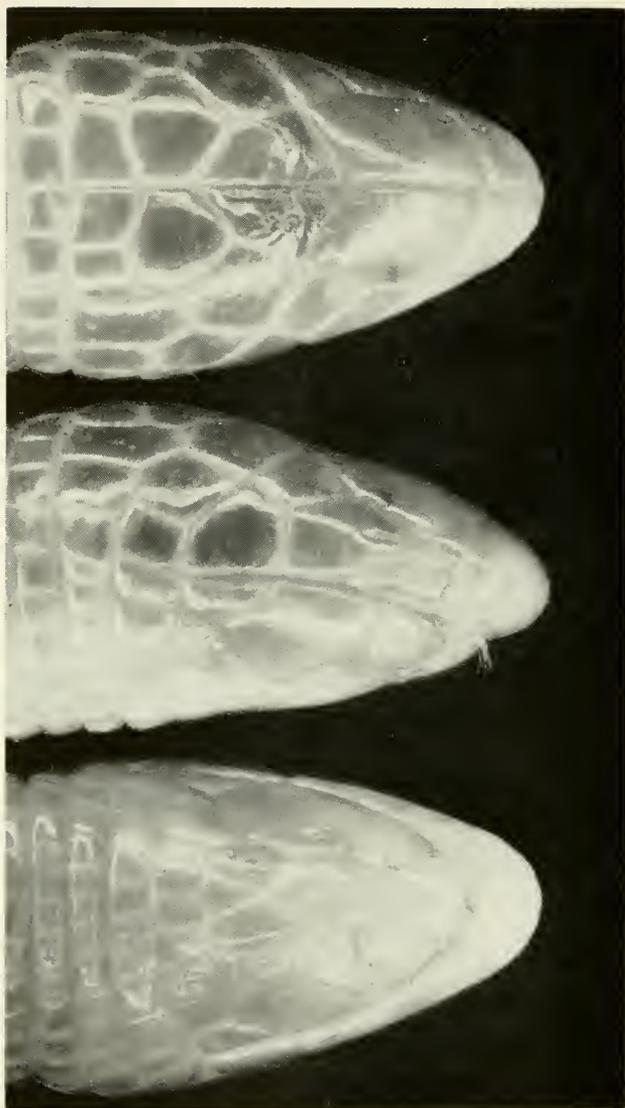


FIG. 6. *Amphisbaena pericensis*. Dorsal, lateral and ventral views of the head of the holotype, M.C.Z. 14631.

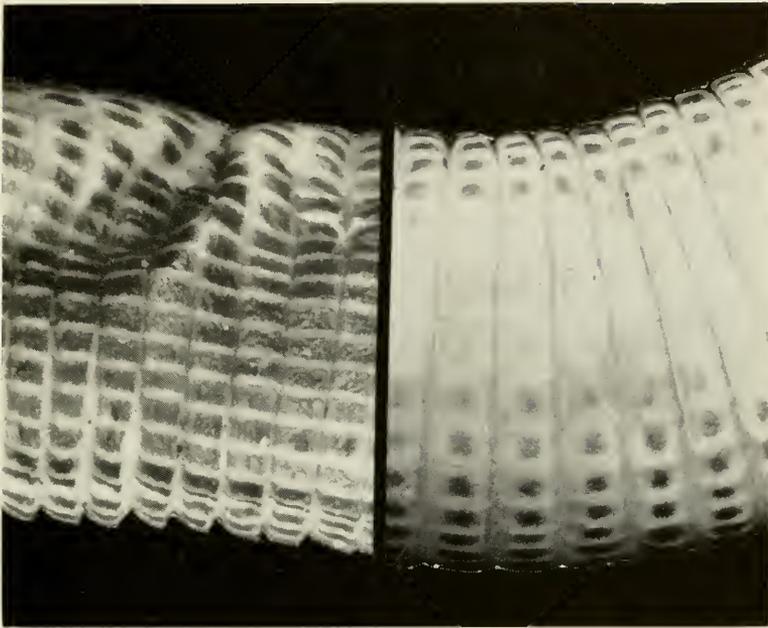


FIG. 7. *Amphisbaena pericensis*. Dorsal (left) and ventral (right) views of the holotype at midbody to show size and pigmentation of segments.

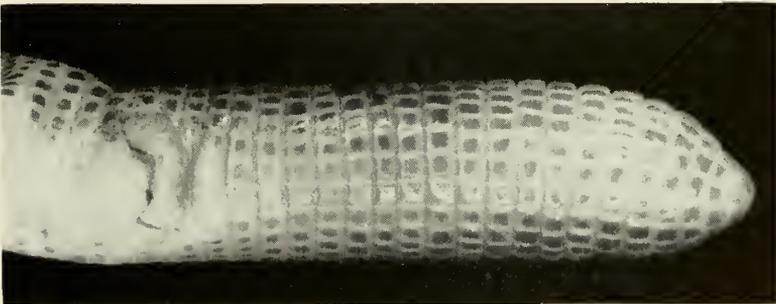


FIG. 8. *Amphisbaena pericensis*. Ventral view of cloaca and tail of the holotype, to show pigmentation, segment arrangement and the hardly apparent autotomy constriction.

B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS.

SEPTEMBER 30, 1963

NUMBER 190

CHARACTERS AND SYNONYMIES AMONG THE GENERA OF ANTS.

PART III. SOME MEMBERS OF THE TRIBE PONERINI (PONERINAE, FORMICIDAE)

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INTRODUCTION

The present part¹ is concerned with some genera and species in the tribe Ponerini of subfamily Ponerinae. It consists mainly of the justification for some rather radical revisionary changes in the tribe at the generic level. It is felt that these findings should be presented here in order that they should not distract from the "final" reclassification results eventually to be presented in synoptic form for the Ponerinae and for all Formicidae. This paper by no means exhausts the necessary changes that must be made in the generic classification of the Ponerini, but it deals with some of the most fundamental ones that require more than summary proposal. Some synonymies proposed or suggested at the species level are to be considered a by-product of the research into generic limits. At various stages during the last two years, the work on ponerine reclassification has been supported by grants from the Bache Fund of the National Academy of Sciences, from the Society of the Sigma Xi, and from the National Science Foundation (G-23680). This help is gratefully acknowledged.

SOME OLD AND NEW GENERIC CHARACTERS OF PONERINI

Tribe Ponerini, the largest in subfamily Ponerinae, has undergone no basic classificatory changes since the appearance of

¹ Part I. *Breviora*, Mus. Comp. Zool., no. 11: 1-13 (1953).
Part II. *Ibid.*, no. 18: 1-8 (1953).

Emery's fascicle covering the subfamily in the *Genera Insectorum* in 1911. Emery's treatment was really a refinement of his earlier reclassification of the ponerines published in 1901. In his well-known key to the genera of ants, Wheeler (1922) followed Emery's classification of the Ponerini for the most part, but worked in the additional genera described up to 1922.

The Emery classification employed a number of characters of worker and female in distinguishing his genera of tribe Ponerini, but the two most stressed were (1) the number of segments in the maxillary and labial palpi, and (2) the number of tibial spurs on the middle and hind legs.

Unfortunately, the palpal character saw extensive use only during some of the early years of ant systematics. Emery, Mayr, and even Frederick Smith often gave the count of segments in their descriptions, but curiously, after Emery used the palpal counts as a foundation stone of his 1901 classification, these appendages were almost completely ignored by most later describers of ponerine species, probably due to the fact that the smaller mouthparts are so small and difficult of access. Later authors seem to have relied more on habitus than on truly diagnostic characters when they placed new (or supposed new) species to genus. As a result, some species have been described as new over and over again in different genera and subgenera (consult the case of "*Trachymecopus*" *brunoi* and its synonyms, discussed below). The primitive number of worker-female palpal segments appears to be 4, 4 (4 maxillary, 4 labial — the formula always stated in that order); in the male it is 6, 4, the basic number for all ants. In many Ponerini, especially the smaller or cryptobiotic species and their derivatives, the number is much reduced, and reaches as low as 0, 1 in the worker, while less consistent reduction occurs in the male. Palpal segmentation is undoubtedly important in generic classification and in the analysis of phyletic trends, but due to its neglect in species descriptions, it remains unknown for a majority of forms. Work is now going forward to correct this deficiency, and some results are incorporated in the present paper.

The other major character in question is the number and state of development of the tibial spurs. The trait is an ambiguous one, as can be seen from its employment in keys. Wheeler's 1922 key to the genera of the Ponerini states it this way in the very first couplet:

Middle and hind tibiae with two spurs. 2.

Middle and hind tibiae with a single, well-developed spur, which is always pectinate; the lateral spur is rudimentary or absent 19.

This couplet really expresses the difference thought to separate the "lower" Ponerini, mostly large in size, from the "higher" members, which tend to be smaller (e.g., *Ponera*, *Cryptopone*). Generally speaking, the genera with smaller-sized species do tend to lose the lateral spurs of the middle and hind tibiae, while genera having larger-sized species normally retain the extra spur, although usually in a more or less reduced condition. The difficulty, of course, lies with distinguishing between the condition "two spurs" and "lateral spur rudimentary," especially when one finds that in most species the lateral spur is considerably smaller than its mate. Furthermore, the threshold at which a "vestigial spur" becomes just another apical seta of the tibia is unspecified along a gradual morphocline of species. In short, the lateral tibial spur, as an allometric character, cannot be used to split the Ponerini into two main groups, and in fact probably cannot even be used by itself as a diagnostic character at the generic level.

Other adult characters of value in classification still remain: the shape of the clypeus has been and still is an important generic character. The tarsal claws may be simple, or may have one or more teeth, or may even be pectinate, as in the case of most *Leptogenys* species. I consider the pectination of the claws, imperfect in some African species of the genus, to be insufficient as a tribal character in view of the several other strong characters shared by both adult and larval Ponerini and *Leptogenys*, and accordingly I am placing tribe Leptogenyini as an included synonym of Ponerini (**new synonymy**).

Another character of some importance is the presence of heavy, conical, spine-like setae on the extensor surfaces of the middle tibiae and tarsi. These structures, which appear to promote movement through soil or rotten wood by improving traction, are found in certain cryptobiotic genera (e. g., *Centromyrmex*, *Wadeura*, *Cryptopone*, *Promyopias*) as well as in a number of fossorial wasps (many pristocerine Bethyliidae, most non-parasitic Scoliioidea, for instance), all of which seek their prey underground or in other confined circumstances. Emery cited the presence of such spine-like, as well as merely bristle-like, setae as characteristic of *Euponera* subgenus *Trachymesopus*, which he named (in 1911) accordingly. The heterogeneity of *Trachymesopus* in this regard, as well as in other respects, made it a perfect catch-all for miscellaneous species of medium-to-small Ponerini from the very beginning, and it has continued in this role right down to the present. As a matter of fact,

heavy, conical spine-like setae that arise over half or more of the mid-tibial extensor surface are found only in a particular group of "*Trachymesopus*," and this group (*ochracea* and allies) shares this and several other characters with the members of *Cryptopone*. The relationship between *Trachymesopus* and *Cryptopone* has long been discussed by E. O. Wilson and myself (see Wilson, 1958: 352), and now the discovery of the concordance between the tibial armament and other characters, particularly the basal mandibular pit, makes the solution of this problem obvious. The "*Trachymesopus*" species with these characters are all really *Cryptopone*, and are transferred accordingly, as discussed under that genus below.

One of the chief *Cryptopone* characters just mentioned is a particularly interesting one; this is a prominent oval pit or fovea near the base of the mandible in its dorsolateral surface. This pit, or its obvious homolog, is also found in all *Brachyponera*, in the members of the "*Trachymesopus*" *sharpi* group, in *Hagensia*, in *Euponera sikorae* Forel (type species of *Euponera*!), and in a few other African species formerly placed in *Euponera* or other genera, but is lacking in *T. stigma*, the type species of *Trachymesopus*, and its closest relatives. All known species with the basal pit are from the Old World, and chiefly from Africa, with the exception of *Cryptopone gilva* and (perhaps) *C. guatemalensis*, which apparently represent a *Cryptopone* invasion of the New World that has spread through North America and reached Central America. In the other direction, *Cryptopone* has reached southeastern Australia and New Caledonia, but curiously, no true *Cryptopone* are known to occur in Ethiopian Africa.

The basal mandibular pit in ponerine species was early noted as a character by Gustav Mayr and occasionally mentioned by later authors in species descriptions, but only Arnold used it as a generic character in his 1951 review of *Hagensia*, a genus in which the pits are unusually distinct. In most species that have it, the pit has been overlooked completely in descriptions, particularly after 1900. Many Ponerini, especially among the larger and presumably more primitive species, bear another character in the form of an oblique groove across the dorsal face of the mandible, curving outward from the inner base and usually continuing into the lateral longitudinal mandibular sulcus that runs to the apex. This channel, which may be functioning to

distribute some product from the mandibular glands, is probably not homologous with the basal pit. It is oriented differently, and at least one species of "*Bothroponera*" has both the pit and the groove.

In the former *Trachymesopus*, species without the truly spine-like mid-tibial setae (except for 2-3 of these setae at the tibial apex) are divided into three groups: the *stigma* and *darwini* groups, which have no basal mandibular pit and no anal lobe on the hind wing of the sexes, and the *sharpi* group, which has the pit, and the lobe in the male only, so far as known. The *sharpi* group is close to *Brachyponera*, with which it shares the pit and the lobe, but further information may dictate a separate genus for each of these groups.

In what remains of *Trachymesopus*, the *stigma* group (e. g., *stigma*, *cautus*, *pachynodus*, *rufonigrus*) has palpal segmentation 3, 3, while *darwini* has 4, 3. Thus, it may be seen that *Trachymesopus* is a heterogeneous grouping even after the removal of the *Cryptopone* species; its reclassification will have to await the study of more of the larvae and adult winged forms.

Among the most promising of characters to be used in ponerine systematics are those of the larvae. The Wheelers (1952) have laid the groundwork for a comparative study of the larvae of the genera of Ponerini, but for the great majority of species of the tribe, the larvae have never been studied. The larvae of Ponerini are usually covered with peculiar medullate projections, called by the Wheelers "tubercles." In consonance with the morphological terminology applied to other holometabolous larvae, particularly Lepidoptera, I propose that these projections be called by the more specifically descriptive term *chalaza* (sing.), *chalazae* (pl.). The chalazae of Ponerini are matched by apparently homologous structures in tribes Thaumatomyrmicini and Odontomachini, which are close to Ponerini on the basis of adult characters as well. Some of the smaller ponerine genera bear special paired mushroom-shaped chalazae on one or more abdominal tergites; these have long been known to function as "hangers" by which the larvae are stuck to the ceiling and walls of the nest by a glutinous substance covering the head of the chalaza. The number and placement of these fungiform chalazae is important in generic taxonomy, but they must be used with care owing to the fact that they may change in number and form, or be lost altogether, as the instars metamorphose one into another.

REVISIONARY OBSERVATIONS ON SOME PARTICULAR GENERA

CRYPTOPONE Emery

Worker: Small in size, generally under 4 mm total length, depigmented (ferruginous or yellowish); eyes absent or extremely reduced, body compact; mandibles downcurved, with a few (4-6) coarse teeth set on more or less oblique masticatory borders. Dorsolateral mandibular surface with a conspicuous basal pit or fovea, circular or elliptical in outline. Middle tibiae with stout spinules covering about $\frac{2}{3}$ or more of their extensor surfaces. Palpal segmentation 2, 2 or less.

Female: Aside from well-developed compound eyes, ocelli, thorax and the other obviously female characters, fit the worker diagnosis. Hind wings without anal lobe, but with two basal cells.

Male: Small, slender, dark-colored, with pygidial spine so common among Ponerini. Hind wing without anal lobe.

Species: Those placed here by Wilson (1958), plus the former *Trachymesopus* species *crassicornis* (Emery), *gilva* (Roger), probably *guatemalensis* (Forel), *ochracea* (Mayr), *rotundiceps* (Emery), *sauteri* (Wheeler), *taivanae* (Forel) and its probable junior synonym *takahashii* (Wheeler). Of species formerly placed in *Ponera*, *P. typhla* (Karawajew) is clearly a *Cryptopone*, and is probably a synonym of *C. testacea* (Emery); the Australian *P. mjobergi* Forel is a junior synonym of *C. rotundiceps* (**new synonymy**). Among species to be deleted from the *Cryptopone* roll, *C. rufotestaceus* Donisthorpe belongs in *Trachymesopus* as that genus is presently constituted, and is the same as the large variant of *T. darwini* hitherto known as *T. lamarki* Santschi (**new synonymy**). True *Cryptopone* has not been taken in Africa south of the Sahara, and *C. angustata* Santschi (type examined) and *C. hartwigi* Arnold should be transferred to *Ponera* as that genus is currently constituted. I have not checked this list of species for exhaustiveness, but it should serve to give a general idea of *Cryptopone* in the sense of the present work.

TRACHYMESOPUS Emery

As already explained above, *Trachymesopus* (without the *Cryptopone* species) contains at least three groups of species. The type species, *T. stigma*, is common and widespread in both the Indo-Australian region and in the warmer parts of the New World. The Old World synonymy is extensive, and has been

dealt with by Wilson (1958:355). In the New World, the synonymy of *stigma* is not yet clear. *T. cognata* (Emery) has never been differentiated satisfactorily, and *T. succedanea* (Roger) could be either *stigma* or the closely related *cautus* Mann. *T. compressinodis* Borgmeier is a synonym of *T. cautus* Mann (types compared; **new synonymy**). Agreeing with *stigma* and *cautus* in palpal segmentation (3, 3) and in the lack of an anal lobe on the hind wings of both sexes, are two Australian species, *rufonigra* (Clark), transferred from *Brachyponera*, and *pachynodus* Clark (wings unknown in the latter). Two other species that apparently are close to this group are *lunaris* (Emery) and *ferrugineus* (F. Smith), though so little is known about these forms now that they cannot be confidently assigned.

The second group consists of *darwinii* and relatives. These are medium-small species known only from the ferruginous-colored females, which are taken commonly at light throughout wide areas of the Old World tropics. These females lack an anal lobe on the hind wing, and their palpal formula is 4, 3. They lack a mandibular pit and have no spine-like setae on the outer face of the middle tibia. They are found from northern Australia, Indonesia and the Philippines westward through India to tropical Africa. They vary considerably in size, but the variation may be continuous; in fact, all of these forms may well represent a single species. As mentioned above, the species described as *Cryptopone rufotestacea* by Donisthorpe belongs here and is a synonym of *T. lamarki* Santschi, which in all likelihood is only a size variant of *darwinii*. It seems likely also that Motschulsky's *Amblyopone testacea* belongs in this complex.

The third group is the group of *sharpi* Forel, which consists of medium-small species, all castes blackish in color, with a distinct elliptical mandibular pit; palpal segmentation (as seen in 2 African specimens of *brunoi* only) is 4, 4. Anal lobe lacking in 2 *brunoi* females from Liberia, but present (though separated by a relatively shallow cleft) in a single male from Southern Rhodesia; perhaps in this group the character is variable or sexually dimorphic. Mid-tibiae without spine-like setae on extensor faces.

Some of the species (*brunoi*, *malayanus*, *katangana*) were described originally in *Ectomomyrmex*, or were placed in that genus later. Actually, these species are all very close to *sharpi*—in fact, *malayanus* is almost certainly a straight synonym of *sharpi*. The form of *sharpi* from China and Japan has the propodeum

wider and more opaque above; it was described by Wheeler as subspecies *pilosior*, but should be considered as a good species until more is known about the variation in this complex, which, if it matches the variation found in *brunoi* in Africa, may be considerable. *T. pilosior* occurs westward to the scarp of the Tibetan Plateau, where I collected a worker on Mt. Omei, Szechuan Province, in 1945; *Euponera* (*Trachymesopus*) *chosonensis* Teranishi, 1940, from Osaka, Japan, is its **new synonym**. The Oriental and African forms of this group are also very close, and deserve careful comparison. The *sharpi* group does not really belong to *Trachymesopus*, and will eventually have to be moved out. But in order to avoid one additional round of name changes, I am leaving it where it is until the limits of other closely related groups, especially *Brachyponera*, are clarified.

TRACHYMESOPUS BRUNOI comb. nov.

Pachycondyla (*Ectomyrmex*) *brunoi* Forel, 1913, Deutsche ent. Zeitschr., beih., p. 205, worker. Type loc.: Bulawayo, S. Rhodesia. Syntype examined.

Euponera (*Trachymesopus*) *nigeriensis* Santschi, 1914, Boll. Lab. Zool. Portici, 8: 316, worker. Type loc.: Olokomeji, Nigeria; also from Aburi, Gold Coast. Syntype examined. **New synonymy**.

Euponera (*Trachymesopus*) *bayoni* Menozzi, 1932, Ann. Mus. Civ. Stor. Nat. Genova, 56: 97-98, worker. Type loc.: Kome, Sesse Archipelago, Victoria Nyanza, Uganda. **New synonymy**.

Ectomyrmex nigricris var. *katangana* Santschi, 1933, Bull. Ann. Soc. Ent. Belg., 73: 96, Type loc.: Pweto, Elisabethville, Belgian Congo. Syntype examined. **New synonymy**.

Euponera (*Mesoponera*) *dentis* Weber, 1942, Proc. Ent. Soc. Wash., 44: 43, fig. 9, dealate female. Type loc.: Lotti Forest, Imatong Mts., Sudan. Type examined. **New synonymy**.

Euponera (*Trachymesopus*) *lamottei* Bernard, 1953, Mem. Inst. Fr. Afrique Noire, 19 (1): 195, fig. 2g, h, i, dealate female. Type loc.: Keoulenta Savannah, French Guinea. **New synonymy**.

This species occurs widely in Africa south of the Sahara. In addition to the types mentioned above, I have seen samples from Liberia, Camerouns and the Kalahari Desert. There is some small variation among these samples in relative head width and in strength and opacity of the sculpture, but this appears to be both size-linked (allometric) and continuous.

ECTOMOMYRMEX Mayr

The taxonomy of this genus has been considerably simplified at the species level by the partial revisions of Wilson (1958) and Yasumatsu (1962), but an even more fundamental change needed is the removal of the species *brunoi* and *malayanus*. These, as has been demonstrated above, are members of the *sharpi* group of "*Trachymesopus*." With these deletions, *Ectomomyrmex* is once more restored to the status of a strictly Indo-Pacific genus, ranging from India and northwestern China eastward to Japan and Korea, Samoa and northern Queensland. It is now also possible to define the genus.

Ectomomyrmex consists of medium-sized to large, usually basically black-colored forms, the workers and females of which tend to have the posterior cranium somewhat prismatic, and the posterior face of the petiolar node strongly striate, or at least rugose-punctate. Worker-female palpi segmented, so far as is known, 4, 4; mandibles without basal pit, the oblique basal groove present and weak, or absent. The oblique mesepisternal suture is present and reasonably distinct in the worker. Compound eyes fairly to rather well developed and multifaceted in the worker.

CENTROMYRMEX Mayr

Centromyrmex Mayr, 1866, Verh. zool.-bot. Ges. Wien, 16: 894. Type:

Centromyrmex bohemannii Mayr, 1866, monobasic.

Spalacomyrmex Emery, 1889, Ann. Mus. Civ. Stor. Nat. Genova, 27: 489.

Type: *Spalacomyrmex feae* Emery, 1889, monobasic.

Typhloteras Karawajew, 1925, Kouowia, 4: 128. Type: *Typhloteras hamulatum* Karawajew, 1925, monobasic.

Glyphopone Forel, 1913, Rev. Zool. Afr. 2: 308. Type: *Glyphopone bequaerti* Forel, 1913, monobasic. **New synonymy.**

Glyphopone subgenus *Leptopone* Arnold, 1916, Ann. S. Afr. Mus., 14: 163.

Type: *Glyphopone (Leptopone) rufigaster* Arnold, 1916, monobasic.

New synonymy.

The type female of *Glyphopone bequaerti* has been compared directly with a winged female kindly sent by Dr. Arnold (Abercorn, Northern Rhodesia, 10-12-1943, Arnold leg. et det.). These two specimens are virtually identical and are surely conspecific, as indicated in the formal synonymy expressed below. The median lobe of the clypeus is hardly to be considered "bicarinate," but the median portion of its surface is very slightly concave when viewed in the proper light. Although these are

large females, with dark forebody and rufous gaster, they bear the general characters of *Centromyrmex*, and in any case, they are probably no larger or darker than the female of *C. gigas*, judging from the workers of *gigas* I have seen. It seems best to consider *Glyphopone* a synonym of *Centromyrmex* until the worker of *G. bequaerti* is found and we are able to determine whether it has the definitive characters.

CENTROMYRMEX BEQUAERTI Forel comb. nov.

Glyphopone Bequaerti Forel, 1913, Rev. Zool. Afr., 2: 308, fig. 1, alate female. Type loc.: Kibombo, Belgian Congo; examined.

Glyphopone (Leptopone) rufigaster Arnold, 1916, Ann. S. Afr. Mus., 14: 163, figs. 10, 10a, alate female. **New synonymy.**

PROMYOPIAS SILVESTRII Santschi

Myopias (Promyopias) Silvestrii Santschi, 1914: 324, fig. 10, worker. Type loc.: Mamou, French Guinea; one syntype worker examined.

Promyopias asili Crawley, 1916, Entomologist, London, p. 30, fig., alate female. Type loc.: "Nyasaland," [according to label on holotype: Mlanje, Nyasaland, 15-IV-1913, S. A. Neave leg.]. Holotype in British Museum, examined. **New synonymy.**

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B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS.

DECEMBER 5, 1963

NUMBER 191

THREE NEW SPECIES OF *MANGORA* (ARANEAE, ARGIOPIDAE) FROM CENTRAL AMERICA

BY ARTHUR M. CHICKERING

In my paper dealing with the genus *Mangora* in Panama (1954) I recognized eight species then known to exist in that country. This conclusion involved the recognition and description of three new species together with the establishment of considerable new synonymy.

During my collecting trips back to the Panama Canal Zone and parts of Panama outside of the Canal Zone in 1954 and 1957-1958 a considerable number of specimens belonging to this genus were taken but no new species were found among these. I have also had the opportunity to study all of the *Mangora* collections from Central America now in the Museum of Comparative Zoology at Harvard College. Some of this material has only recently been sorted out of general collections which have been awaiting attention for many years. From all of this material I have been able to separate out what I believe to be representatives of three new species. These are described in this paper in accord with my usual formula.

If recently established new synonymy is taken into consideration together with the new species recognized in this paper, the complete list of species in the genus *Mangora* O. P.-Cambridge, 1889, now definitely known from Central America, may be given as follows: *M. bimaculata* (O. P.-Cambridge); *M. calcarifera* F. P.-Cambridge; *M. candida* Chickering; *M. conspicua* sp. nov.; *M. distincta* sp. nov.; *M. mobilis* (O. P.-Cambridge); *M. montana* Chickering; *M. passiva* (O. P.-Cambridge); *M. pia* Chamberlin and Ivie; *M. picta* O. P.-Cambridge; *M. schmierlari* Chickering; *M. spinula* F. P.-Cambridge; *M. sufflava* sp. nov.; *M. trilineata* O. P.-Cambridge. Banks (1898) reported *M. gibberosa* (Hentz) from Lower California. I have not been able to examine these specimens but I regard it as highly unlikely that the species exists in that

part of Central America and, for this reason, the species is not included in the list given above. Kraus (1955) reported *M. gibberosa* (Hentz) from El Salvador. Again, I think there is serious question regarding the validity of this identification. I am rather strongly inclined to believe it belongs to the species which I am regarding as *M. conspicua* sp. nov. but, in view of the uncertainty, I am omitting it from my list. Only males are known for *M. distincta* sp. nov., *M. picta* O. P.-Cambridge, and *M. sufflava* sp. nov. Only females are known for *M. passiva* (O. P.-Cambridge), *M. schmierlai* Chickering, and *M. trilineata* O. P.-Cambridge.

All types established in this paper together with my entire collection of Araneae are deposited in the Museum of Comparative Zoology at Harvard College.

Genus MANGORA O. P.-Cambridge, 1889

MANGORA CONSPICUA sp. nov.

(Figures 1-7)

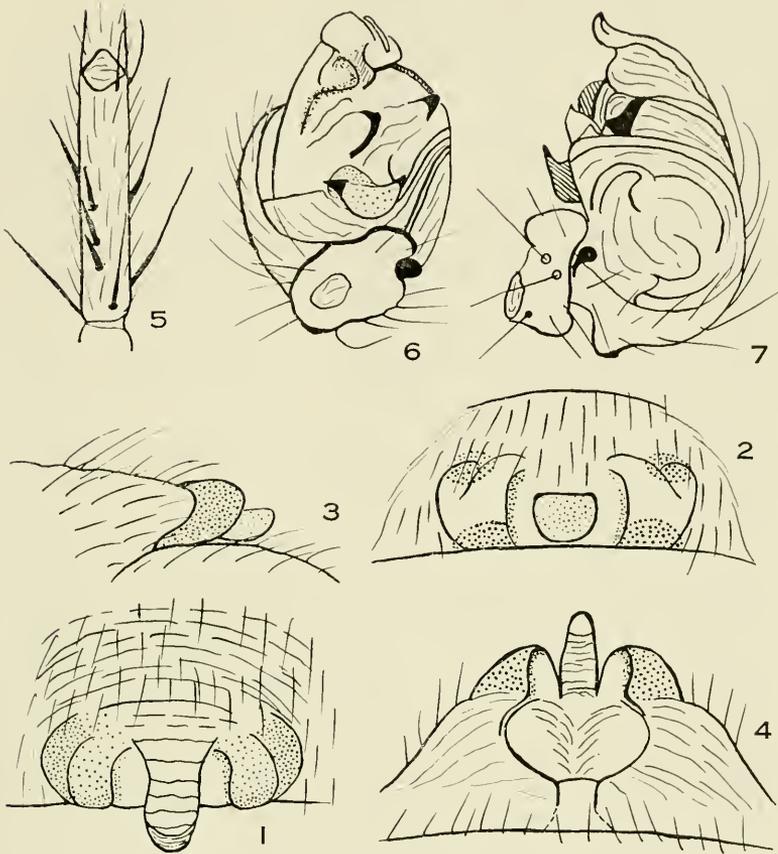
Female holotype. Total length 3.77 mm. Carapace 1.408 mm. long; .99 mm. wide opposite interval between second and third coxae where it is widest; .66 mm. tall at level of greatest width and, therefore, two-thirds as tall as wide; median fovea a narrow, longitudinal groove.

Eyes. Eight in two rows as usual. LE on very slightly raised tubercles; AME protrude somewhat over clypeus. Viewed from above, anterior row strongly recurved, posterior row slightly so. Viewed from in front, posterior row procurved, anterior row recurved, all measured by centers. Central ocular quadrangle wider in front than behind in ratio of about 20 : 17; slightly longer than wide in front. Ratio of eyes AME : ALE : PME : PLE = 8 : 5.5 : 6.5 : 6. AME separated from one another by about 1.25 times their diameter, from ALE by slightly less than that distance. PME separated from one another by about ten-thirteenths of their diameter, from PLE by eleven-thirteenths of their diameter. Height of clypeus equal to about the radius of AME.

Chelicerae. Typical of the genus. Promargin of the fang groove apparently with three teeth; retromargin apparently with only two.

Maxillae and *Lip.* Typical of the genus; with details regarded as unnoteworthy.

Sternum. Quite convex; longer than wide in ratio of about 13 : 11; sternal suture strongly procurved; not directly continued between fourth coxae but a sclerite is present there; fourth coxae separated by nearly two-thirds of their width.

EXTERNAL ANATOMY OF *Mangora*Figures 1-7, *M. conspiciua*

Figs. 1-3. Epigynum from below, in posterior view, and in profile from right side, respectively.

Fig. 4. Epigynum from a paratype, turned forward to reveal the dorsal surface.

Fig. 5. Left second tibia of male allotype, showing ventral spines.

Figs. 6-7. Two views of the male palpal tibia and tarsus.

Legs. 1423. Width of first patella at "knee" .217 mm., tibial index of first leg 15. Width of fourth patella at "knee" .227 mm., tibial index of fourth leg 16.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in mm.)					
1.	1.474	.440	1.050	1.320	.638	4.922
2.	1.350	.440	.924	1.166	.610	4.490
3.	.748	.330	.528	.638	.438	2.682
4.	1.474	.450	.968	1.122	.550	4.564

All legs with fairly robust spines. The long, branched hairs on the third tibiae appear to be arranged in two oblique rows of five and four, respectively, but short trichobothria are closely contiguous. Tarsal and palpal claws appear as usual in the genus.

Abdomen. 2.795 mm. long; 1.826 mm. wide; ovoid; with attachment to cephalothorax only slightly anterior to middle; otherwise as usual in the genus.

Epigynum. General pattern resembles that of *M. mobilis* (O. P.-Cambridge) and *M. passiva* (O. P.-Cambridge) but the central tongue is longer than in either of these species and other differences are also visible. Features as shown in Figures 1-4.

Color in alcohol. This is a very clearly marked species and all three females available are remarkably consistent in their color pattern. Carapace yellowish with a narrow, median, black stripe reaching from just behind PME through the median groove where it is extremely narrow; there is a marginal stripe beginning a little behind PLE and extending to about opposite the second coxae where it widens and continues nearly to the posterior border as a gray area. The sternum is dark brown with a light spot in the middle just behind the sternal suture. The legs are basically yellowish but are rather conspicuously spotted because each spine is surrounded at its base by a small black dot. The first and second femora each have a ventral black dot on the membrane at the joint between the trochanter and the femur, then an irregular black stripe reaches nearly to the distal end where there is a curved black band; there is also an indistinct gray stripe on both of these femora just prolateral to the black stripe. The gray stripe is lacking on some paratypes but the fourth femur has a dark, gray, retrolateral stripe extending through the middle of the segment. The abdomen is also conspicuously colored by numerous small white flecks and dark brown or black stripes. Beginning about one-third from the base there is a narrow median, brownish stripe and on each side of this there is an irregular black stripe. White dominates the whole dorsum except for these stripes. The lateral sides each have four narrow, irregular, dark brown or black, oblique stripes extending to the venter. The latter part is yellowish anterior to the epigynum;

behind the epigynum there is a broad, median stripe with a group of white flecks on each side. There are also three small, white spots on each side of the group of spinnerets.

Allotype male. Three males apparently belonging to this species are in the collection but they are all defective for one reason or another. For this reason the female has been chosen as the holotype and a male with normal palps as the allotype. The abdomen of the allotype male was crushed and of little value. Total length of a paratype male 2.134 mm. Carapace of allotype male 1.122 mm. long; .718 mm. wide opposite interval between second and third coxae where it is widest; about .44 mm. tall. Otherwise essentially as in female.

Eyes. Essentially as in female; details regarded as unnoteworthy.

Chelicerae. Difficult to see teeth along fang groove; apparently the number is the same as in female.

Maxillae, Lip, and Sternum. Each maxilla has a tooth which is in apparent opposition to a chitinized tubercle on the palpal femur; otherwise these structures are essentially as in female.

Legs. 1243. Width of first patella at "knee" .162 mm., tibial index of first leg 13. Width of fourth patella at "knee" .152 mm., tibial index of fourth leg 15.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in mm.)					
1.	1.232	.418	.880	1.056	.594	4.180
2.	1.056	.360	.682	.990	.550	3.638
3.	.638	.242	.396	.506	.374	2.156
4.	1.034	.330	.704	.792	.462	3.322
Palp	.220	.120	.098	—	.462	.900

Spines on legs are considerably more conspicuous and much longer than in females. The curled hairs on the third tibiae apparently are arranged in two oblique rows of four and three, respectively. Additional trichobothria are also present but their exact distribution has not been determined. The second tibia has specialized spines; those seen in ventral view are represented in Figure 5. The first coxa has the ventral hook and the second femur has the corresponding groove and ridge.

Palp. Complicated; parts are small and generally inconspicuous but the clavis is clearly visible. Both patella and tibia are short; the latter is broad, angular, and very irregular in outline (Figs. 6-7). The femur has the chitinized tubercle as already stated.

Abdomen. This part of the body is badly crushed and unsuitable for study; apparently it is essentially like that of the female.

Color in alcohol. The color in general is similar to that of the female holotype but it is less conspicuous. The marginal stripes on the carapace of the female are merely indistinct grayish areas in the male allotype. The sternum is nearly surrounded by a dark gray margin with the greater part yellowish with small grayish areas. The legs are much as they appear in the female but the black dots at the bases of the spines are less conspicuous and the proteral, grayish stripes on the first and second femora are absent in the male. Abdomen: there are numerous white, chalky flecks on the dorsum; there are two black dots in the middle line in the anterior half of the dorsum; the posterior half of the dorsum contains a dark, rectangular, fairly broad spot composed of a series of black marginal spots more or less connected by very narrow, black lines extending through a brownish area.

Type locality. The holotype female is from Mexico, Nuevo Leon, El Potosi, Cerro Potosi, June 13, 1938 (H. Hoogstraal). One paratype was taken with the holotype. Another in the collection is from the same general region, Sabinas Hidalgo, 1000 ft. elevation, June 13, 1940. Three females in the collection are from Honduras, Escuela Agr. Panam., 27 km. S. of Tegucigalpa, San Antonio del Oriente. Two males accompany the females. One was mature; it had undergone severe injury to its abdomen but was selected as the allotype; the other was immature. The Honduran specimens were collected by A. and M. Carr at 3800-4000 ft. elevation, November 17, 1945. Two other males in the collection are from Mexico: Nuevo Leon, Villa de Santiago, Hacienda Vista Hermosa, 2000 ft. elevation, July 19, 1940 (H. Hoogstraal). Both of these males have their tarsal bulbs so distended as to be useless for description.

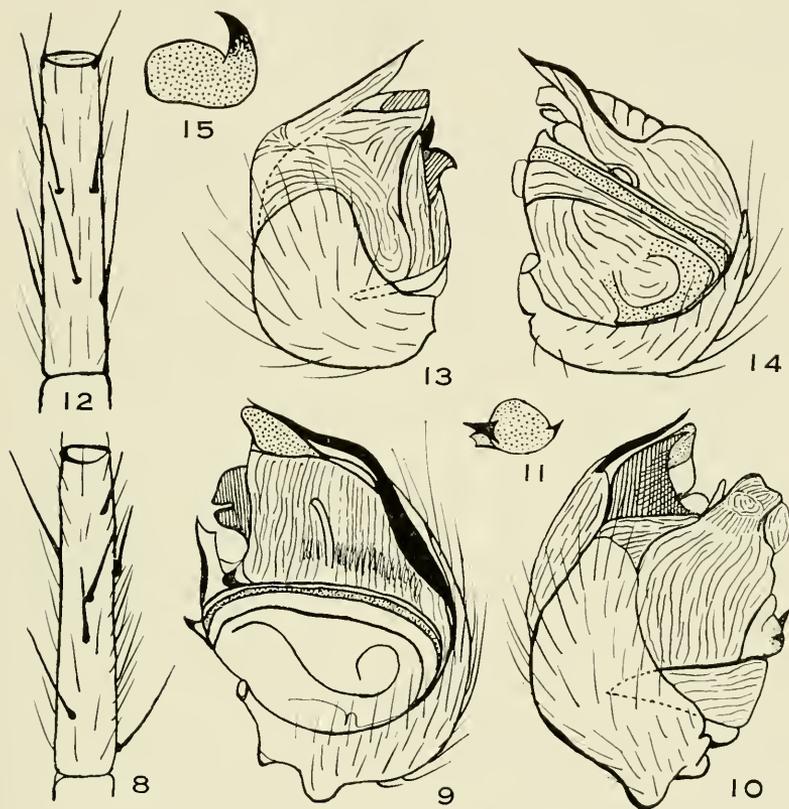
MANGORA DISTINCTA sp. nov.

(Figures 8-11)

Male holotype. Total length 2.535 mm. Carapace 1.202 mm. long, .902 mm. wide opposite interval between second and third coxae where it is widest, .484 mm. tall and, therefore, about .54 as tall as wide; gently arched with tallest point nearly at level of greatest width; median fovea a rather deep, narrow, longitudinal groove.

Eyes. Eight in two rows as usual; LE on slightly raised tubercles; AME protrude prominently over clypeus. Viewed from

above, anterior row strongly recurved, posterior row slightly so. Viewed from in front, anterior row slightly recurved, posterior row moderately procurved, all measured by centers. Central ocular quadrangle wider in front than behind in ratio of 19 : 16; slightly



EXTERNAL ANATOMY OF *Mangora*

Figures 8-11, *M. distincta*

Figures 12-15, *M. sufflava*

- Fig. 8. Left second tibia to show ventral spines.
 Figs. 9-10. Two views of the palpal tarsus.
 Fig. 11. Tarsal clavis.
 Fig. 12. Left second tibia to show ventral spines.
 Figs. 13-14. Two views of the palpal tarsus.
 Fig. 15. Tarsal clavis enlarged.

longer than wide in front. Ratio of eyes AME : ALE : PME : PLE = 6 : 5 : 6 : 5. AME separated from one another by their diameter, from ALE by slightly less than this distance. PME separated from one another by slightly more than their radius, from PLE by their diameter. LE separated only by a line. Height of clypeus about equal to the diameter of AME (surrounding pigment makes it difficult to obtain exact measurements of eyes and their relative positions).

Chelicerae. General features as usual in the genus. Unable to observe teeth along fang groove without injury to holotype.

Maxillae and Lip. Maxillae with a sharply pointed tooth near their bases; probably used in opposition to the chitinized tubercle on the palpal femur. In general, both structures appear to be typical of the genus.

Sternum. Scutiform; strongly convex; somewhat depressed in anterior portion; sternal suture quite procurved; widest between second coxae where it is nearly as wide as long; continued broadly between fourth coxae which are separated by 8/11 of their width.

Abdomen. Ovoid; quite typical of the genus; details regarded as unnoteworthy.

Color in alcohol. Legs and mouth parts generally yellowish; each chelicera has a small, irregular, grayish area in front near the base. The carapace is yellowish with a narrow central stripe from a little behind PME and extending two-thirds of the distance to the posterior border. The sternum is yellowish with a very irregular light grayish marginal area. Abdomen: yellowish with whitish flecks dorsally and dorsolaterally; in the posterior half of the dorsum there are three narrow brownish stripes; in the region of the spinnerets there are several black and white dots; on each lateral side there is a narrow oblique grayish stripe followed by an area of many small white flecks and finally a rounded irregularly grayish spot; the venter is generally yellowish but just in front of the genital groove there is an oval grayish spot and behind the genital groove there is an irregularly grayish, rounded spot containing a group of white flecks.

Type locality. The holotype is from Honduras, Escuela Agr. Panam., 27 km. S. of Tegucigalpa, San Antonio del Oriente, Nov. 17, 1945, 3800-4000 ft. elevation (A. and M. Carr). There are no paratypes and the female is unknown.

MANGORA SUFFLAVA sp. nov.

(Figures 12-15)

Male holotype. Total length 2.6 mm. Carapace 1.3 mm. long, .99 mm. wide opposite interval between second and third coxae where it is widest, .638 mm. tall at about the level of its greatest width and, therefore, about half as tall as wide; median fovea a narrow, well defined, longitudinal groove; considerably overlapped by anterior end of abdomen. Other features as usual in the genus.

Eyes. Eight in two rows as usual. Viewed from above, anterior row strongly recurved, posterior row moderately so. Viewed from in front, anterior row moderately recurved, posterior row moderately procurved, all measured by centers. Central ocular quadrangle wider in front than behind in ratio of 7 : 6; slightly longer than wide in front. Ratio of eyes AME : ALE : PME : PLE = 7.5 : 6 : 6.5 : 6. AME separated from one another by about their diameter, from ALE by about two-thirds of their diameter. PME separated from one another by about two-thirds of their diameter, from PLE by about 1.3 times their diameter. LE separated only by a broad line. Height of clypeus equal to about four-fifths of the diameter of AME.

Chelicerae, Maxillae, Lip and Sternum. All apparently typical of the genus.

Legs. 1243. Width of first patella at "knee" .200 mm., tibial index of first leg 13. Width of fourth patella at "knee" .162 mm., tibial index of fourth leg 14

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in mm.)					
1.	1.364	.506	.990	1.100	.649	4.609
2.	1.320	.484	.902	1.078	.627	4.411
3.	.792	.308	.506	.528	.418	2.552
4.	1.292	.418	.770	.880	.528	3.888
Palp	.286	.119	.119	—	.440	.964

All legs with well developed spines and hairs. Second tibia with modified spines; those seen in ventral view shown in Figure 12. The long, slender, branched hairs on the prolateral side of third tibia appear to be arranged in two oblique rows of three each. The first coxa bears the usual hook and the second femur has the corresponding prolateral, proximal groove and chitinized ridge. Tarsal claws appear to be as usual in the genus.

Palp. The patella has the usual long, slender, terminal, dorsal spine. Both patella and tibia are short. Important tarsal features shown in Figures 13-15. The clavus appears to be different from any other found in the collection. The tooth is probably present on the maxilla together with the chitinized tubercle on the palpal femur but neither can be clearly seen without danger of damage to the holotype.

Abdomen. 1.625 mm. long; 1.170 mm. wide near middle; ovoid. At the base are two long, slender, dorsal, spine-like bristles. Other features typical of the genus.

Color in alcohol. Carapace yellowish with a grayish median stripe extending from AME to middle third of steep posterior declivity; the center of the grayish stripe is a narrow, black line. The sternum is broadly grayish around the margin but yellowish in the center. The legs and mouth parts are yellowish with many variations in the depth of color. Abdomen: this part of the body has a rather unusual color pattern; dorsolaterally there is a fairly broad, white stripe on each side extending nearly the length of this part of the body; there is a large, median, grayish yellow spot in the anterior half of the dorsum containing a pair of small white dots in the posterior half with another pair of small white dots at its posterior border; the posterior half of the dorsum has a pair of dark gray stripes separated by a yellowish stripe; these stripes do not reach to the posterior end of the abdomen; the venter is yellowish with faint gray irregularities.

Type locality. The holotype male is from Boquete, Chiriqui, Panama, August, 1950. This specimen was overlooked among specimens belonging to different genera at the time of completion of my previous paper on *Mangora* (1954) and only recently found. There are no paratypes and the female is unknown.

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B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS.

DECEMBER 5, 1963

NUMBER 192

A DESCRIPTION OF *DINOPIS LONGIPES*

F. P.-CAMBRIDGE, 1902

(Araneae, Dinopidae).

BY ARTHUR M. CHICKERING

F. P.-Cambridge described this highly interesting species entirely by means of figures and a statement of the total lengths of the two sexes. It may be that one reason for this extreme brevity was due to the fact that fully mature individuals have extraordinarily long and fragile legs and the body is usually badly distorted in the preservative. This results in considerable difficulty in getting specimens sufficiently intact to make description significant. It has usually been assumed that this is a rare species but this is probably because collecting activities have not been sufficiently intensive. At any rate, I now have in my collection several mature specimens of both sexes and numerous immature individuals.

Because of the extreme brevity of the original description it has been thought advisable to prepare a detailed description of both sexes in order to make clear the fundamental features of the species. After a careful search through the collection, individuals of both sexes have been selected for detailed description in accord with my usual formula. The selected male is smaller than some other individuals of the same sex but its parts are quite well preserved and its legs are much less fragile than in most of the other available specimens. It appears to have been captured soon after the last moult and before its full size had been reached. The female selected for description had probably reached her full mature size.

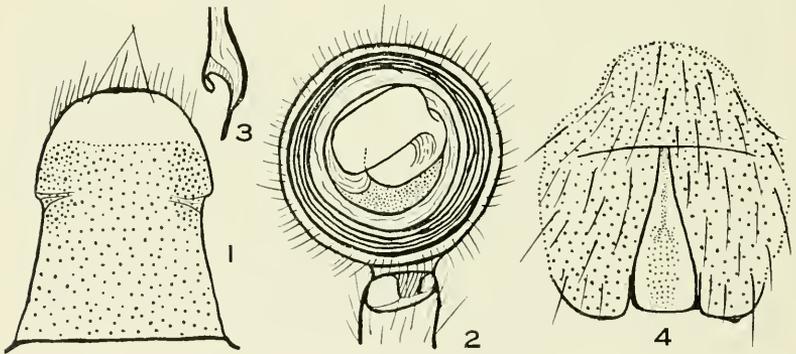
Genus *DINOPIS* Macleay, 1839

DINOPIS LONGIPES F. P.-Cambridge, 1902

Male. Total length 16.282 mm. Carapace 4.42 mm. long; about 2.73 mm. wide; extremely flat; with a shallow median depression continued posteriorly by a long, very narrow groove; with several very short spines.

Eyes. Eight in three rows with arrangement typical of the genus; posterior centrals enormously enlarged and moved forward to dominate the optical area. Viewed from above, only posterior eyes seen in two rows. Viewed from in front, anterior row definitely procurved. Ratio of eyes AME : ALE : PME : PLE = 13 : 15 : 32 : 16. AME separated from one another by $18/13$ of their diameter, from ALE by $42/13$ of their diameter. PME separated from one another by about $2/3$ of their diameter, from PLE by nearly $3/2$ of their diameter. (All measurements are made from the inner margin of the iris and not the margin where the cornea becomes continuous with the cuticle, which is often difficult to determine.) The iris of the PME is purplish and the border of the cornea is bright red. The clypeus is lacking because of the marginal position of the first row of eyes. The AME are located on a common tubercle; each ALE is also mounted on a fairly prominent tubercle.

Chelicerae. Rather small for the size of the animal; basal segment about .77 mm. long; distal half of medial surface with many long, curved, stiff, brownish bristles. Fang evenly curved, without special features. Fang groove fairly well defined; with 5 definite small teeth plus a terminal nodule along the promargin; with 10-12 minute teeth along the retromargin, some of which are no more than nodules; some irregularities have been noted on left and right sides and in different specimens.



EXTERNAL ANATOMY OF *Dinopis longipes*

- Fig. 1. Lip.
 Fig. 2. Palpal tarsus of male showing coiled embolus and central apophysis.
 Fig. 3. Distal end of embolus; removed from a second male.
 Fig. 4. Epigynum from below.

Maxillae. Nearly parallel in general; massive in proximal halves; narrowed and somewhat diverging in distal halves; with well developed scopulae.

Lip. General features shown in Figure 1.

Legs. 1243. Width of first patella at "knee" .550 mm., tibial index of first leg 3. Width of fourth patella at "knee" .440 mm., tibial index of fourth leg 4.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in mm.)					
1.	13.780	1.950	14.495	20.150	5.460	55.835
2.	11.700	1.755	11.310	12.675	3.510	40.950
3.	9.750	1.280	7.410	7.280	1.625	27.345
4.	10.855	1.690	10.075	10.725	1.755	35.100
Palp	2.015	.845	.520	—	1.170	4.550

Spines: Numerous femoral spines are present but apparently all are very small and, perhaps, irregularly placed; no patellar spines have been observed; tibial and metatarsal spines are numerous and of moderate size. Three tarsal claws are present with each upper claw provided with a single row of about six teeth; the third claw is simple and without teeth; there are also numerous spurious claws present. Numerous trichobothria have been observed on tibiae and metatarsi; they are not confined to "ventral surface at base of tibia" as stated by Dr. Petrunkevitch (1939). The calamistrum is moderately well developed on the proximal half of the fourth metatarsus of immature specimens; on the specimen here described in detail it is, apparently, much reduced.

Palp. Both patella and tibia are short, simple and lacking apophyses or other special modifications; the cymbium is a deep cup-shaped structure containing the bulb which has an extraordinarily long, coiled embolus; enclosed in the center of the circular coils of the embolus is a somewhat distinctive structure noted by F. P.-Cambridge and again noted in this study. Figures 2 and 3 show the chief features of the palp as observed by this author. The length of the free part of the embolus seems to vary in different individuals. In one example there were apparently ten circular coils making a total length of the embolus approximating two inches. In the specimen described here in detail the free part of the embolus is much shorter; when stretched out it resembles a clock spring. The median apophysis surrounded by the coiled embolus also exhibits different shapes in different specimens. The significance of these differences is not at all clear.

Abdomen. Long, stender; of nearly uniform width; with a pair of very small dorsal tubercles slightly behind the middle. The six spinnerets and eribellum appear typical in males of the genus. The abdomen is well supplied with plumose hairs.

Color in alcohol. Carapace: the basic color is a yellowish brown; with a narrow darker median stripe and a fairly broad and still darker dorsolateral stripe on each side; white plumose hair extends between the PLE up to the enlarged PME. The sternum is yellowish, with a very irregular, broken, narrow, brown border and several irregular whitish subchitinous patches. The legs are yellowish with sparsely located small black dots; the coxae are much spotted with black ventrally. Abdomen: light brownish dorsally and laterally; with a darker, median, dorsal stripe; the lateral sides possess several alternating, light and dark longitudinal stripes; the venter has a fairly broad, brownish, variegated, median stripe and many small, whitish, subchitinous, irregular spots on each side of the darker median stripe.

Female. Total length about 24.7 mm. Carapace about 8.58 mm. long; 4.225 mm. wide opposite interval between second and third coxae where it is widest; much narrowed immediately in front of first coxae where it is about 2.405 mm. wide; surface with numerous shallow depressions.

Eyes. General features as in male. Ratio of eyes AME : ALE : PME : PLE = 9.5 : 11 : 44 : 12.5.

Chelicerae. Essentially as in male except for teeth along the fang groove. The specimen from which this description is chiefly taken shows seven teeth along the promargin of which the second, fifth, and seventh are very small. Along the retromargin there are five or six teeth of moderate size and many minute teeth, little more than minute tubercles; immediately behind the last tooth of moderate size there is a series of five very minute teeth some of which are on the lower part of the larger tooth itself; some of the minute teeth occur in the fang groove. The fang groove in another female specimen showed the promargin with six teeth of which the fourth and sixth were small, the others of moderate size; the retromargin had eight teeth in an irregular row together with numerous minute tubercles. There is a well defined scopula along the promargin of the fang groove.

Maxillae. Essentially as in male.

Lip. This structure is abnormal in the specimen chiefly used for this description. Another specimen has the lip essentially as shown in Figure 1.

Sternum. Also essentially as in male.

Legs. 1243. Width of first patella at "knee" .88 mm., tibial index of first leg 4. Width of fourth patella at "knee" .902 mm., tibial index of fourth leg 6.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in mm.)					
1.	18.525	2.925	17.680	18.850	4.160	62.140
2.	18.200	2.860	16.900	16.900	2.929	57.789
3.	13.780	2.015	10.400	10.725	1.950	38.870
4.	14.170	2.665	12.545	11.895	1.950	43.225

I have found difficulties in making leg measurements as accurate as usual because of fragility and breakage. The palpal claw has three prominent teeth; the palpal tarsus bears many stiff bristles and numerous spines. The calamistrum is fairly well developed on the proximal third of the fourth metatarsus. All legs are richly provided with spines of two kinds; the usual type are numerous, short and, apparently, not regularly placed; the second type is a slender, highly branched, unusual kind. Trichobothria have not been observed in females, perhaps because of the multiplicity of spines.

Abdomen. Badly distorted by the preservative. Apparently as in male in all essential general features except that the dorsal tubercles somewhat in front of the middle are moderately well developed in contrast to the minute tubercles in the male; each tubercle has its posterior surface covered by a coating of short, white hairs. The cribellum is well developed and undivided.

Epigynum. Essentially as represented in Figure 4.

Color in alcohol. Essentially as in male except that the whole coloration is darkened to a dull brown in general; the dorsal surface of the abdomen bears a series of isolated, small, white dots caused by clusters of short, white hairs.

Collection records. Both specimens chiefly used for this description were collected on Barro Colorado Island, C. Z., July, 1954. Several other adults and numerous immature specimens are in the collection from many localities in the Canal Zone and Boquete, Chiriqui, Panama. The species seems to be fairly abundant on Barro Colorado Island. All specimens referred to in this paragraph are now deposited in the Museum of Comparative Zoology at Harvard College.

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B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS.

DECEMBER 5, 1963

NUMBER 193

A MIOCENE TOAD FROM COLOMBIA, SOUTH AMERICA

BY RICHARD ESTES¹ AND

RICHARD WASSERSUG²

The fossil toad described here is part of the large vertebrate assemblage of the La Venta fauna (Fields, 1959), and was collected by R. W. Fields during the 1949 University of California field expedition to the upper Magdalena Valley, Huila, Colombia, South America. It is the same specimen identified by D. Savage (1951) as a leptodactylid, cited by Estes (1961) as a bufonid close to the living *Bufo alvarius* and *B. crucifer*, and discussed briefly by Tihen (1962b, p. 14) as *Bufo* sp., near *B. marinus*. Tihen's very useful paper on bufonid osteology (1962a) now makes it possible to give a much more accurate and clear-cut assessment of the relationships of this animal. Few fossil *Bufo* have been recorded previously from South America (Tihen, 1962b).

Both authors wish to express their gratitude to Drs. E. E. Williams, R. F. Laurent, J. A. Tihen and J. M. Gallardo for their many helpful suggestions, and to Mr. Howard Hamman, who prepared the illustrations. This work was supported by National Science Foundation Grant NSF G-18905, held by the senior author, and research time for the junior author was provided through the Thayer Academy Advance Studies in Science Program (also supported by the National Science Foundation). We are grateful for this support.

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Class AMPHIBIA
Superorder SALIENTIA
Order ANURA
Family BUFONIDAE
BUFO MARINUS Linnaeus

Referred specimen—University of California no. 41159, postorbital portion of skull, eight articulated vertebrae, both scapulae with articulating proximal ends of the humeri, both distal ends of humeri in articulation with proximal ends of radioulnae, two fragments from the region surrounding the acetabulum of the pelvic girdle, distal end of right femur, proximal ends of both tibiofibulae, distal extremity of right tibiale-fibulare, and two unidentified fragments. Two bone shafts which were collected at the same time, and have the same specimen number, are probably mammalian.

Horizon—University of California locality V-4517, Monkey unit, Honda group (Fields, 1959, p. 419, and fig. 2).

Age—Late Miocene.

Fauna—La Venta.

Preservation—The skeleton was apparently complete before exposure and erosion disarticulated and destroyed parts of it. The matrix is a silty mixture of claystone and sandstone, and the cavities have been filled either with this material or with calcite. In some cases, calcite or matrix have remained as endocasts of parts of the bones. Breakage has apparently been the result of erosion, and has occurred at the weakest and thinnest points.

The shoulder and elbow complexes are articulated in flexed positions, and the vertebral column has a slight ventral curve, similar in both cases to their positions in life in a normal resting position. It is possible that the toad died and was buried in such a position.

Description—The maximum width of the skull across the posterior arms of the squamosals is 39.5 mm. A height measurement of the skull taken from the dorsal extremities of the prootic part of the otoparietal (in *Bufo*, paired processes directly dorsal to the foramen for the ninth and tenth cranial nerves) to the parasphenoid-ptyergoid suture is 10.0 mm. A ventral measurement along the median line from the exoccipital condyles to the posterior border of the sphenethmoid is 11.7 mm. In occipital view, the skull roof appears flat, except for the strong postorbital crests and suggestions of the supraorbital crests. The foramen magnum is about 65 per cent wider than deep, and the foramina for ninth

and tenth cranial nerves are prominent. Only the left columella is present and its tip was broken in handling. Its true length, as indicated in the figures, was taken from a photograph made before the breakage occurred. The prootic parts of the otoparietal are strongly ossified laterally and ventrally and form the ventral borders of strongly marked troughs for the columellae. The pterygoids

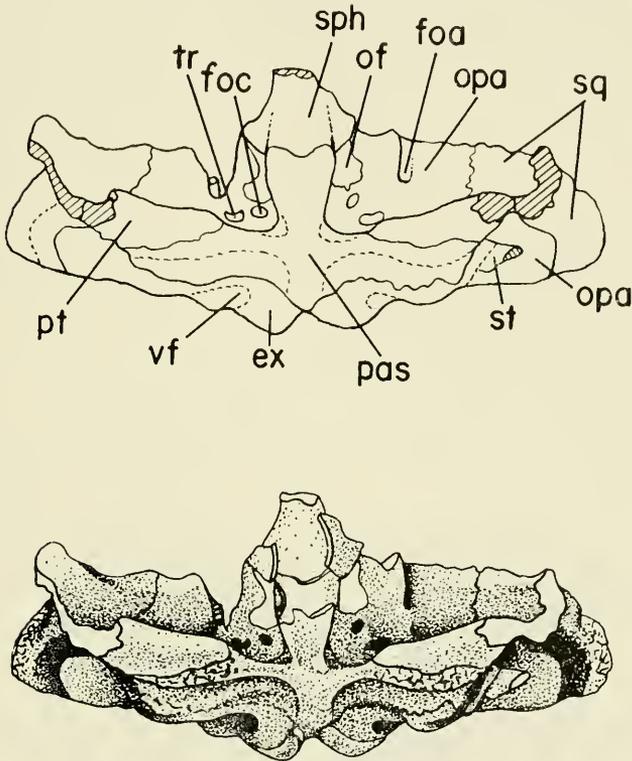


Figure 1. *Bufo marinus*, U. C. no. 41159, ventral view of skull, anterior to the top; above, outline, and below, shaded drawing; X2. On the outline, solid lines indicate sutures, dotted lines are contours, and cross-hatching indicates breakage. Abbreviations: *ecc*, endocranial cast; *ex*, exoccipital; *foa*, canal for occipital artery; *foc*, oculomotor foramen; *fom*, foramen magnum; *for*, foramen for maxillo-mandibular branch of trigeminal nerve; *fps*, frontoparietal suture; *ma*, attachment for nuchal muscles; *oc*, exoccipital condyle; *of*, large opening into braincase for optic and trochlear nerves; *opa*, otoparietal; *pas*, parasphenoid; *pt*, pterygoid; *sph*, sphenethmoid; *sq*, squamosal; *st*, columella auris; *tr*, foramen for fifth, sixth and seventh cranial nerves; *vf*, foramen for ninth and tenth cranial nerves.

are broken just medial to the point at which they would have given off their quadrate and palatal processes, and the descending quadrate processes of the squamosals are broken off at approximately the same level. The cultriform process of the parasphenoid is broken off just posterior to its juncture with the sphenethmoid, but the bone shows nothing unusual. The squamosal-prootic and prootic-parasphenoid sutures are difficult to discern, especially on the right side, and it appears that almost complete fusion has occurred.

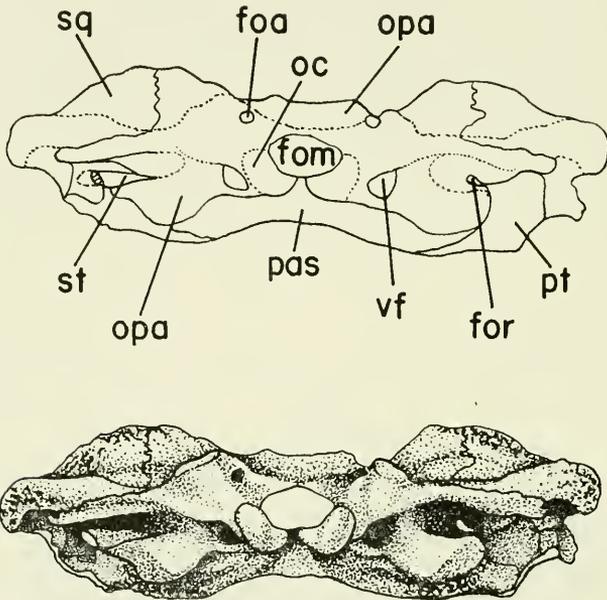


Figure 2. *Bufo marinus*, U. C. no. 41159, posterior view of skull; above, outline, and below, shaded drawing; X2. Comments and abbreviations as in Figure 1.

In dorsal view, the dermal ornamentation lacks strong protuberances other than the postorbital and orbital crests, though weak parietal crests are present, and two small bumps occur near the midline. The all-over pattern of the dermal ornament is a pitted and wrinkled one, in which the wrinkles extend more or less transversely across the top of the skull.

The frontoparietal portions of the otoparietals appear to be fused to each other, though an anterior groove, shown in Figure

3, perhaps indicates part of their suture. Conjoined, these frontoparietal areas are 21.7 mm. at their widest point. The anterior section of the frontoparietal area is broken off before its contact with the nasals. The occipital groove (Tihen, 1962a), is enclosed to form a canal. On the right side, breakage has removed the overlying bone and exposed the endocast of this canal.

In ventral aspect, much of the brain cavity appears as an endocranial cast. Small posterior fragments of the sphenethmoid, along with the anterior arms of the prootics and the cultriform process of the parasphenoid, completely surround an opening which was membrane covered in life and through which the optic

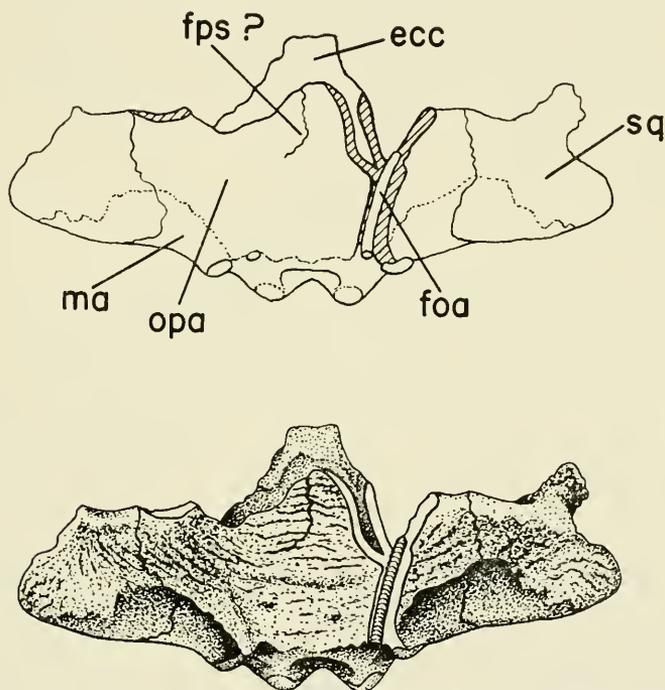


Figure 3. *Bufo marinus*, U. C. no. 41159, dorsal view of skull, anterior to the top; above, outline, and below, shaded drawing; X2. Comments and abbreviations as in Figure 1.

and trochlear nerves passed. This opening is somewhat squared-off, with notches in anterodorsal and posteroventral corners. Because of greater ossification, especially on the posterior border of the sphenethmoid, the opening is relatively smaller than that of

Recent *Bufo*. The lateral wings of the parasphenoid are broadly overlapped by rugose medial processes of the pterygoids. The foramen for cranial nerves five, six, and seven, and the oculomotor foramen are as in Recent *Bufo*. The occipital grooves (here enclosed to form canals) open on the ventral surface of the orbital portions of the frontoparietals, and are continued for a short distance as channels on the roof of the orbit. These paired canals, which in life transmitted the occipital arteries, diverge slightly as they pass anteriorly, but lie essentially parallel to the midline. Dorsal to the suture between the prootic and the pterygoid, immediately lateral to the foramen for cranial nerves five, six, and seven, and on a level with it, is a groove which passes through the prootic and emerges immediately lateral to the base of the columella. The maxillo-mandibular branch of the trigeminal nerve

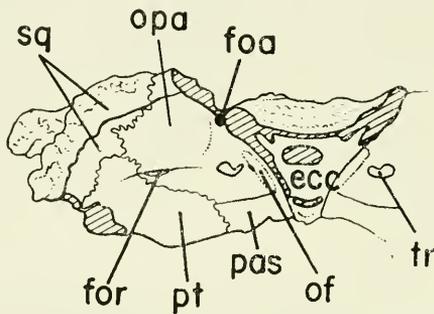


Figure 4. *Bufo marinus*, U. C. no. 41159, anterior view of right half of skull, outline only, showing posterior wall of orbit; X2. Comments and abbreviations as in Figure 1.

is found in this groove in *Rana* (Holmes, 1924, p. 296) and dissection showed this to be the case in *Bufo* as well. The groove in *Bufo* terminates on the lateral borders of the prootic, leading into the suprapterygoid fenestra (Tihen, 1962a, p. 160), but in this specimen there has been extremely high ossification in this area and portions of the prootic, squamosal, and pterygoid have completely closed the fenestra, and enclosed the groove in a foramen.

The thick and massive vertebral column is complete from the atlas back to about the level of the anterior third of the eighth vertebra, though all of the transverse processes are badly broken. The column was originally articulated with the skull, but was removed by the senior author in order to study the configuration of the exoccipital condyles and atlantal cotyles. An approximate

overall measurement of the seven presacral vertebrae is 42.5 mm. The atlantal cotyles are separated by a shallow notch. The neural spines are flattened and capped with dermal bone that has a slightly pitted texture. None of the broken transverse processes are long enough to give positive information about their true length or orientation, though they seem to have been oriented as in Recent *Bufo*. The zygapophyses are robust, as are the centra.

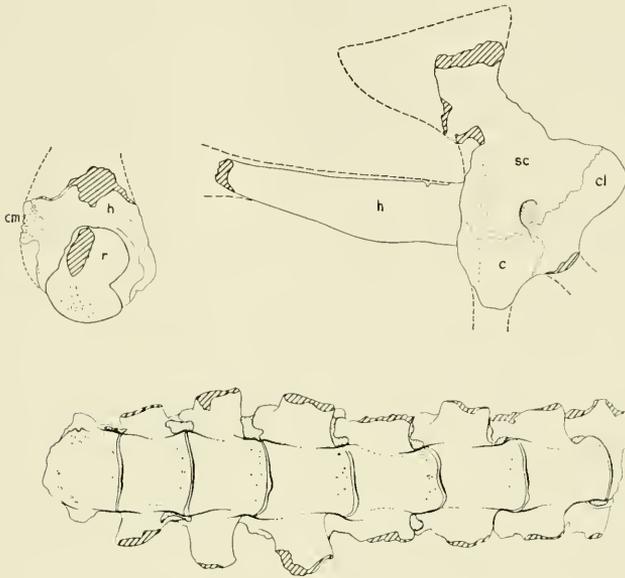


Figure 5. *Bufo marinus*, U. C. no. 41159, right, medial view of left scapula and humerus (*h*), showing sutural contacts of scapula (*sc*), coracoid (*c*), and clavicle (*cl*); left, anterior view of distal end of left humerus and proximal end of radioulna (*r*), to show *crista medialis* (*cm*); below, ventral view of vertebral column, anterior to left; all X2.

The right scapula is the better preserved. Its dorsal edge is broken parallel to, and near, the original natural border. The left scapula is broken at about the same point, but its posterior half is missing. In the glenoid fossa, the small band of cartilage that separates the scapula from the clavicle in the Recent species is completely replaced by a firm bony suture. In Bufonidae, the *pars acromialis* of the scapula (Proctor, 1921, p. 197) forms a strong prominence which is relatively larger in the fossil (on the right side; it is broken on the left) than in the Recent species. The

paraglenal cartilage (Ecker, 1889, p. 40), between the scapula and the coracoid, usually forms a noticeable portion of the floor of the glenoid cavity in modern anurans, but is absent in the fossil and replaced by a firm suture of these two bones. The large foramen in the glenoid fossa is, as a result of the heavy ossification in this region, slightly smaller than in the Recent forms.

The deltoid crest of the humerus is quite prominent, and is about as high from base to peak as the circumference of the humerus at the same point. The shafts of both humeri are missing, distal to the crests.

The radioulnar articulations are similar to those of Recent *Bufo*. On the distal segment of the left humerus, the *crista medialis* is well developed, and has a strongly rugose muscular attachment surface.

All that remains of the pelvic girdle is the ventroposterior corner of the ischium and a ventral piece of the ilium from near the acetabulum.

The proximal articulation surfaces and short segments of shafts of the tibiofibulae show no differences from Recent *Bufo*. The right tibiofibula has the longest shaft preserved. The grooves separating fused tibial and fibular components are deep but no more so than in the Recent species. The distal end of the right femur is no longer in natural articulation with the tibiofibula but still makes a perfect fit.

Both proximal and distal extremities of the right tibiale-fibulare are present. The diaphyses of the bones have been broken so that a natural fit is no longer possible.

Two small fragments may represent a posterior section of the ilial shaft and a section of tibiofibula, but are insufficient for positive identification.

Discussion—Tihen (1962a, p. 163) defines the *valliceps* species group of *Bufo* as follows: frontoparietals broad, usually produced into crests; roofing bones ornamented; occipital groove enclosed to form a canal; frontoparietals and prootics fused. He then divides the *valliceps* group into three essentially geographical subgroups: the Mexican section in Central and North America; the South American section in South and Central America; and the Caribbean section, throughout the Neotropical Region, "partaking to some extent of the characteristics of each of the others, besides developing its own features."

This fossil is placed in the *valliceps* group on the basis of presence of all of the above characters. Within this group, it is eliminated from the Mexican section by having a strong overlap of the

medial wings of the pterygoids onto the wings of the parasphenoid and complete closure of the suprapterygoid fenestra (*ibid.*, p. 168). The strongly-overlapping pterygoids are characteristic of the South American section, and do not usually occur in the Caribbean section, but the occluded suprapterygoid fenestra is present in the latter (*ibid.*, p. 171). This single resemblance to the members of the Caribbean section will be discussed below.

Bufo chilensis of the South American section and *B. retiformis* of the Caribbean section were the only species not available for this study. The dermal ornamentation of the fossil is most like that of the South American section, which has crests of only moderate extent and development and a lined or wrinkled sculpture; while crests in members of the Caribbean section are often extensive, exaggerated, and the sculpture is pustular.

A final factor used in allocating the fossil to the South American section was the width of the vertebral centra, which are perceptibly narrower in proportion to their length in the Caribbean group. As might be expected, the results are correlated with size, so that only specimens of relatively large size appear to be well separated. Many specimens of the Mexican section resemble the Caribbean forms in also having the narrow centrum.

The above considerations indicate that the fossil belongs to the South American section, but it differs from these forms in one characteristic of importance to Tihen's classification. He indicates (*ibid.*, pp. 165-166) that the suprapterygoid fenestra is not markedly occluded in the South American section of the *valliceps* group, while it is often nearly closed by flanges of pterygoid and squamosala in members of the Caribbean section. The fenestra is completely closed in the fossil, thus indicating a possible relationship to the latter group in terms of the classification based on skeletons of Recent species. However, the suprapterygoid fenestra, as a taxonomic character, may be weak in some cases (as Tihen realized), owing to its qualitative nature. Tihen points out (*ibid.*, p. 174) that *B. typhonius* of the Caribbean section lacks an occluded suprapterygoid fenestra. One specimen of *B. peltcephalus* of the Caribbean section (M. C. Z. no. 23564) also has an open fenestra. Within the South American section, one specimen of *B. paracnemis* (M. C. Z. no. 343) has the fenestra closed on one side of the skull. It is possible that closure of the fenestra in Recent specimens may be both variable within the species as a whole, and be partly a function of age of the specimen. In addition, since there has been a trend in many groups (including anurans) toward deossification, geologic age can be a modifying factor as well. The

latter is probably the most important with respect to this fossil, since a number of regions, e.g. shoulder girdle (see above) and prootic show a greater amount of ossification than comparable regions in any Recent specimen of either New or Old World *Bufo* seen by us.

The *crista medialis* of the humerus is of some interest in this specimen, because it is a secondary sexual characteristic in some Recent frogs. The *crista* forms the attachment for the *M. flexor carpi radialis*, which aids in flexing the wrist and is important in amplexus. Ecker (1889, pp. 42-43) indicated that the *crista* was present in males of *Rana esculenta*, *R. temporaria*, and *R. oxyrhinus*. Holmes (1924, p. 241), in discussing the same species, states that it is present in both males and females, but is more prominent in males. Inasmuch as the methods of embrace and courtship are more or less uniform throughout the Salientia (Noble, 1931, p. 111), this characteristic may be of similar significance in other anurans as well. Table I gives the results that were derived from specimens of *Bufo* related to the fossil.

TABLE I

Taxon	MCZ no.	sex	<i>crista medialis</i>
<i>B. peltocephalus</i>	29600	♀	absent
	23564	♂	present
<i>B. arenarum</i>	1263	♀	absent
	30650	♂	present
<i>B. blombergi</i>	29669	♀	absent
<i>B. marinus horribilis</i>	21439	♀	present but small
	29028	♂	absent — small specimen
<i>B. ictericus</i>	321	♂ ?	present

Only a small number of the M. C. Z. collection of New World *Bufo* were sexed at the time of skeletonization, and of the others, only a few have the ridge to any great extent. *B. marinus horribilis* (M. C. Z. no. 29028), a male which lacks the *crista medialis*, was the smallest individual of that species in the osteological collection and may not have reached maturity. The fossil is thus most probably a male, though exceptions such as the above render this uncertain.

SPECIFIC ASSIGNMENT OF THE FOSSIL

As indicated above, the specimen clearly belongs to the South American section. Tihen (1962a, p. 165) includes the following

species within this group: *Bufo arenarum*, *B. blombergi*, *B. chilensis*, *B. crucifer*, *B. ictericus*, *B. m. marinus*, *B. m. horribilis*, and *B. paracnemis*. The fossil differs strongly from *Bufo blombergi* in having strong supraorbital and postorbital crests. *B. arenarum* has very high cranial crests, which are rugose and slightly flattened on their dorsalmost surfaces, and has a relatively smooth skull surface between the crests—both characters in contrast to those of the fossil. *B. crucifer* has a sculpture pattern much finer in texture and more deeply incised than in the fossil, has strong parietal crests, and has a relatively smooth skull surface between the crests, as in *B. arenarum*. The remaining taxa are very closely related, and all have been included in a single undifferentiated species, *B. marinus*, by some workers, or treated as subspecies or full species by others. We have followed Tihen's taxonomy (1962a) for convenience in discussion. M. C. Z. specimens of *B. m. horribilis* indicate that this primarily Mexican group tends to have thin, fine, almost pitted sculpture, and relatively low cranial crests, unlike the fossil. Specimens of *B. ictericus* contrast with the fossil in having prominent parietal crests, though this is a variable character. Both skeletons of *B. paracnemis* available to us resemble the fossil in sculpture and crest pattern, but on each side have a very strong anterior angulation of the posterior skull margin, in contrast to the fossil and the other species included in the South American section, though the consistency of this character is not determinable at this time. Hence the strongest resemblance between the fossil and any Recent group, on the basis of the available specimens, is with *Bufo marinus marinus*. The tendency toward obliteration of sutures, the relatively greater ossification in prootics, suprapterygoid fenestra, and shoulder girdle, as well as the general robustness of some of the bones themselves, do not, in our opinion, warrant nomenclatorial recognition at the specific level, but merely reflect the often greater ossification seen in many fossils (discussed above on p. 9) and probably indicates a stage in the evolution of *Bufo marinus* in the broad sense. In identifying this specimen with the Recent *Bufo marinus*, we realize, with Taylor and Smith (1945, p. 541) and J. Savage (1960, p. 235) that the concept of *B. marinus* as currently used is a broad one, yet further refinement in the assessment of relationships of this fossil cannot precede re-evaluation of the Recent *Bufo marinus* complex.

The beginnings of such a re-evaluation have been provided by Bertini and Cei (1962), who studied the serological relationships

between some of the species involved. *Bufo marinus*, a predominantly Amazonian aquatic species, appears to be the most primitive type, and has given rise to xerophilic continental, and moisture-loving coastal populations in the southern half of the continent. Identification of this fossil with the populations usually referred to as *B. m. marinus* is thus consistent with the northern occurrence of the fossil within South America, and with the primitive nature of *B. m. marinus*.

Blair (1963, p. 11) has discussed evolutionary patterns in *Bufo*, and has suggested that the ancestral stock of the *marinus* group "somehow crossed into South America during its time of isolation from North America in the Tertiary." There is still insufficient fossil material to make any positive statement, but most recent work on fossil anurans suggests that by the late Cretaceous or Paleocene, family groups were well differentiated, and lines resembling many modern genera were already present. It is thus quite possible that the ancestral stock for the *marinus* group entered South America by a land connection with North America which persisted until late Paleocene time. If this is so, then it is not necessary to propose that they reached South America by some sort of "sweepstakes" method after the connection was severed.

SUMMARY AND CONCLUSIONS

A late Miocene toad from the upper Magdalena Valley, Huila, Colombia, South America, is referred to the Recent species *Bufo marinus*. Within this poorly understood group, it seems to show closest resemblance to *B. m. marinus* from northern South America. It differs from *B. marinus* only in having slightly greater ossification in the suprapterygoid fenestra, lateral parts of the prootics, and glenoid region of the shoulder girdle. This condition is insufficient evidence for recognizing a taxonomic difference from *B. marinus*, at least until restudy of the Recent forms is effected. The broad geographic and altitudinal range of the Recent species precludes ecologic interpretation. The species is aquatic, and common today along large river courses and may have been so on the Miocene floodplains as well. The fossil, in combination with the lizards described by Estes (1961), is another indication of the modernity of the herpetological elements of the late Miocene La Venta fauna, and of the greater extent of the floodplain-aquatic habitat in northern South America during the late Miocene.

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B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS.

DECEMBER 31, 1963

NUMBER 194

A NEW SUBSPECIES OF *TROPIDOPHIS GREENWAYI* FROM THE CAICOS BANK

By ALBERT SCHWARTZ

The species of small boa, *Tropidophis greenwayi*, has heretofore been known only from Ambergris Cay.¹ No additional specimens of *T. greenwayi* have been taken since the type and paratype were collected in 1936. At the time of their review of the Caribbean snakes of the genus *Tropidophis*, Schwartz and Marsh (1960) examined the two extant specimens and separated them from the Cuban and Bahaman species *T. pardalis* (with which they had been nomenclatorially associated) and *T. canus* (to which they might be expected on geographic grounds to be related).

From January 11 to 22, 1961, the writer and David C. Leber collected on South Caicos and its adjacent Long Cay and visited the Ambergris Cays as well in order to secure additional specimens of *T. greenwayi* and to ascertain if this snake were more widely distributed on the Caicos Bank. We were unable to find the boa on the Ambergris Cays, but a series of fourteen individuals was collected for us on South Caicos and Long Cay by residents of these islands. Comparison of this large series with the two specimens of topotypic *T. greenwayi* indicates that the South Caicos and Long Cay populations represent a different form, which may be called:

TROPIDOPHIS GREENWAYI LANTHANUS, new subspecies

Type: Museum of Comparative Zoology (MCZ) 69630, from 0.5 mi. north of Cockburn Harbour, South Caicos, taken 22 January, 1961, by a native for A. Schwartz.

Paratypes: MCZ 69619, 0.5 mi. east of Cockburn Harbour, South Caicos, 13 January, 1961; MCZ 69632, same locality, 14

¹Actually, "Ambergris Cay" is one of a pair of cays, both known as the Ambergris Cays, which lie about 13 miles southwest of Cockburn Harbour on South Caicos.

January, 1961; MCZ 69620, same locality, 19 January, 1961; MCZ 69621, 7 mi. northeast of Cockburn Harbour, South Caicos, 20 January, 1961; MCZ 69622, 0.5 mi. east of Cockburn Harbour, 21 January, 1961; MCZ 69623, Cockburn Harbour, 21 January, 1961; MCZ 69624-25, Long Cay, off Cockburn Harbour, South Caicos, 21 January, 1961; MCZ 69626-28, same locality, 22 January, 1961; MCZ 69629, 69631, same data as type. All specimens were collected by natives for A. Schwartz.

Distribution: Known only from South Caicos and adjacent Long Cay on the Caicos Bank.

Diagnosis: A subspecies of *T. greenwayi* differing from the nominate form in higher number of ventral scutes and in coloration and pattern.

Description of type: An adult spurred male with the following measurements and counts: total length, 257 mm., tail, 30 mm.; ventral scutes 160, subcaudal scutes 28; supralabials 9/10; infra-labials 11/11; parietals in contact; preoculars 1/1, postoculars 3/2; dorsal scales smooth, rows 25-27-19; dorsal paramedian blotches 42/49; tail blotches four. Coloration: Head uniformly

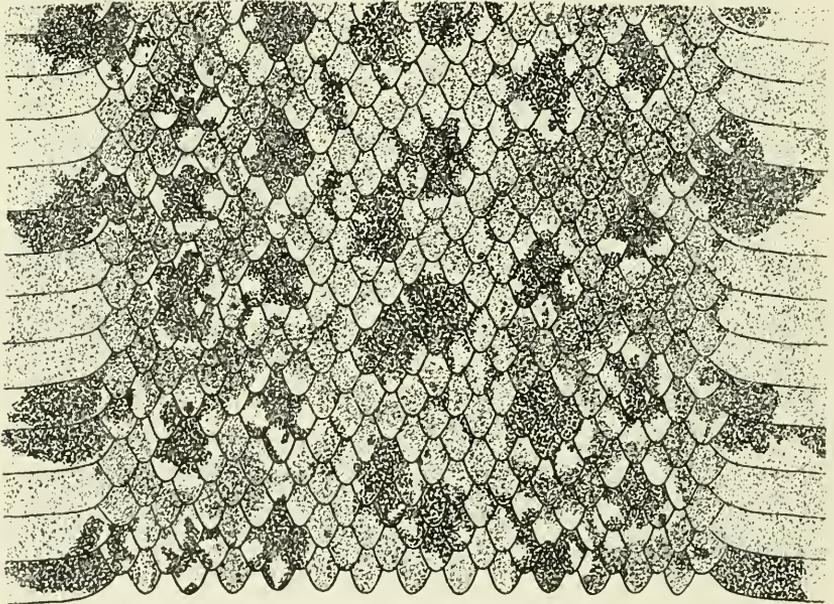


Figure 1. Dorsal midbody pattern of *Tropidophis greenwayi lanthanus* (MCZ 69630, type).

dark brown dorsally; neck slightly paler, quickly grading posteriorly into a grayish-tan middorsal zone about ten scales wide, this zone including the two paramedian rows of dark brown dorsal blotches, each blotch faintly outlined with pale gray, the dorsal zone continuing posteriorly onto the upper surface of the tail, where it merges imperceptibly with the yellow coloration of the tail tip. Sides darker brown, becoming more reddish ventrally, and enclosing three rows of lateral blotches, the uppermost two rows the least conspicuous (because of the closeness of their color to that of the ground color and the reduction of pale outlining), the lowermost row outlined by gray especially along the posterior margins. Ventral surface reddish-tan with two rows of dark brown blotches, which may extend dorsally onto the first two scale rows, do not coalesce medially on the venter, and are outlined posteriorly in white. Supralabials dark brown, the posterior three somewhat flecked and blotched with cream. Hemipenes extruded, weakly bifurcate and weakly spinose distally.

Paratypes: The paratypes include three males and ten females: I cannot discern any difference in coloration, pattern or scalation between the sexes nor between the snakes from South Caicos and Long Cay, and all are discussed as one unit. All three males are spurred, as is the type. Two of the males are juveniles, each with a total length of 140 mm. Males range in total length from 140 mm. to 320 mm., whereas females vary between 250 mm. and 336 mm. Ventrals range between 156 and 165 (mean 161.2), caudals between 26 and 30 (mean 28.0). All have 1/1 preoculars. Postoculars vary from 2/2 (two snakes), 2/3 (six, including type), and 3/3 (five), thus showing a tendency toward having three postoculars in 85 per cent of the population; one snake has the head scales so damaged that its data are omitted. Paramedian blotches vary from 27 to 49 in the series, the largest discrepancy between right and left counts on the same snake being seven blotches, as in the type and one other individual. The average blotch number is 39.9. One snake, as noted below, lacks blotches completely. Scale rows at midbody are either 25 (eleven snakes) or 27 (three snakes). The number of rows of blotches around the body are eight or ten, with only one snake showing the reduction to eight rows of blotches. The tail/total length ratio ($\times 100$) averages 10.5 (9.4–12.1; the highest ratio is shown by one of the juvenile males). All of the paratypes have the parietals in contact, and have the dorsal scales smooth. Upper labials vary from 9 to 10, and lower labials from 9 to 12.

Coloration of the paratypes: All the adult paratypes except one agree very closely with the type. All have a lighter median zone containing two rows of paramedian blotches; this middorsal zone was noted in life as matching in various individuals (color notations from Maerz and Paul, 1950): Pl. 14A5, Pl. 15C7, Pl. 13A6, Pl. 14A4, Pl. 12A6, all of which are shades of buffy tan to grayish tan. The sides are somewhat darker (Pl. 15A9, Pl. 16A6, Pl. 13A10, Pl. 15C8, Pl. 15C8), then becoming lighter on the lower scale rows and venter to a more red coloration (Pl. 14G10, Pl. 15A4, for example). The blotches themselves are always dark brown. The venter varies from a rich reddish tan to an almost chocolate brown, at times relieved by rather extensive white borders to the brown ventral blotches. One snake, an adult female, is unusual in that the pattern consists merely of the paler middorsal zone and darker sides, without any indication of lateral or ventral blotches; the paramedian blotch rows are represented by a rather diffuse dark brown smudging along the middle of the back. The tail tips are dark in two snakes and light (yellow) in ten; two are indeterminate.

The two juvenile paratypes are very like the adults in coloration and pattern; the pattern elements are not appreciably brighter than in the adults (in contrast to juvenile and adult *T. canus* where the juveniles show the dorsal pattern much more distinctly than the adults). There is also no evidence of the lateral nuchal stripe which is a common feature of both juvenile and adult *T. canus* (Schwartz and Marsh, *op. cit.*: 61) and especially prominent in the juveniles.

In addition, the young paratypes have white, rather than brown, venters; apparently the darker pigmentation comes with increase in size.

Comparisons: *T. g. lanthanus* requires comparison only with the typical form. It is quite distinct from the adjacent Bahaman and Hispaniolan forms of *Tropidophis*. The comparison is hampered, however, by the paucity of specimens of the nominate form. If the type and paratype represent a fair sample of *T. greenwayi* on the Ambergris Cays (and it is possible that they do not), then *lanthanus* is certainly very distinct from the snakes on these outlying cays. Comparison of the illustration (Figure 1) of *T. g. lanthanus* with that of the type of *T. g. greenwayi* (Schwartz and Marsh, *op. cit.*: fig. 7) at once demonstrates the pattern differences. In the nominate form there is no indication of the dorsal pale zone, the entire dorsal surface has a mottled or stippled effect,

with blacks, browns, tans, and whites more or less intermixed; the blotches are extremely obscured by the mottled and stippled markings on the interspaces. Such is not the case in *lanthanus* where in all specimens but one (the blotchless female mentioned above) the blotches are quite distinct and there is no interspace stippling. It might be argued that the *greenwayi* coloration is a peculiarity of extreme age or adulthood; in fact the type of *greenwayi* is the largest specimen of the species presently available. However, in the largest specimen of *lanthanus*, the trend is obviously just the reverse of that in the nominate snakes, and the pattern is completely obliterated except for the dorsal pale zone. Another feature of *greenwayi* is the "salt-and-pepper" effect on the dorsal surface of the head; such a condition does not occur in *lanthanus*, where the head is always uniformly dark brown. In number of ventrals, *lanthanus* embraces the 157-158 ventral counts known from the two *greenwayi* (both are males). However, the specimen of *lanthanus* which has the lowest count for that race (a female with 155) stands alone in the series; all other *lanthanus* have counts ranging from 160 to 165. I regard this single specimen as being somewhat aberrant. When large series of topotypic *greenwayi* finally become available, I suspect that they will have ventral counts lower than those of *lanthanus*.

Both specimens of *greenwayi* have 2/2 postoculars, whereas only two of thirteen *lanthanus* have such a count; the remainder have counts of 2/3 or 3/3, the third postocular being wedged between the fifth and sixth supralabials. It is possible that a tendency toward 3/3 postoculars is characteristic of *lanthanus*.

Remarks: Perhaps the most interesting feature of the new specimens of *T. greenwayi* here reported is their uniformity. For example, the species was partly defined (Barbour and Shreve, 1936:2) by having the parietals in contact. Schwartz and Marsh (*op. cit.*:57) noted that this character, as with all scale characters in this assemblage of small boas, was variable; the same comment applies equally to dorsal scale carination and number of dorsal scale rows. But all new specimens of *T. greenwayi* do indeed have parietals in contact and smooth scales. In fact, *T. greenwayi* can be in addition characterized as being a *Tropidophis* with smooth dorsals usually in 25 scale rows and typically ten rows of blotches, all features which were uncertain at the time of the review of the Caribbean *Tropidophis*. Likewise, additional data are now available on tail/total length ratio in *T. greenwayi*; the ratio averages 10.5, which is the lowest mean of any member of

the assemblage, most closely approached by that of *T. canus canus* (10.7).

Even with additional material available, I am unable to guess as to the affinities and origin of *T. greenwayi*. With two juveniles now at hand, the relationships of this species to *T. canus* seems even more remote than it did previously (Schwartz and Marsh, *op. cit.*: 62). This snake appears to have been long isolated from its relatives, whatever they may have been, and other than to remark that it is a member of the *pardalis-maculatus* assemblage, little can be said.

I suspect that *T. greenwayi* will be found to occur on the other major islands of the Caicos Bank. It is surprising that it has been so long overlooked on South Caicos where the natives knew of it as soon as approached about small snakes. The name *lanthanus* is an allusion to the fact that the species has been overlooked on South Caicos. This boa appears to be genuinely lacking from Grand Turk and probably other islands on the Turks Bank, which is separated from the Caicos Bank by the Turks Island Passage: natives there were aware of *Epicrates* on some of the outer cays, but did not know of any snakes at all on Grand Turk. No snakes of any species were encountered in the one week spent by us on Grand Turk.

Figure 1 was executed by Ronald F. Klinikowski. I wish to thank him for his efforts on my behalf.

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B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS.

DECEMBER 31, 1963

NUMBER 195

CAYMAN ISLANDS *TROPIDOPHIS* (REPTILIA, SERPENTES)

By RICHARD THOMAS

New material from the Cayman Islands, gathered principally through the efforts of Dr. Albert Schwartz during his collecting in the West Indies, has provided a large enough series of *Tropidophis* from each of the three islands so that a clearer picture of the relationships can be seen. Specimens examined have been under the curatorship of Dr. Doris Cochran, United States National Museum (USNM), Dr. Ernest Williams, Museum of Comparative Zoology (MCZ), Dr. Albert Schwartz, field collection (AS), and in the author's private collection (RT). The illustrations are the work of Ronald F. Klinikowski.

The Cayman group consists of three islands: Grand Cayman, Cayman Brac, and Little Cayman. Grand Cayman is situated about 180 miles west-north-west of Jamaica and 150 miles south of Cuba; it is about 22 miles long and eight miles wide at maximum width. Cayman Brac, 89 miles east-north-east of Grand Cayman, is about 12 miles long with an average width of a mile. Little Cayman, five miles to the west of Cayman Brac, is ten miles long with a maximum width of two miles. The long axis of each island lies in a generally east-west direction. They are low-lying islands formed of calcareous rocks.

Battersby (1938) described *Tropidophis melanurus caymanensis* from Grand Cayman; Grant (1940) further recorded *T. m. caymanensis* from Cayman Brac and described *Tropidophis parkeri* from Little Cayman. Schwartz and Thomas (1960) on the basis of obvious affinities with *melanurus* called *parkeri* a subspecies of *T. melanurus*.

The new material recently acquired from the Caymans indicates that, despite affinities of the Cayman *Tropidophis* with *T. melanurus*, these snakes are distinct and should be known as

Tropidophis caymanensis caymanensis and *Tropidophis caymanensis parkeri*. *Tropidophis caymanensis* may be distinguished from *Tropidophis melanurus* by the following characters:

1. Size: The average total length of *caymanensis* from all three islands (48 specimens) is 369.5 mm with a range of 202-564 mm. The average size of *melanurus* from Cuba and the Isle of Pines (77 specimens) is 607.1 mm with a range of 253-1057 mm.

2. Scale-rows: Caymanian *Tropidophis* have usual scale-row counts of 23-25-17 (*caymanensis*), 25-27-17 (*parkeri*), or 23-25-17 (Brac *Tropidophis*). *Tropidophis melanurus* has a usual scale-row formula of 25-27-19.

3. Light tail tip: All specimens of Caymanian *Tropidophis* examined have a light tail tip; of 16 specimens of *parkeri* seen in the field all but three (with incomplete tails) had yellow tail tips, and one of the three with incomplete tails showed traces of yellow pigmentation on the remaining tip. Old specimens show a slight darkening on the dorsum of the tip, but the rest of the tip is yellow. Specimens from Grand Cayman and Cayman Brac, which were not seen alive by the writer, have plain but distinctly light tail tips, presumably as a result of the yellow fading in preservation; field color notes on one adult (AS16230) from Grand Cayman describe a yellow tail tip. In *melanurus* the yellow tail tip is a distinctly juvenile condition and in the adult becomes either unicolor with the ground color or black.

4. Dorsal body pattern: In *caymanensis*, the two rows of paramedian dorsal spots are squarish (2-4 scales long by 2-3 scales wide) and distinct from the ground color; these spots are more discrete than in *melanurus*, with pale edging frequently occurring on the median edges, and in addition they are distinct from the middorsal stripe. *T. melanurus* typically has paramedian dorsal spots much less distinctly developed and they are apt to be broadly confluent at the midline and not distinct from the middorsal stripe, when the latter is present. The light edging is confined to the outer edges of the spots.

Tropidophis caymanensis is, therefore, a species with closest affinities to *melanurus* but distinguished from that species by its dwarf size, lower number of scale rows, persistence of the yellow tail tip in adults and bolder dorsal spotting.

Examination of the series of 16 specimens from Cayman Brac shows that they may be distinguished from the Grand Cayman population with which they had previously been considered identical. I take great pleasure in naming this new subspecies

for Dr. Albert Schwartz, who suggested this problem, in honor of his zoological work in the West Indies; it may therefore be known as:

TROPIDOPHIS CAYMANENSIS SCHWARTZI subsp. nov.

Type: MCZ 69618, an adult male from The Creek, 8 mi. NE of West End, Cayman Brae, collected 25 August 1961 by a native for A. Schwartz.

Paratypes: MCZ 69603-04, Cayman Brae, The Creek, 8 mi. NE of West End, 22 August 1961; MCZ 69605, Cayman Brae, 6 mi. NE of West End, 23 August 1961; MCZ 69606, Cayman Brae, The Creek, 8 mi. NE of West End, 23 August 1961; MCZ 69607-608, Cayman Brae, The Creek, 8 mi. NE of West End, 24 August 1961; MCZ 69609-11, Cayman Brae, West End, 25 August 1961; MCZ 69612-13, Cayman Brae, Spot Bay, 25 August 1961; MCZ 69614-17, Cayman Brae, The Creek, 8 mi. NE of West End, 25 August 1961. All specimens were collected by natives for A. Schwartz.

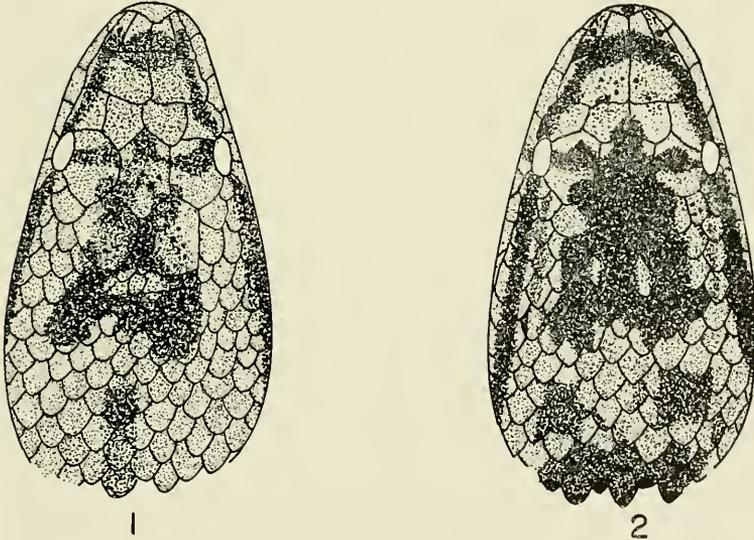


Fig. 1. Dorsal cephalic pattern of *Tropidophis caymanensis schwartzi* (MCZ 69618, type).

Fig. 2. Dorsal cephalic pattern of *Tropidophis caymanensis caymanensis* (AS 16230).

Diagnosis: a race of *caymanensis* with a normal scale-row count of 25-25-15, rather than 23-25-17 (*T. c. caymanensis*) or 25-27-17 (*T. c. parkeri*), differing also from *T. caymanensis* in the coloration of the head and in a higher mean ventral count and from *T. c. parkeri* in a somewhat lower mean ventral count.

Description of type: An adult male, total length 435 mm, tail 50 mm. Body relatively stout, slightly compressed, head distinct from neck; scales weakly keeled except for five lowermost rows on each side, smooth scales becoming reduced to three lowermost rows posteriorly; middorsal row enlarged and bicarinate on posterior fifth of body, ending anterior to vent; dorsal scale-rows 25-25-17; ventrals 200; subcaudals 39; anal single; spurs present; preoculars 1/1; postoculars 3/3; temporals 3-4/3-4; supralabials 10/10, 4 and 5 entering the orbit; infra-labials 12/12. Dorsal pattern: two rows of 55 and 61 paramedian dark spots, 2 to $3\frac{1}{2}$ scales long by 2 to $2\frac{1}{2}$ scales wide; light edging to spots mostly lateral, but some median edging occurs also; lighter middorsal stripe present, broadly connected to median edges of spots. Sixth and ninth scale rows with fine, light centered, dark lines; row of small spots between lines on sixth and ninth scale-rows; two rows of staggered, dark spots on lower five scale-rows; venter irregularly stippled with dark pigment (see Figure 3); lowermost row of lateral spots becoming enlarged and migrating to venter on posterior fifth of body: about seven spots on dorsum of tail; subcaudal surface with two rows of about seven dark spots. Dorsal ground color of body light grey changing to cream below sixth scale-row and on venter; tip of tail light. Cephalic pattern: trapezoidal, dark, dorsal cephalic figure much invaded by light stippling (see Figure 1); posterior center of figure light; anterior portion of cephalic figure separated off to form interocular bar; nipple-like, anterior projection of interocular bar not extending beyond frontal; dark, oval spot on internasals and prefrontals narrowly joined on each side to preocular portion of lateral head stripe, which continues posteriorly onto neck to level of ninth ventral after which it is broken up into a lateral row of spots.

Variation: The paratypes include seven males and nine females; the largest male is 435 mm (the type); the largest female is 358 mm. The males of this series average larger than the females, having an average total length of 362.8 mm (202-425); females average 336.8 mm (297-358). Ventrals in males, including the type, average 195.6 (191-202); females 200 (195-205); subcaudals in males average 36.6 (34-39), in females 36.2 (31-39).

All specimens have 1/1 preoculars and 3/3 postoculars; all have the scale-row formula of 25-25-17 except for two with counts of 25-25-15. The model supralabial count is 10/10 with other counts of 12/10 (1) and 9/10 (2). Tails of males average 10.6 per cent of total length with a range of 9.1-11.8 per cent; tails of females average 11.2 per cent of total length (10.8-12.0%).

Pattern and color are fairly uniform in the paratype series. In all of the specimens the dorsal cephalic pattern is much invaded and broken up by solid, light areas and by heavy stippling of light pigment; in all examples but three the interocular pigmented area is separated from the cephalic figure to form an interocular bar; in the three exceptional specimens the interocular bar is but narrowly joined to the dorsal cephalic figure by a median strip of dark pigment made hazy by light stippling. Typically there are several (usually 4) dark spots on each side of the lower labials. The dorsal pattern in the paratype series is much the same as in the type; the average number of dorsal spots is 60.1 in males and 58.9 in females. Ventral coloration in the paratype series varies from a uniformly clear cream to a rather heavy, irregular, dark mottling over nearly the entire undersurface; the typical ventral coloration for the series is like that described for the type. All specimens, except one with an incomplete tail, have light tail tips.

Comparisons: A recently acquired series of 16 *T. c. parkeri* agree with Grant's (1940) original diagnosis of it as a 27 scale-row form with a ventral count of over 200; the ventrals of the nine males average 201.0 (199-204), those of the females 205.1 (201-212); the normal scale-row count for the series is 25-27-17 with variants of 25-27-16 (1), 25-27-18 (1), and 25-27-19 (1). *Schwartzi* may be distinguished from *parkeri* by the possession of a normal scale-row count of 25-25-15. Chromatically there does not seem to be much difference in the populations; the fresh *parkeri* material has a richer, deeper coloration, whereas *schwartzi* is much lighter. The difference, however, is likely due to fading, since field color notes on one specimen of *schwartzi* ("dorsal ground color orange tan; dorsal blotches brown, not outlined posteriorly with orange") agree with the typical *parkeri* coloration. *Parkeri* tail tips are yellow; those of *schwartzi* are definitely light and probably faded from the yellow condition. The cephalic figure in *parkeri* tends to be broken up and invaded with lighter pigmentation much as in *schwartzi*, though the figure is frequently broken into two or three disjunct portions in *parkeri* as opposed to simple invasion by light pigment

in *schwartzi* to form an erose margin and light center. The average number of paramedian, dorsal spots in *parkeri* is 54.7 for males and 55.9 for females, slightly lower than the averages for *schwartzi*. In *parkeri* the females average larger than males; 11 females average 400.3 mm (230-564); nine males average 373.3 mm (306-444); the tails of male *parkeri* average 10.6 per cent

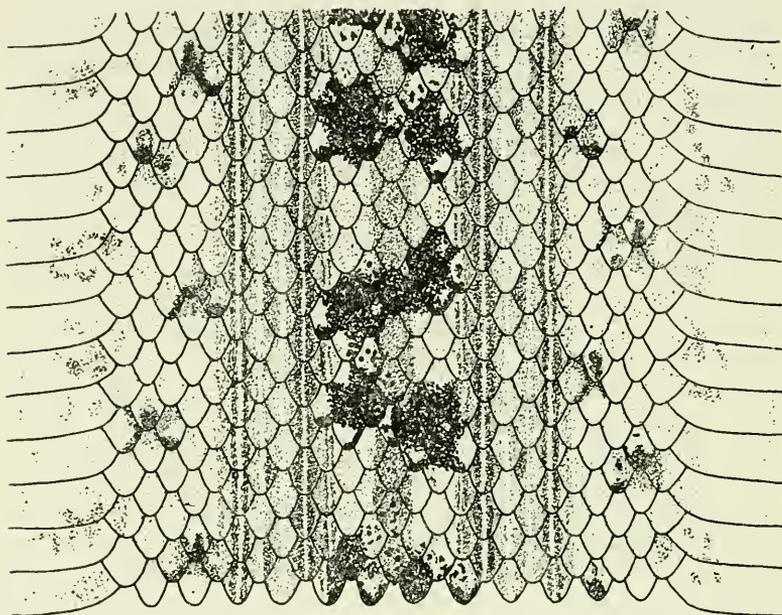


Fig. 3. Dorsal midbody pattern of *Tropidophis caymanensis schwartzi* (MCZ 69618, type).

of the total length, those of females 9.4 per cent. The slight sexual dimorphism evident in average total length and average tail/total length ratios for *schwartzi* is present but reversed in *parkeri*.

The ten specimens of *caymanensis* which were examined have a modal scale-row count of 23-25-17 with variants of 23-25-19 (1) and 25-25-19 (1). These agree closely with Battersby's (1938) type and paratype which had scale-row counts of 23-25-17. *Schwartzi* is distinguishable from *caymanensis* by the possession of 25-25-17 scale-rows. Grant (1940) thought that the type of *caymanensis* was abnormal in having only 191 ventrals; he also mentioned a male with 183 ventrals. In his analysis,

he apparently omitted both of these specimens from consideration and speculated that they might be members of a localized population along the north coast characterized by a reduced number of ventrals. The material at hand shows that similar low ventral counts are not restricted to the north coast; counts of 183, 187 and 191 are found on specimens from Georgetown in the southwest. Grant also mentioned five females and five males in his own collection which, along with the female paratype, average 205 and 193 ventrals, respectively. However, he only listed seven specimens in his own collection from Grand Cayman; just what the provenance of the other three specimens is cannot be determined. Counts from the new material plus the counts on the type, paratype, and the individual with 183 ventrals noted by Grant (Br. Mus. No. 1939.2.3.78) yield an average of 192.6 (183-200) for seven females, 191.7 (183-195) for six males. Therefore, *caymanensis* is seen to average lower in ventrals than *parkeri* and *schwartzi*, there being almost no overlap between *caymanensis* (183-200) and *parkeri* (199-212). There are apparently no significant differences in body pattern and color between *caymanensis* and *schwartzi*. However, *schwartzi* can be distinguished from *caymanensis* on the basis of the cephalic figure. In *caymanensis* the cephalic figure is much more solidly pigmented with black and uniform in outline; the edges are not highly indented and eroded by invasion of light pigment as in *schwartzi*, and the light areas within the figure are more restricted and well defined, not extensive and hazy in outline by virtue of light stippling (see Figure 2). Seven female *caymanensis* average 392.0 mm total length (222-488) and five males average 368.8 mm (192-538); tails of males average 12.2 per cent of the total length, those of females average 10.8 per cent of the total length. Once again, apparent sexual dimorphism is the reverse of that in *schwartzi*.

Remarks: The author was able to do some collecting on Little Cayman in December of 1962. Some impressions were gathered concerning *Tropidophis c. parkeri* and are probably applicable to the species generally. A series of sixteen *parkeri* was collected during the visit to Little Cayman. These snakes gave the impression of being more secretive than *T. melanurus*, which is most frequently found prowling abroad at night. *Parkeri* was never collected in the open; the majority were found beneath fragments of limestone which litter the island. Two were taken within rocks themselves, being secreted in eroded chambers; one was taken among the leaves of a dead *Agave*, and another was

found three feet off the ground in the leaf base of an epiphyte. One specimen was found approximately eight feet above ground in the roof of an outhouse, where it was partly concealed beneath corrugation in the tin roof. One specimen was found beneath rocks and litter under a sea-grape tree; it was this "beach situation" wherein the natives claimed the snake to be most often found. A large female specimen found resting in a tin can disgorged a large *Hyla septentrionalis* shortly after capture. Many specimens autohemorrhaged freely upon capture or at subsequent disturbance; the "shutter" effect noted by Hecht, Walters and Ramm (1955) for Bimini *Tropidophis* was also observed; this effect is produced by the sudden and transient appearance of blood under the brille during autohemorrhage. Most of these snakes coiled in a tight, defensive ball and would so remain for long periods with their heads completely hidden. This habit is not in keeping with *melanurus*, which might be said to be less timid; experience with *melanurus* in the field indicates also that

Comparative material: Tropidophis caymanensis caymanensis: USNM 108042-43, Grand Cayman; MCZ 44862-4, Grand Cayman; AS 16209-11, 16230, Grand Cayman, Georgetown; AS X4876, Grand Cayman, Georgetown. *Tropidophis e. parkeri*: USNM 108009, Little Cayman; MCZ 44865 (type), Little Cayman; MCZ 44866-8 (paratypes), Little Cayman; AS X4890-X4904, Little Cayman, western end; RT 36, Little Cayman, western end. *Tropidophis melanurus*: 79 specimens, Cuba and the Isles of Pines.

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B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS.

DECEMBER 31, 1963

NUMBER 196

A NEW GENUS AND SPECIES OF BATHYPELAGIC
OPHIDIOID FISH FROM THE WESTERN
NORTH ATLANTIC

BY DANIEL M. COHEN

U. S. Fish and Wildlife Service
Washington, D. C.

Through the kindness of Dr. Richard H. Backus of the Woods Hole Oceanographic Institution and Dr. Giles W. Mead of the Museum of Comparative Zoology I have had the opportunity to study the three fishes reported upon below. Although they were taken off the southern edge of Georges Bank, hardly a zoologically unknown area, they represent the first of their kind ever captured. And, indeed, they are so different from any other known ophidioid that still another name must needs be added to the already lengthy roster of genera in this group.

THALASSOBATHIA gen. nov.

Diagnosis. Chin barbel absent. Vertical fins continuous; ventral fins each with two rays, originating close to the level of the posterior margin of the preopercle and a short distance behind the symphysis of the cleithra; the ventral fins covered with thick skin, short, extending only to the level of the origin of the pectoral fin; pectoral fin rounded, without separate elongated rays. Branchiostegal membranes separate; gill rakers reduced in number and size; branchiostegal rays seven. Preopercular spine present beneath skin. Anterior nostril lacking a tube, placed high on snout. Teeth present on premaxillary, vomer, palatine and dentary, lacking on basibranchials. Maxillary not expanded posteriorly, not sheathed. Premaxillary not protractile, bound to the snout anteriorly by a broad frenum. Head compressed, its height greater than its width. Eyes well developed. Body compressed, relatively short and stubby. Two lateral lines.

Peritoneum dark. Swimbladder reduced, its cavity completely occluded; bladder not bound to vertebrae. Neural spines on abdominal centra not depressed; their tips not truncate.

Type species. *Thalassobathia pelagica* sp. nov.

The name *Thalassobathia* is derived from the Greek $\theta\alpha\lambda\alpha\sigma\sigma\alpha$, the sea; $\beta\alpha\theta\upsilon\varsigma$, deep. The gender is feminine.

Relationships. The main problem encountered in establishing this genus has been to determine its relationships rather than to distinguish it from any presently known genera. The curiously reduced ventral fins and the general shape and consistency of the body might suggest relationship with the liparid fishes; however, there is not the slightest trace of either a suborbital stay or a sucking disc. In addition, the branchiostegal membranes are separate from each other and from the isthmus, and the gill opening extends far up on the side of the body in typical ophidioid fashion. The last character also separates *Thalassobathia* from the Zoarcidae (not including *Lycodapus*). The non-protractile premaxillaries and attached broad frenum suggest the condition of the upper jaw found in salarime blennies; however, very different dentition, branchiostegal membranes, ventral fins, caudal fin connections and other characters separate *Thalassobathia* from the Salarinae. In addition, the absence of a one-to-one correspondence between dorsal and anal fin rays and vertebral centra separates *Thalassobathia* from any of the blennioids.

Among the ophidioids the closest known relatives of *Thalassobathia* appear to be the *Bythites* — *Oligopus* — *Cataetyx* group of genera recently discussed by Cohen (in press). Some reasons for deriving *Thalassobathia* from this group are the similarly compressed and foreshortened body, the typical bythitine dentition, and especially the double lateral line system, which greatly resembles that found in some of the species of *Oligopus* (Cohen, in press).

Although at first glance *Thalassobathia* does not appear to be a bathypelagic fish, closer examination reveals that many of its characteristics are adaptations to a midwater life. The skeleton is so poorly ossified that X-ray photographs are very indistinct. Scales are completely lacking. The swimbladder is a small, tissue-filled organ similar to those which have been found in many other species of bathypelagic fishes. The above characters and their significance in floating fishes have been treated by Denton and Marshall (1958) and Marshall (1960). Other structures which may help to keep *Thalassobathia* aloft are its subdermal fatty

layer and enlarged liver. Among the most characteristic features of ophidioid fishes are the naked ventral fin rays which probably serve as tactile organs in benthic species (Herald, 1953, and serve as tactile organs in benthic species (Herald, 1953 and Briggs and Caldwell, 1955, have confirmed this for two species of benthic Ophidiidae). These structures would of course be useless in midwater, and *Thalassobathia* has reduced ventral fin rays which are covered with thick skin.

Because of its midwater habitat, *Thalassobathia* should also be compared with the ophidioid subfamily Aphyoninae (Nybelin, 1957) which comprises a small group of bathypelagic species. Aphyonines are small, pale fishes with thin, scaleless skin, weak musculature, reduced ossification and no swimbladders. Although they are livebearing, they have a copulatory apparatus which is very different from that found in benthic livebearing ophidioids. They also lack well developed eyes and lateralis systems. I believe that neoteny has played an important part in the evolution of the aphyonines. *Thalassobathia*, with its large eyes, well developed lateralis system and bythitine dentition, seems, on the other hand, to be one more offshoot of the highly adaptive *Bythites* group of genera, and although it shares a common environment with the Aphyoninae, the two are not at all closely related.

Specimens examined in preparing the foregoing section are listed in Cohen (in press). In addition I have examined the aphyonine material described by Nybelin (1957), specimens of *Aphyonus* in the Museum of Comparative Zoology and in the British Museum (Natural History), and specimens of *Barathronus* in the U. S. National Museum and the Chicago Natural History Museum. I thank the fish curators in Cambridge, Chicago, Göteborg, London and Washington for their kindness.

THALASSOBATHIA PELAGICA sp. nov.

Figures 1, 2

Holotype. MCZ 42161, 221 mm standard length, collected by Richard H. Backus on board the "Capt. Bill III," haul RHB 913; October 13, 1962; 39° 26' N., 71° 00' W. to 39° 32' N., 71° 00' W.; depth to gear 390 fms. (approx. 713 m), depth to bottom 1400-1350 fms. (approx. 2561-2469 m); time 1020 to 1505 hrs. EDT; 64 foot open midwater trawl.

Paratypes. MCZ 42162 (2); data as for the holotype.

Description. Body compressed and foreshortened, greatest depth between three and four in total length. Head relatively

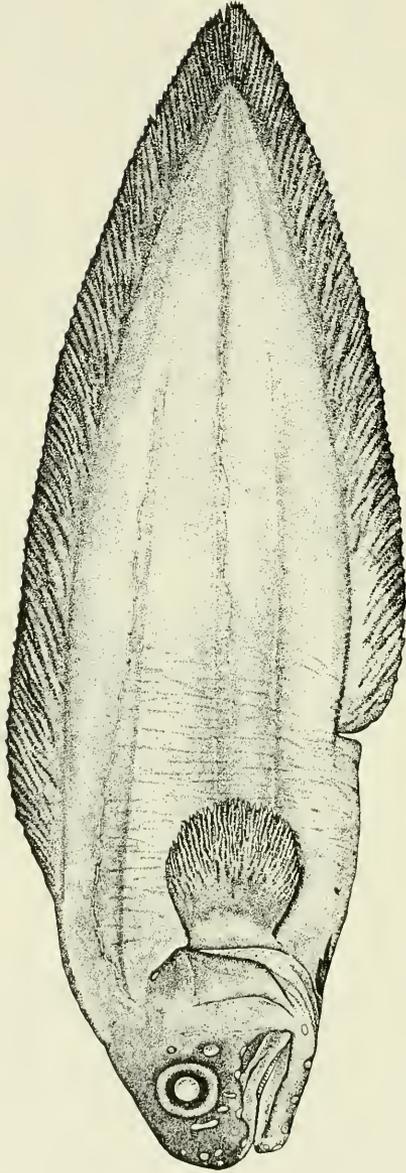


FIG. 1. *Thalassobathia pelagica*, holotype, 221 mm standard length. Drawn by Mildred H. Carrington.

short, between five and six in total length. Snout rounded, mouth slightly inferior. Interorbital area flat or slightly convex. Outlines of head converging anteriorly when viewed from above. Eye prominent, horizontal diameter of cornea about three and one-half in head. Posterior nostril an elongate slit immediately in front of ventral half of eye, anterior nostril small and round, closer to tip of snout than to orbit. Body quite flexible due to weak ossification, feeling much the same as icosteid fishes.

All fins covered with thick skin. The dorsal fin appears to originate a short distance behind the level of the posterior margin of the opercle; it is preceded by rayless pterygiophores and pterygiophores bearing very reduced rays. The exact number of these elements is in doubt as their weak ossification makes them difficult to count on an X-ray photograph. Pectoral fins inserted vertically, broadly rounded; in the holotype and smallest paratype the pectoral fin extends about two-thirds of the way from its origin to the vent, in the other paratype the pectoral fin extends only about one-half of the pectoral origin to vent distance. The ventral fins much reduced and covered with thick black skin (Fig. 2C), the longer, inner ray extending only slightly beyond the level of the base of the pectoral fin. One pectoral fin was cleared and stained to verify the number of rays.

Teeth short, needle-like, extending on the dentary in a single line from the angle of the gape to the symphysis, where a broader patch of teeth is present; premaxillary teeth arranged similarly to those on the dentary; vomerine teeth in a roughly circular patch; palatine teeth in an elongate patch, about three or four times longer than wide. Suprabranchial tooth patches present; however, I have been unable to find any basi-branchial teeth. Tongue massive, lacking teeth and lacking an anterior prow-like extension. The first gill arch with rakers reduced to a few fleshy flaps and protuberances laterally (Fig. 2A), medially (Fig. 2B) with seven or eight small rakers. A prominent pseudobranch located lateral to the upper arm of the first arch. Gill filaments of moderate length, about equal to diameter of lens.

Color brown-grey over the body, the grey due mainly to a mucous coat; the fins and head darker.

Prominent pores on the head. The lateral canal with a single pore near the upper angle of the opercle; supraorbital canal with two or three pores, one above the upper nostril, another below and slightly ahead of the upper nostril, a median pore in the interorbital region of the largest paratype; infraorbital canal

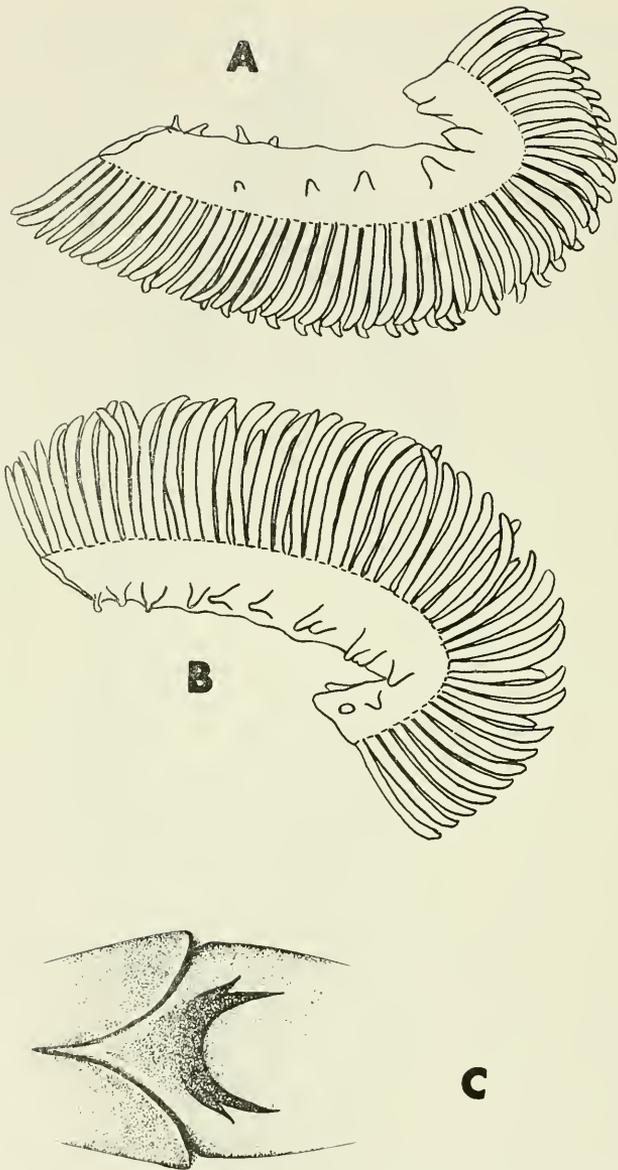


FIG. 2. *Thalassobathia pelagica*. A, First gill arch from left side of smallest paratype, lateral view. B, First gill arch from left side of smallest paratype, medial view. C, Ventral fins of largest paratype. Drawn by Mildred H. Carrington.

with nine pores, the anteriormost below the anterior nostril and immediately behind one of the supraorbital pores, six in an irregular row in the loose skin above the upper jaw, and two behind the eye; preoperculo-mandibular canal with five or six pores located along the ramus of the lower jaw; in the smallest paratype the pair of pores located closest to the midline of the lower jaw have joined to form a single pore.

Lateral line with an upper and lower section, the upper line originating above the opercle and arching upward and back to the level of the origin of the dorsal fin, where it extends posteriorly about midway between the dorsal profile and the midline; the dorsal line disappears at about two-thirds of the distance between the posterior margin of the opercle and the base of the tail; the ventral line originates slightly behind the level of the vent and extends posteriorly to the tail in the midline of the body. Each of the two lateral lines along the body is marked by about 30, small, dark, papillae; similar structures are sparsely distributed over the body and head.

Each specimen has a broad, fleshy hood over the genital area. The largest paratype has a pair of large ovaries which contain small eggs at the bases of numerous villi. The smallest paratype contains small paired ovaries with developing eggs.

The swimbladder of the smallest paratype is a white, bean-shaped organ about 14 mm long. The lumen appears to be completely occluded by white tissue.¹

The liver is prominent in both paratypes, and the thick skin has a subdermal fatty layer.

The brain case is cartilaginous. The olfactory nerves extend anteriorly in the orbit and are separated from each other by the cartilaginous interorbital.

All three specimens bear numerous round marks left by squid tentacles. The smallest paratype has the top of its head bitten off.

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¹ I am indebted to N. B. Marshall for his kindness in examining the swimbladder.

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TABLE 1

Counts and measurements in mm of *Thalassobathia pelagica*

	Holotype	Paratype	Paratype
Dorsal rays	79	72	74
Anal rays	65	58	61
Pectoral rays	23	24	27
Vertebrae ¹	49	48	48
Caudal rays	10	10	10
Standard length	221	173	200
Head length	44.0	13.5	42.0
Snout	10.0	—	7.4
Orbit	11.9	—	11.0
Interorbital	16.0	—	13.3
Upper jaw length	30.0	21.8	22.2
Prenal	87.9	71.0	87.2
Greatest body depth	59.4	47.2	64.0
Body depth at vent	54.1	45.4	50.0
Pectoral fin length	28.2	23.4	25.4

¹ Not including hypural.

B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS.

DECEMBER 31, 1963

NUMBER 197

ANOLIS WHITEMANI, NEW SPECIES FROM HISPANIOLA (SAURIA, IGUANIDAE)¹

BY ERNEST E. WILLIAMS

Miss Cochran in 1941 commented on the apparent extreme variability of *Anolis cybotes cybotes*, mentioning among other points that "some of the specimens have heavy keeling on the ventrals; in others from precisely the same locality, taken at the same time, the ventrals are perfectly smooth." Inspection of material referred to *cybotes* in the Museum of Comparative Zoology, the United States National Museum, and in the unreported collections of the American Museum of Natural History revealed that this phenomenon of sharp dimorphism in regard to keeling was curiously localized and that many of the localities were in the Cul de Sac Plain in Haiti and in its continuation in the Dominican Republic. A closer look at the specimens from this area showed further that there were indeed two kinds of *cybotes*-like anoles represented, and that they were in fact reported as taken at exactly the same localities by the same collector on the same dates. There seemed, however, to be not a difference in a single character but in several independent characters. The suspicion thus arose that species difference and not intraspecific dimorphism was involved. The suspicion was sharpened when P. S. Humphrey, collecting for Yale University and the University of Florida in 1959, brought back only two *cybotes*-like anoles from the Cul de Sac region, one of each type. The fresh material permitted also an increased confidence in a color difference which had seemed to exist in the specimens long in collections. When, therefore, in August 1959, E. E. Williams and A. S. Rand planned a visit to Haiti, one of the objectives was to obtain and examine alive a series of the keeled *cybotes*-like anole from the Cul de Sac.

¹ Notes on Hispaniolan herpetology no. 9.

This objective was achieved, and the keeled form in the Cul de Sac Plain proves indeed to be a new species, which we name in honor of M. Luc Whiteman of Port-au-Prince who has assisted in the recent Haitian explorations.

Since 1959, more material of *A. whitemani* has been obtained by A. S. Rand and J. D. Lazell, Jr. at Mole St. Nicolas on the northwest peninsula of Haiti — an arid area very similar to the arid portions of the Cul de Sac Plain in which *whitemani* was first found. In addition to these (MCZ) specimens and the material in the United States National Museum (USNM) and the American Museum of Natural History (AMNH), further specimens have been found in the collections of the Hamburg Museum. The latter, from Monte Cristi in the Dominican Republic, extend the range of *whitemani* considerably to the east but still along a dry coast.

ANOLIS WHITEMANI new species ¹

Type: An adult male, MCZ 60055, **road to Eaux Gaillees, Haiti**, E. Williams and A. S. Rand collectors, 13 August, 1959.

Paratypes: **Haiti**. MCZ 60056-9, same locality as the type, E. Williams and A. S. Rand coll. MCZ 62844, same locality as type, A. S. Rand and J. Lazell coll. YPM 3193, *Eaux Gaillees*, P. S. Humphrey and S. Van Vleck coll. AMNH 70588, *Eaux Gaillees*, A. Curtiss coll. USNM 117217-8, *Trou Caiman*, A. Curtiss coll. USNM 54189, *Thomazeau*, A. Curtiss coll. MCZ 62827-43, *Mole St. Nicolas*, A. S. Rand and J. Lazell coll. **Dominican Republic**. AMNH 50147, 50200, MCZ 61843, *Las Baitoas near Duverge*, W. G. Hassler coll. Hamburg Museum 5198 (3), *Monte Cristi*.

Diagnosis: Very close to *A. cybotcs* but differing in squamation (dorsal scales larger, the middorsals hardly larger than adjacent scales, rather than abruptly larger; the ventrals smaller, hardly larger than middorsals, narrow and keeled, rather than wide, smooth and cycloid), and in color (body color very pale, nearly grey instead of distinctly brown, dewlap unmarked white, rather than grey with yellow streaks or yellowish or pinkish with grey streaks).

Description. *Head*: Head massive, snout to posterior border of eye about as long as tibia. Head scales mostly smooth. Five scales across head between second canthals. A shallow frontal

¹ Named for M. Luc Whiteman, who has helped so much in amassing the recent collections from Haiti.

depression. Naris in front of canthal ridge. Anterior nasal scale in contact with rostral.

Supraorbital semicircles narrowly in contact, partly in contact with supraocular disks. Supraocular disks consisting of about 8 enlarged keeled scales separated by 4-5 rows of granules from the scales of the supraciliary rows. One to two elongate supraciliaries continued backward by a double row of moderately enlarged scales. Canthus distinct, canthal scales 4, the second largest, decreasing gradually forward. Loreal rows 6-7, the lower row the largest. Supratemporal scales somewhat enlarged, flat, grading into the enlarged scales surrounding the interparietal. Interparietal larger than ear, separated from supraorbital semicircles by 1-2 scales.

Suboculars separated from supralabials by one row of scales, anteriorly separated from the canthal ridge by one scale, posteriorly continued behind eye for a short distance. Six supralabials to center of eye.

Mentals somewhat broader than long, in contact posteriorly with 4 throat scales. Infralabials narrow, in contact with 3 large, wide, nearly lunate sublabials. Throat scales small, swollen, not keeled, only the anterior ones elongate.

Trunk: Middorsal scales keeled, hexagonal, not much larger than adjacent scales which grade very gradually into granules on flanks. Ventrals not much larger than middorsals, relatively narrow, distinctly keeled, the keels in lines. Postanal scales small, poorly differentiated.

Gular fan: Moderate, scales cycloid, keeled, larger than ventrals.

Limbs and digits: Head and foot scales multicarinate. About 17 lamellae under phalanges 2 and 3 of fourth toe. Largest scales of limbs unicarinate, those of arm as large as, of thigh larger than ventrals.

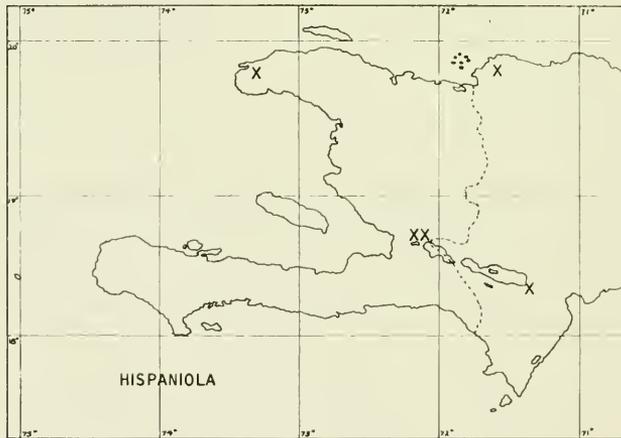
Tail: Compressed. Each verticil surmounted by 4 keeled scales, ventrally 3 pairs of somewhat larger keeled scales per verticil.

Color in life: Four topotypes taken on road to Eaux Gaillies: 1. Type ♂. Dewlap *white*. Ground color grey with indistinct transverse bands. Scattered brown spots on flanks and on sides of belly. 2. ♂. Dewlap pure white. Dorsum grey and cream. Pattern very obscure. Venter pure white. 3. ♀. Dorsum pale grey. Belly pure white. 4. ♂. Juvenile. Dewlap pure white. Dorsum cream and grey.

Notes by W. G. Hassler 1935 (Las Baitoas paratypes): “*Anolis*?-like *cybotes*: in grass on mountain side *above* road and forest. These anoles very grey or grey-brown. Pattern faint. Sides slightly yellowish grey. Belly and throat *white*. ♂ similar to ♀. Faint yellowish brown-grey longitudinal bars like ordinary *cybotes* but much lighter, less red and all very faint. Throat (very faint vermiculations), belly and fan *WHITE*.”

SPECIES STATUS AND CHARACTER DIFFERENCES

The squamation and color differences between *whitemani* and *cybotes* in the Cul de Sac Plain are striking but hardly more striking than those between *cybotes* and “*Audantia*” *armouri* Cochran from the Massif de La Selle. New evidence, however, shows that the latter taxon, formerly considered a distinct genus, intergrades with *cybotes* at intermediate elevations in the foothills of the La Selle range, e.g. at Furey, 10 miles S. of Port-au-Prince. Some of the squamation differences between *whitemani* and *cybotes* are in fact rather similar to those between *armouri* and *cybotes* — although they are greater (Table 1, and Figs. 2-4). Thus the character differences are not *in themselves* great enough to establish species status for *whitemani*.



X *Anolis whitemani* n. sp. in
central and western Hispaniola

FIG. 1. Localities for *Anolis whitemani* n. sp.

TABLE 1.

Differences separating *cybotes*-like anoles in the Port-au-Prince area.

	<i>whitemani</i>	<i>cybotes</i> (Port-au-Prince and vicinity)	<i>armouri</i>
VENTRALS	keeled, narrow.	smooth, eyeloid, wide.	smooth, eyeloid, very wide.
TEMPORALS	granular, but larger than flank scales.	finely granular, even smaller than flank scales.	granular, but larger than flank scales.
MIDDORSALS	enlarged but grading into flank scales.	abruptly larger than flank scales.	enlarged but grading into flank scales.
BODY COLOR	pale tan.	brown to reddish.	olive.
BODY PATTERN	patternless or with pale grey transverse mark- ings.	patternless as adults or with greenish lines on flanks.	often with bold rhombs on flanks = persistence in adults of a juvenile pattern.
DEWLAP COLOR	white	pale yellow or rarely pale pink with white or greyish streaks or greyish with yel- lowish streaks.	pinkish or yel- lowish with green- ish smudges centrally. ¹

SPECIES STATUS AND DISTRIBUTION

In the final analysis the judgment that *whitemani* is a full species rather than a morph of *cybotes*, as Cochran (1941) believed, has been based on observation of the habits and habitats of the two species in the Cul de Sac region.

The topotypic series of *A. whitemani* was taken in open dry scrub along the road to Eaux Gaillées in the full sun of late morning. The same day quite typical *A. cybotes* were obtained in the grove of trees at the spring in the village of Eaux Gaillées and in a similar grove of trees at Manneville further east on the same road, again at a spring.

¹ Color notes from information provided by Dr. Albert Schwartz.

In the Cul de Sac Plain such groves of quite large trees around springs are quite literally oases in a thorn scrub desert. The fauna, like the flora of these oases, is characteristically that of rather moist areas.

The faunas of these oases are obviously disjunct, in effect island populations derived from the faunas of the moist forests of the mountain foothills to the south and to the north. The contrasts between the fauna within an oasis and that outside it are sharp and very characteristic. Within each oasis are animals that could be seen also in a pension garden in Port-au-Prince itself, e.g. *Anolis chlorocyanus*, *A. cybotes*, *A. distichus*, *Celestus costatus*. Outside, in the dry scrub, are *Anolis whitemani*, *Celestus curtissi*, *Lciocephalus semilineatus*.

A. cybotes and *A. whitemani* thus live in the same area but are sharply segregated by ecological preference and sharply distinguished by color and morphology. It is very important that the morphological differences are greater between *cybotes* and adjacent *whitemani* than between *cybotes* and more distant *armouri*; this is a demonstration that these two populations are behaving as good species.

The discovery of *A. whitemani* on the dry northwest coast at Mole St. Nicolas is a very valuable addition to the data on its distribution. When its occurrence seemed limited to the Cul de Sac Plain, *whitemani* was something of an anomaly, since this area has only relatively recently emerged from under the sea. However, with the realization that it is probably to be found all along the dry northwest coast of Haiti and is known as far east as the similar dry coast at Monte Cristi on the north coast of the Dominican Republic, its recent extension into similar arid habitats in the Cul de Sac Plain becomes very plausible. It is probably an autochthon of the dry west and northwest coast of the "northern island"—the portion of Hispaniola north of the former seaway through the Cul de Sac. (For a discussion of the importance of the northern and southern islands in Hispaniola zoogeography, see Williams, 1961.)

It is noteworthy that Humphrey obtained large series of the species *cybotes* on Gonave Id. (an island mostly dry but again with oases around the springs) but no *whitemani*. The latter may thus really be absent there. This requires further confirmation, but the fauna of Gonave has been derived by a limited and erratic sampling of the faunas of the neighboring mainland. The absence of any individual species is therefore not in itself surprising and need not imply oversight in collecting.

ACKNOWLEDGMENTS

I am indebted to Dr. Albert Schwartz, Dr. Philip Humphrey, Dr. Doris Cochran, Mr. C. M. Bogert and Dr. W. Lädiges for the privilege of examining specimens. National Science Foundation Grant G 5634 and a grant from the American Philosophical Society provided funds for expeditions to Haiti. National Science Foundation Grant G 16066 continues to support research on Hispaniolan and other anoles.

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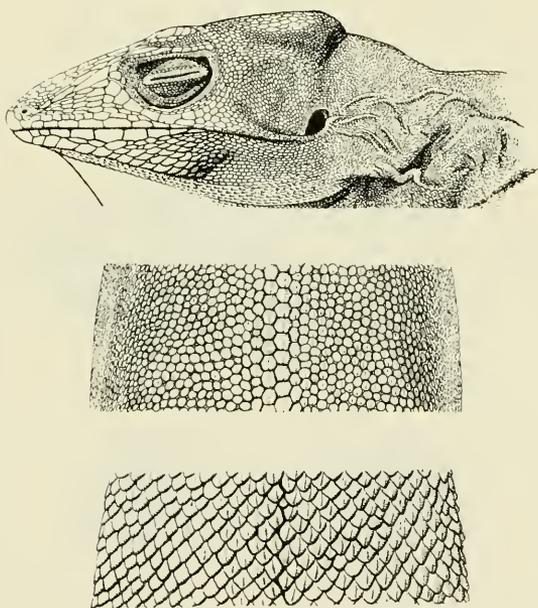


FIG. 2. *Anolis whitemani* n. sp. Paratype. MCZ 60056. *Top*: Side view of head. *Middle*: Dorsum at midbody. *Bottom*: Venter.

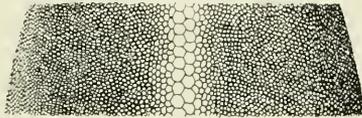
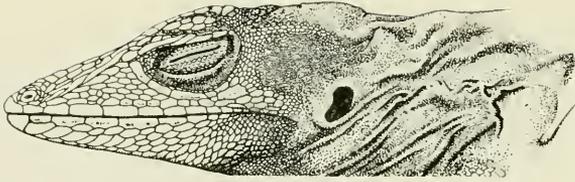


FIG. 3. *Anolis cybotes cybotes*. MCZ 59883. *Top*: Side view of head. *Middle*: Dorsum at midbody. *Bottom*: Venter.

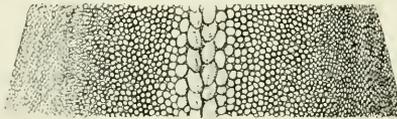
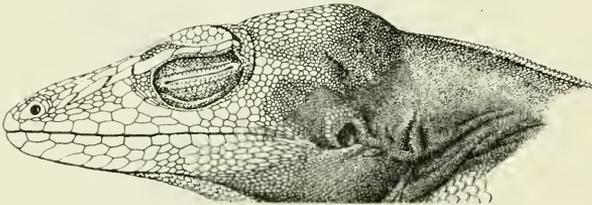


FIG. 4. *Anolis cybotes armouri*. MCZ 61051. *Top*: Side view of head. *Middle*: Dorsum at midbody. *Bottom*: Venter.

B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS.

MARCH 10, 1964

NUMBER 198

AMPHISBAENA SCHMIDTI, A THIRD SPECIES OF THE
GENUS FROM PUERTO RICO¹ (AMPHISBAENIA:
REPTILIA).

By CARL GANS

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The island of Puerto Rico is unique among the islands of the Greater Antilles in possessing two almost certainly sympatric species of *Amphisbaena*. One of them, *A. cacca*, ranges over the entire island, while the second, *A. bakeri*, is restricted to the central portion of the northwestern corner of Puerto Rico (Fig. 1). *A. cacca* has been shown to vary more widely in the western than in the eastern portion of its range (Grant, 1932; Gans and Alexander, 1962).

A recent study of the systematics and variations of the several Antilles species (Gans and Alexander, 1962; here followed for terminology) disclosed three individuals from Puerto Rico that clearly differed from both described forms in five characteristics, i.e. in more ways than the former differed from each other. The specimens were left *incertae sedis* for three reasons: two specimens came from a rather old collection; the third specimen had been collected on the diametrically opposite end of the island; and only these three out of more than 200 Puerto Rican specimens showed this character pattern.

Dr. H. Heatwole has now made available three additional specimens that stem from two coastal localities adjacent to that of the first two specimens. They make it desirable to call attention to the probable existence of yet a third species of *Amphisbaena* on the island, a situation that may have some interesting zoogeographical implications.

¹ Notes on amphisbaenids No. 11.

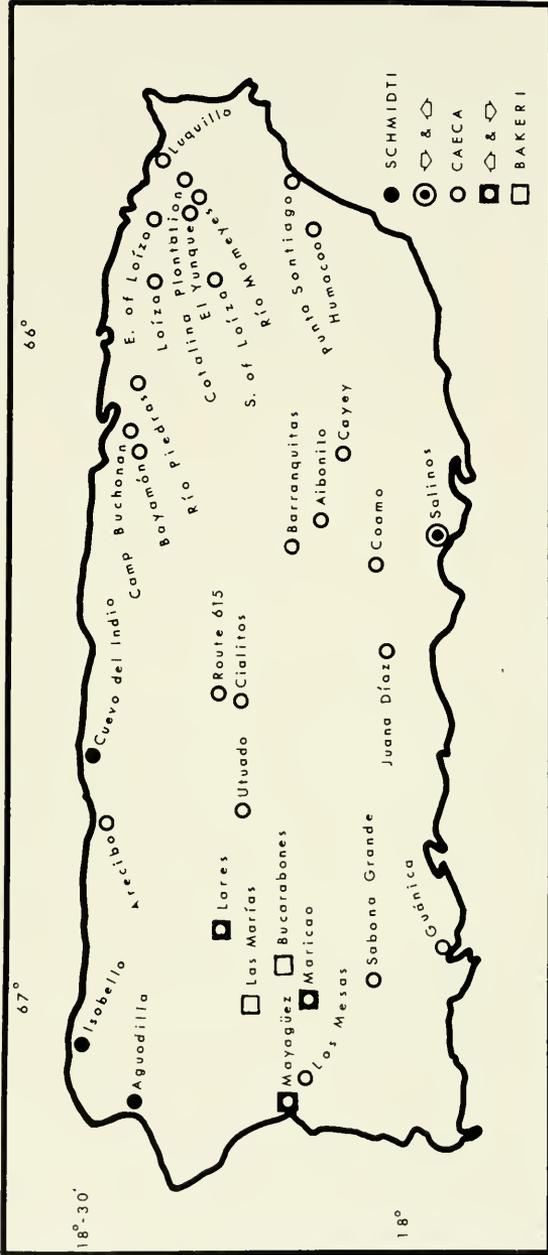


Fig. 1. *Amphisbaena*. Sketch map of the island of Puerto Rico showing the relation of the localities from which specimens have been examined. Localities from Gans and Alexander (1962) except for Coamo and Route 615 recorded on the basis of specimens now in the Michigan and UPRR collections.

I take great pleasure in naming this form for the late Karl Patterson Schmidt. The specimens belong in the collections of the Carnegie Museum (CM), the Universitetets Zoologiske Museum of København (KM), and the University of Puerto Rico at Rio Piedras (UPRRP). One of the individuals from Rio Piedras has been sent on exchange to the Museum of Comparative Zoology (MCZ). I am grateful to the curators of the several institutions, particularly to Dr. F. W. Braestrup who went to considerable trouble to check the original catalogs, and to Dr. H. Heatwole and students who made an effort to collect additional specimens. A. A. Alexander and E. E. Williams contributed by discussing this situation. Dr. Virginia Cummings prepared the drawings and Miss Charlyn Rhodes furnished technical assistance. These studies are supported by Grant G-21819 from the National Science Foundation.

KEY TO PUERTO RICAN *AMPHISBAENA*

1. Body annuli more than 205, caudal annuli fewer than 18, tail markedly shorter (Fig. 4), generally no enlarged parietals 2
 Body annuli 205 or fewer (198-202), caudal annuli 18 or more (20-22), tail markedly longer (Fig. 4), parietals very large *schmidti* sp. nov.
2. Body annuli 218-236, tail slightly longer (Fig. 4), internasal suture considerably shorter *cacca*
 Body annuli 239-255, tail slightly shorter (Fig. 4), internasal suture considerably longer *bakeri*

AMPHISBAENA SCHMIDTI sp. nov.

Diagnosis: A form of *Amphisbaena* without fusion of head segments; with markedly enlarged parietals; having 198 to 202 body annuli along the ventral line; 20 to 22 caudal annuli; 14 dorsal and 16 to 17 ventral segments to a midbody annulus; two rows of postgenial and one row of postmalar chin shields and 4 precloacal pores. The tail is cylindrical and its end rounded. The autotomy constriction is noticeable at the seventh to eighth postcloacal annulus and autotomy takes place here.

Holotype: MCZ 73115, a female collected by M. J. Velez, Jr., at Orilla (Cunta) Carreamo, Isabella, Puerto Rico, on 21 February 1960.

Paratypes: UPRRP 1290, a male collected with the holotype; CM 36277 from Salinas, Puerto Rico; KM R-4414 and R-4416 collected by Dr. Meinert at Agnadilla, Puerto Rico, in January

1892; and UPRRP 2502 collected by H. Heatwole along highway P.R. 681, 2 miles east of Cueva del Indio, Puerto Rico, on 14 January 1963.

Discussion: The demonstrated differences indicate that the new form is very distinct morphologically. They do not show whether it is a separate species, a (coastal?) race of *A. cacca*, or of *A. bakeri*. A case may be made for each of these. I have decided to treat the form as a full species for the following reasons: (1) The degree of morphological difference is greater than that found between conspecific populations among related species. It exceeds that between the two presently recognized species on the island. (2) The sample from Salinas contains five specimens of *A. cacca* and one of *A. schmidtii*. The coastal record of *A. cacca* from Arecibo lies midway between two records of *A. schmidtii*. Both of these cases suggest a limited degree of sympatry. (3) Specimens of *A. schmidtii* from opposite ends of the island indicate almost no geographic variation, in contrast to the situation of *A. cacca*. (4) Designation of the form as a full species does not prejudice the open question of its affinities.

Description: Meristic characters are listed in the table. Figure 2 shows the head scalation, Figure 3 the segmentation of cloaca and tail, and Figures 5 to 7 are photographs showing details of color pattern and midbody segmentation. Figure 4 shows the body proportions.

Specimens are a dark brown with very slight ventral counter-shading. None of the specimens show a dropping out of pigment on the midventral area. The smaller specimens have each segment more or less uniformly pigmented, but the two largest show a considerable additional darkening of the rectangular segmental centers. The intersegmental raphes are always lightened. Dorsal surfaces of head and tail are a uniform dark violet brown in freshly preserved specimens.

The head scalation is characterized by lack of major fusions. An azygous rostral invisible in dorsal view is followed by a pair of contacting nasals, very large elongate prefrontals, frontals, and wide and long parietals. The latter may be divided (transversely) or not. There are three supra- and three infralabials, but the angulus oris lies very slightly anterior to the posterior edge of the third pair. The second of each series is by far the largest; indeed, the second infralabials are larger than any scales but the prefrontals. A small segment lies immediately in line with the slit of the mouth and contacts the posterior half

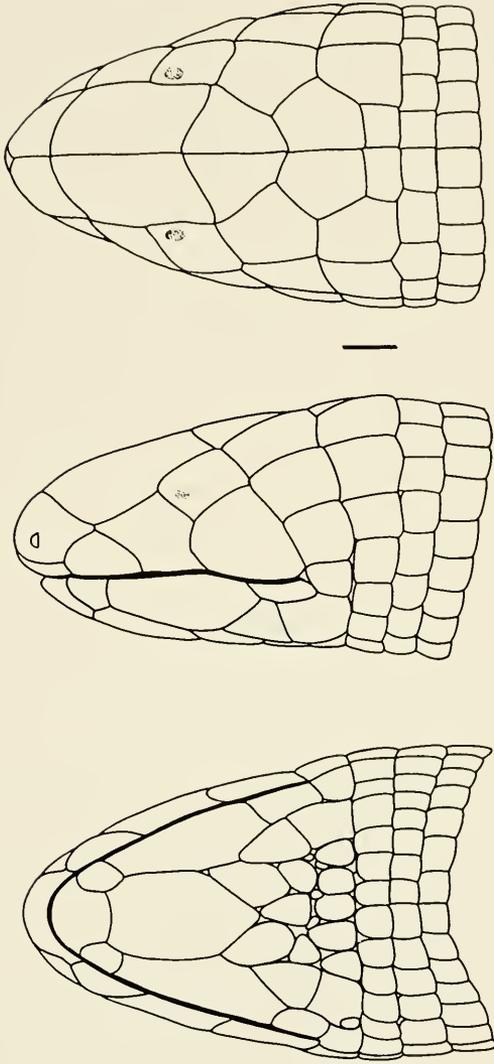


Fig. 2. *Amphisbaena schmidti*. Dorsal, lateral and ventral views of the head of the holotype, MCZ 73115 from Isabella, Puerto Rico. The line equals 1 mm to scale. (V. Cummings, del.)

of the enlarged lateral postmalar segment. The sutures between the supralabials run at angles of 45° to the slit of the mouth. The ocular is quadrangular.

The mental is T-shaped and much larger than the tiny first infralabials. The third infralabials are quite narrow. The postmental is almost as large as a second infralabial. The triangular tips of the two segments of the first postgenial row embrace it posteriorly. There are three second postgenials. The anterior tip of the median one contacts the postmental in some specimens. The malars are relatively small and contact the second and third infralabials, but are clearly excluded from contact with the postmental. The segments of the postmalar row are relatively long, the lateral ones are almost wedge-shaped. Only the anterior half of the lateral ones contacts the third infralabial; the posterior portion reaches the small segment back of the angulus oris. The postmalar row is thus counted as the first body annulus

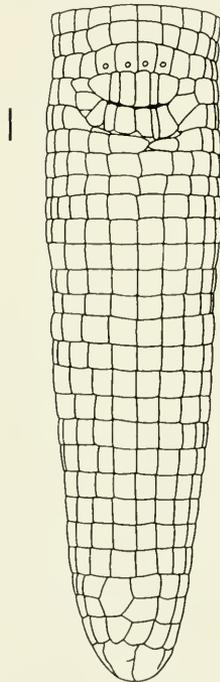


Fig. 3. *Amphisbaena schmidti*. Ventral view of cloaca and tail of the holotype, MCZ 73115 from Isabella, Puerto Rico. The line equals 1 mm to scale. (V. Cummings, del.)

as well. The lateralmost segments of the row are of the same width as the malars, and give the impression that the latter have been split.

Dorsally, the large segments of the first body annulus curve to contact the sides of the frontals. The dorsal portion of the second annulus consists of elongate segments that increase in

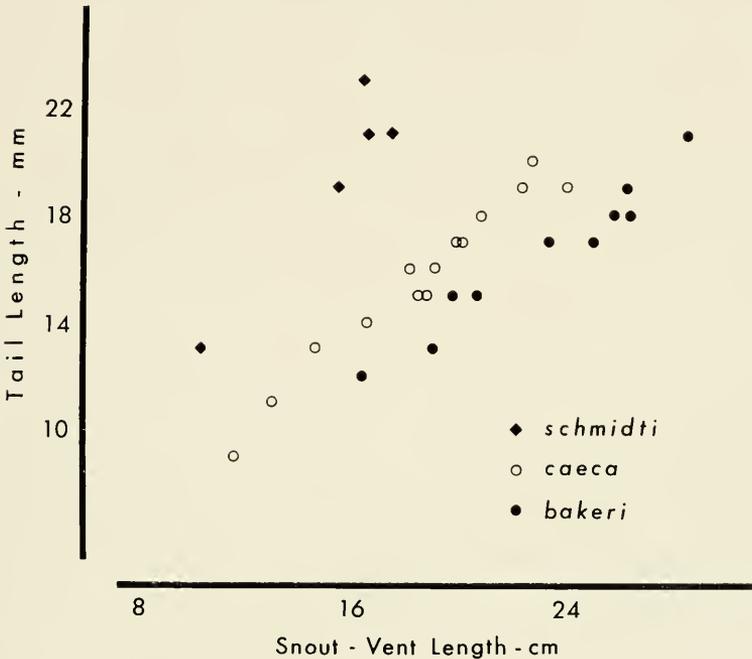


Fig. 4. *Amphisbaena*. Scatter diagram showing plot of tail length versus snout-vent length for all specimens of *A. schmidti* and *A. bakeri*, as well as specimens of *A. caeca* from western Puerto Rico. Inclusion of eastern Puerto Rico material of *A. caeca* would mask the difference between *A. caeca* and *A. bakeri*, but not affect that between the former and *A. schmidti*.

length toward the middorsal line. The posterior edge of the second annulus shows no forward curvature. There is no dorsal intercalated half-annulus, though the parietals are split into two pairs in four specimens and on one side of another.

The head is pointed, depressed, of horizontally oval cross-section. The lower jaw is but slightly shorter than the upper.

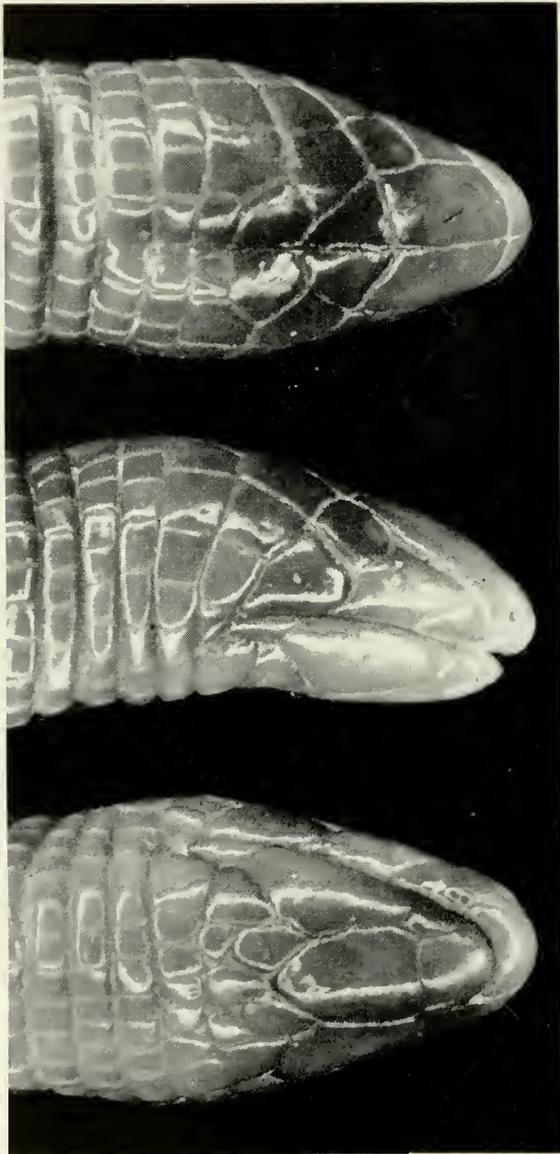


Fig. 5. *Amphisbaena schmidti*. Dorsal, lateral and ventral views of the head of MCZ 73115, to show uniform coloration and the effect of the bulging temporal musculature.

The bulge of the temporal musculature is very noticeable, producing a concave folding of the skin along the middorsal raphe and a clear distinction of the head from the narrower neck.

There are 198 to 202 body annuli from the back of the third infralabial, up to and including the pore-bearing preloacals. The second through fifth annuli are ventrally much narrower than the succeeding ones and their segments do not line up with those following. There is no pattern irregularity in the "pectoral" region, nor are there intercalated dorsal half-annuli. There are 14 dorsal and 16 to 17 ventral segments to a midbody annulus.

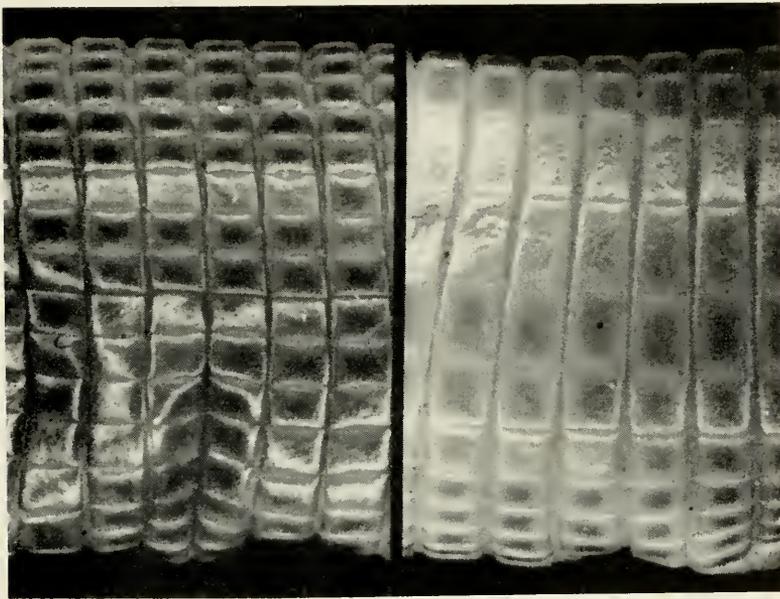


Fig. 6. *Amphisbaena schmidti*. Dorsal and ventral views at midbody of MCZ 73115 to show segment proportions and coloration.

The cloacal region is characterized by 4 round preloacal pores which are strongly expressed in males as well as females. There are 6 preloacal and 9 to 12 postloacal segments and 3 (once, unilaterally, 4) lateral rows. The extreme lateral postloacal segments lie almost directly laterad of the extreme lateral segments of the curved preloacal shield, so that one is tempted to count them as preloacals. The autotomy annulus falls on the seventh to eighth postloacal annulus and autotomy takes place

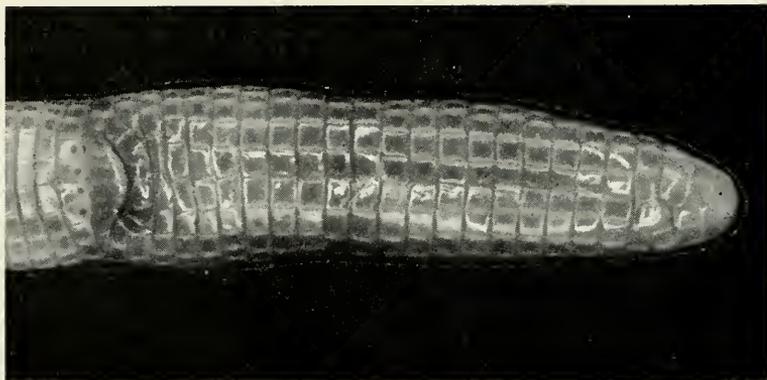


Fig. 7. *Amphisbaena schmidti*. Ventral view of cloaca and tail of MCZ 73115 to show pore size (in a female) and coloration.

here. Specimens have 20 to 22 caudal annuli. The cross-section of the tail is circular throughout and the distal tip is capped by a hemispherical portion.

The lateral sulci are distinctly marked from back of the first quarter of the trunk length to the level of the cloaca. At their widest they are narrower than the width of one of the bordering segments. The dorsal and ventral sulcus and the lateral sulcus in the anterior quarter are indicated only by the alignment of intersegmental sutures.

The dorsal segments of a midbody annulus are approximately one and one-quarter times as long as wide, while the ventral ones are one and one-half times as wide as long.

Habits: Examination of the KM catalogs (by Braestrup) indicates that Dr. Meinert (an entomologist) excavated some termite nests on the days when the two paratypes were taken, and may have found the specimens at that time. The Cueva del Indio specimen was collected under a fallen palm leaf on humus.

Range: Coastal Puerto Rico.

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Data for specimens of *Amphisbaena schmidti*

Collection and number	Sex	A N N U L I body/tail	SEGMENTS dors./vent.	Chin segments	Clouca	Length
KM R-4414	♀	202+3+(7)X	14/16	2-3-7	4-6-9	117+X
KM R-4416	♂	200+3+(8)22	14/16	2-3-7	4-6-12	163+23
MCZ 73115	♀	199+3+(7)20	14/17	2-3-7	4-6-10	154+19
UPRRP 1290	♂	202+3+(7)21	14/16	2-4-7	4-6-12	102+13
UPRRP 2502	♂	200+3+(7)20	14/16	2-3-6	4-6-10	165+21
CM 36277	—	198+3/4+(7)21	14/16	3-4-6	4-6-12	173+21

B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS.

MARCH 10, 1964

NUMBER 199

A NEW SUBSPECIES OF *VARANUS EXANTHEMATICUS* (SAURIA, VARANIDAE)

By R. F. LAURENT

Dr. Williams asked me recently to study a small series of young Savanna Monitors collected by C. J. P. Ionides in southeastern Tanganyika, where many novelties have already been discovered. He had been impressed by their striking color pattern which is quite different from the pattern exhibited by other juveniles of the same species.

In this, he was quite right. However, the morphological features selected by Mertens (1942) as characteristic of the recognized species and races of the genus *Varanus* did not suggest that the six critical juvenile specimens belonged to an undescribed form. In squamation they agreed perfectly well with *Varanus (Empagusia) exanthematicus microstictus* Boettger. Nevertheless, I believe that it is a serious mistake to ignore coloration when this character has the same degree of constancy as is generally considered significant for morphological characters.

The difficulty here seems to be that the diagnostic juvenile patterns gradually fade during the life of the monitors so that the adults are far more similar, uniform and dull, than are the juveniles. As a result, the number of specimens available for comparison is greatly reduced, the adults not being distinguishable.

When I compared the Ionides specimens with other juveniles of *Varanus exanthematicus*, I came to the conclusion that the subspecies recognized by Mertens are themselves geographically variable as far as their juvenile color pattern is concerned.

The six juveniles from southeastern Tanganyika are alike, but obviously different from two specimens from Kenya; likewise, among the so-called southern *albigularis*, two juveniles from Zululand have a striped pattern quite different from the

ocellated pattern of five other juveniles from Transvaal, Bechuanaland and Southwest Africa.

The photographs of specimens here discussed replace advantageously any clumsy and lengthy description. Feeling that six specimens disclosing the same color pattern are enough to infer that the population to which they belong has on the whole peculiarities patently different from those of other populations, I regard them as a new subspecies of *Varanus exanthematicus*:



Fig. 1. Map showing the known localities for *Varanus exanthematicus ionidesi* n. subsp.

VARANUS EXANTHEMATICUS IONIDESI subsp. n.

Holotype: A half-grown individual (MCZ 54494), Kilwa, Tanganyika, 1956, coll. Ionides.

Paratypes: 1 adult, 2 subadults and 1 juvenile (MCZ 52536-39), Liwale, Tanganyika, 1953; 1 juv. (MCZ 54495), Masasi, Tanganyika, 1956; 1 juv. (MCZ 55470), Liwale, Tanganyika, 1957; 1 juv. (MCZ 56176), Kilwa, Tanganyika, 1958; 1 juv. (MCZ 56981), Liwale, Tanganyika, 1958. All collected by C. J. P. Ionides.

Diagnosis. A subspecies of *Varanus exanthematicus* similar to *microstictus* Boettger (type locality, Ethiopia) but differing from it by a very distinctive juvenile color pattern somewhat similar to that of *albigularis*.

The general color is lighter and with less contrast of light and dark colors than in two young *microstictus* from Kenya.

Two black lines start from the posterior border of the eye and approach each other on the neck, stopping abruptly in the scapular region where they form an acute angle. (The same lines exist in *microstictus* and *albigularis*, but they are hardly distinct in *microstictus*.) Between these lines there are three or four blackish marks (these are invisible in *microstictus*).

There are four or five transverse series of 6 light spots (8 to 13 in the typical form, or disposition irregular) generally surrounded by a black border, extending on 4 to 20 scales (in *microstictus* they fill 1 to 4 scales only and they have no black border); the mediiodorsal spots are especially large and they fuse on the vertebral line (except in one individual where they are at least contiguous).

On the tail, the transverse bars are arranged in pairs which, in *ionidesi*, have the appearance of groups of four or even of eight, because the central zone of each bar may become as light as the intervals between the pairs and, in addition, two secondary zones of a less pronounced paling may still intervene on both sides of the central zone. These complications exist only for the first three or four pairs; the distal bands are plain black. These areas of paling of the central zones disappear gradually in *ionidesi*, but they are not at all apparent in the young *microstictus* available for comparison; in the latter, the terminal bars are not darker than the proximals. Lastly, the number of pairs is 9-10 in *microstictus*, but only 6-8 in *ionidesi*. The throat is blackish, as is usual, according to Mertens, for the other races.¹

MORPHOLOGICAL CHARACTERS

As stated previously, the morphological characters are not different from *microstictus*. Table 1 gives scale counts as compared with Mertens' descriptions of *microstictus*, *albigularis* and *angolensis* plus some specimens of *microstictus* (Kenya) and of *albigularis* (southwest Africa and Transvaal) and *angolensis* (Lobito).

Certain measurements have been studied on scatter diagrams. No significant differences have been observed between *ionidesi* and *microstictus*, but it seems that *albigularis* and *angolensis* have the head broader and the snout longer than both *micro-*

¹ This is not the case for the two *microstictus* juveniles from Kenya.

TABLE I

Subspecies	N	Scales around the body	Ventral scales (from gular fold to the groin)	Scales between the commissures of the mouth
<i>ionidesi</i>	5	129-150	88-99	53-63
<i>microstictus</i> (Mertens)	14	122-152	88-94	51-56
<i>microstictus</i> (Kenya)	2	131-134	87-90	50-52
<i>albigularis</i> (Mertens)	19	137-167	85-110	57-64
<i>albigularis</i> (Zululand)	2	139-147	98-99	54-57
<i>albigularis</i> (Transvaal, SW Africa)	5	137-149	88-107	53-60
<i>angolensis</i> (Mertens)	3	110-138	77-92	53-55
<i>angolensis</i> (Lobito, Angola)	4	126-141	94-98(!)	55-56

These data on *angolensis* suggest that this alleged subspecies might be elinally merged with *albigularis*.

stictus and *ionidesi*; the differences are minor and would have to be checked on large series. More interesting perhaps is the fact that the two Zululand specimens, different from all others by their transversely banded pattern, are also different in that their tail is shorter than the snout-vent length. This strongly suggests that another neglected race exists in South Africa, but it would be imprudent to describe this on two specimens with relatively inexact locality. The existence of this race will have to be confirmed by studies on larger samples of *Varanus cranthematicus* from South Africa.

Specimens utilized for comparison with
Varanus cranthematicus ionidesi

Varanus cranthematicus microstictus Boettger, MCZ 41112, Sokoki Forest, Kenya (coll. H. J. A. Turner); MCZ 59154, Kakoneni on Sabaki River, Kenya (coll. M. J. Coe).

Varanus cranthematicus albigularis (Daudin), MCZ 45417-18, Zululand; MCZ 39906, Waterberg, Southwest Africa (coll. W. Hoesch); MCZ 41888, Saltpan, Pretoria Distr., Transvaal (coll. A. Roberts); AMNH 57600, Otjuiarongo, Waterberg, Southwest Africa; CNHM 17141, Gaborones, Bechuanaland (coll. H. Lang); CNHM 75712, Hüttenhain, Southwest Africa (coll. W. Hoesch).

Varanus cranthematicus angolensis Schmidt, AMNH 47721-24, Lobito, Angola.

Acknowledgment. This work has been performed thanks to a grant generously allowed by the National Science Foundation (BG-13987). I take pleasure in thanking Mr. C. M. Bogert and Dr. R. F. Inger for the loan of specimens belonging to the collections of the American Museum of Natural History (AMNH) and the Chicago Natural History Museum (CNHM), respectively.

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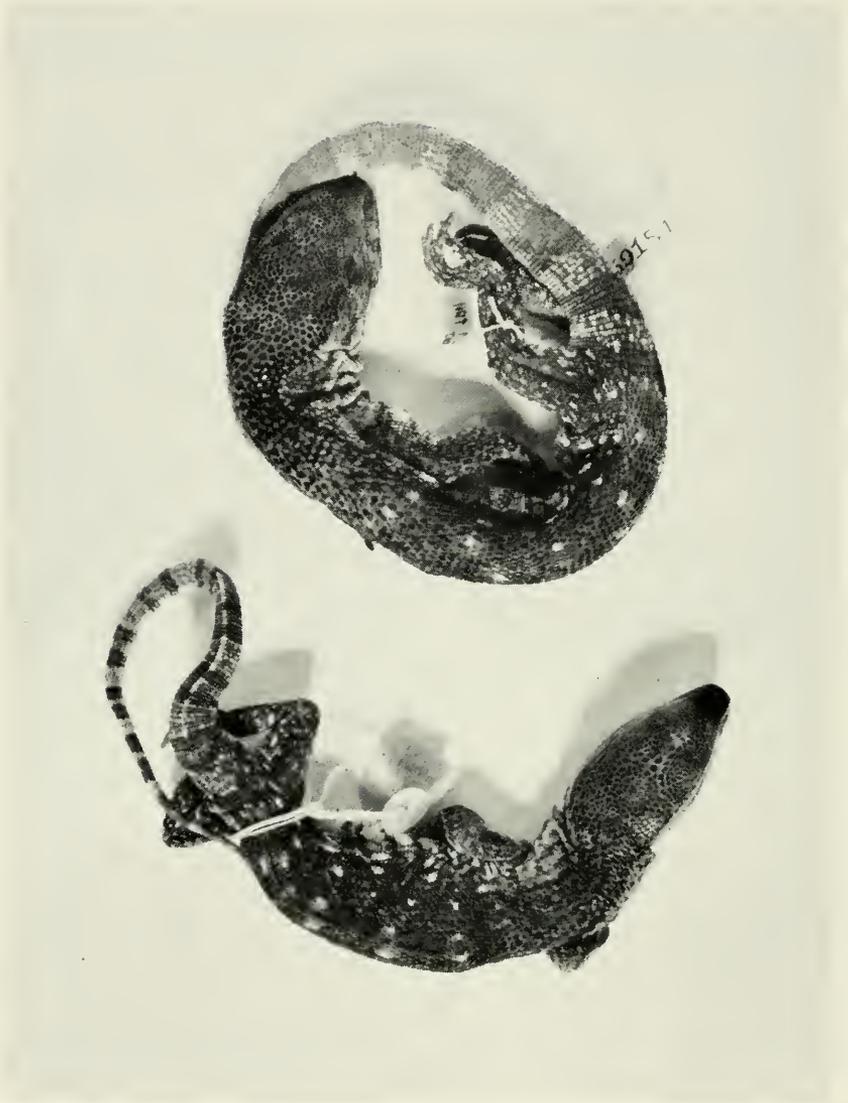


Fig. 2. *Varanus exanthematicus microstictus* juveniles from Kenya.



Fig. 3. *Varanus exanthematicus ionidesi* n. subsp. Holotype surrounded by paratypes.

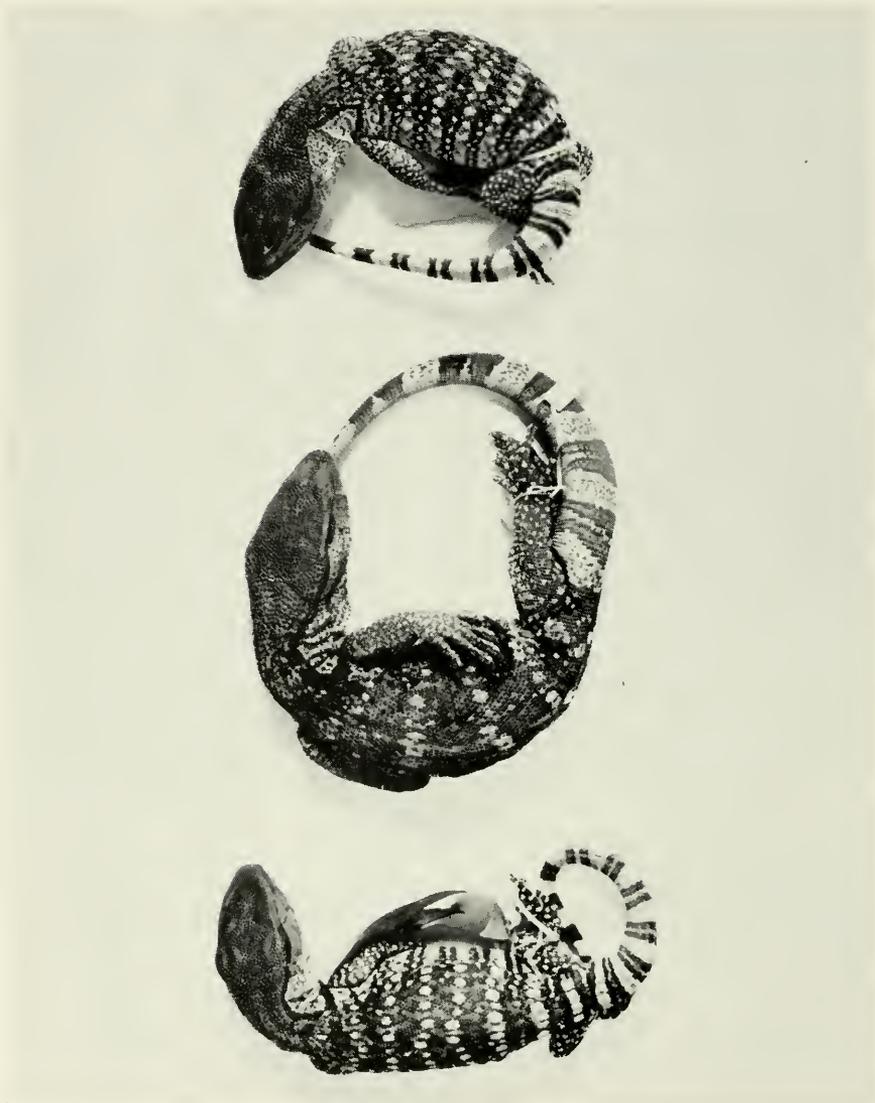


Fig. 4. *Taranus exanthematus albigularis* juveniles, showing the typical pattern.



Fig. 5. *Varanus exanthematicus albigularis* juveniles from Zululand, showing the banded pattern.

B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS.

APRIL 10, 1964

NUMBER 200

AN ANGUID LIZARD FROM THE LEEWARD ISLANDS

By GARTH UNDERWOOD

Department of Zoology, University of the West Indies, Trinidad.

Through the good offices of Mr. L. Kasasian of the University of the West Indies, I received from Mr. J. Phillips, Director of Agriculture in Montserrat, a lizard which I was amazed to see was an anguid of the genus *Diploglossus*; the family had not previously been known, living or fossil, from the Lesser Antilles. Scarcely less amazing was the observation that this lizard resembles the Central American *D. monotropis* in respect of several major differentiating characters, and differs conspicuously from the known Greater Antillean species.

The specimen was collected in Montserrat by Mr. J. Kingsley Howes who tells me that he has only once before seen this lizard, and that twenty-five years ago. On the grounds that I am therefore unlikely soon to see another I describe for the second time (Underwood, 1959a) a new species of *Diploglossus* on the basis of a single specimen. Once again my description contains tedious detail, some of which may be eliminated when more specimens are examined. As explained in the earlier paper, I do not recognize the genus *Celestus* as distinct from *Diploglossus*. In the condition of the claws, prefrontals, nasals, and numerous scale organs on the back, this species resembles only *D. monotropis*. I therefore borrowed two specimens of *monotropis* and prepared the description with these before me; the specimens are MCZ 37139 Yavisa, Panama, and MCZ 15353 Limon, Costa Rica.

The name of the island of Montserrat is Spanish, from the Latin *mons serratus*. As this is quite the most remarkable reptile yet reported from Montserrat, and as no other reptile bears the name of this island, I call it *Diploglossus montisserrati*.

Family ANGUIDAE Cope

DIPLOGLOSSUS MONTISSERRATI new species

Type and only known specimen: adult ♂ MCZ 76924, and from this specimen: left ramus of lower jaw; slide 1, prefrontals, frontal (damaged), frontoparietals, interparietal (damaged), parietals and occipital scales; slide 2, series of 10 scales back from occipital; slides 3a, b and c, 12 longitudinal rows of 10 dorsal scales; slide 4, transverse row of scales from middorsal to midflank; slide 5, three rows of 10 scales forward from groin; slide 6, transverse row of tail scales at level of ankle from middorsal to midventral; slide 7, series of 20 scales back from mental; slide 8, 25 midbelly scales. Collected by J. Kingsley Howes at Woodlands Spring, elevation about 600 feet, Montserrat, West Indies, 16° 45½' N, 62° 13' W.

Diagnosis: A large strong-limbed *Diploglossus* with sheathed claws; three prefrontal scales; contact between nasal and rostral scales; numerous scale organs on dorsal scales but none on belly scales; very numerous scale organs on dorsal tail scales; more than 80 scales from occipital to base of tail; back plain brown, no crossbands.

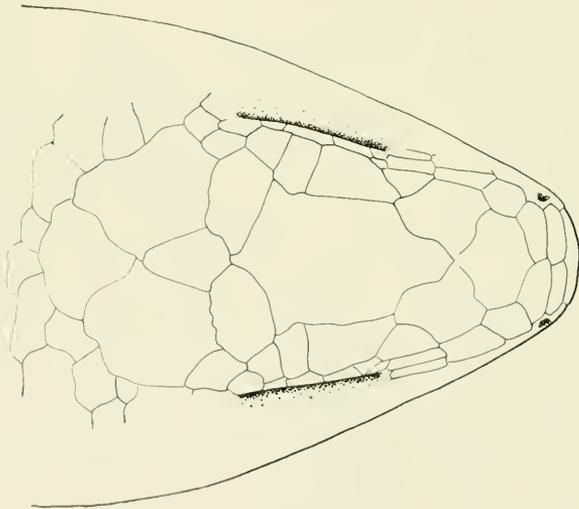


Fig. 1. Dorsal view, head of *Diploglossus montisserrati* type. Area of posterior frontal and frontoparietals may be a little inaccurate owing to damage.

Description: As this species rather closely resembles *monotropis*, I note in square brackets the features in which *monotropis* differs. Upon receipt of the first draft of my manuscript Mr. Benjamin Shreve kindly examined an additional seven specimens of *monotropis* in the Museum of Comparative Zoology for the characters which I had thought useful. His data are incorporated here. Shreve's counts on the type of *montisserrati*, when they differ from mine, are cited in parentheses.

Head broad; width: length to anterior margin of earhole = 0.83:1. Rostral one and a half times as broad as high, in contact with 1st labials, nasals, and supranasals. Pair of supranasals each meeting other supranasal, rostral, nasal, upper postnasal and frontonasal. Pair of frontonasals, each meeting other frontonasal, supranasal, upper postnasal, canthal and median prefrontal. Pair of canthals each meeting frontonasal, 2 prefrontals, 1st and 2nd loreal and upper postnasal [the same or meeting both postnasals and only 1st loreal]. Three prefrontals (sutures separating them incomplete posteriorly). Median prefrontal meets frontonasals, canthals and lateral prefrontals [and sometimes frontal]; each lateral prefrontal meets median prefrontal, canthal, 2nd loreal [1st or 2nd loreal], 1st and 2nd supraoculars [1st and 2nd or 1st only] and frontal.

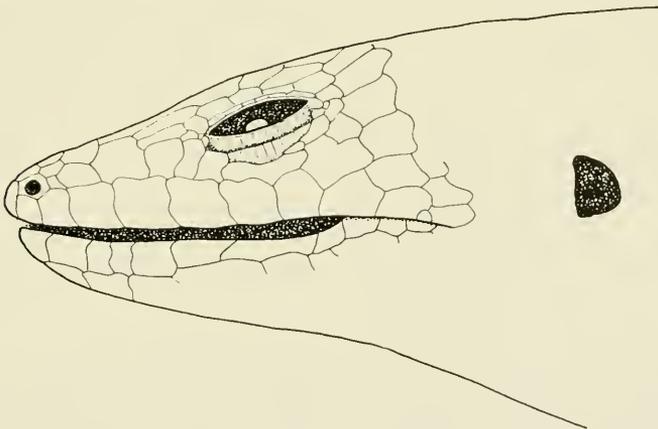


Fig. 2. Lateral view, head of *Diploglossus montisserrati* type.

Frontal tapers to a point anteriorly, wide posteriorly; meets prefrontals, 2nd and 3rd supraoculars, frontoparietals and interparietal; broadly in contact with frontoparietals, narrowly in

contact with interparietal [narrowly or broadly in contact with interparietal], excluded from contact with parietals. Palpebral aperture large. Four supraoculars, 2nd largest; 2nd loreal just meets first supraocular [no loreal meets supraoculars], 3rd loreal separated from supraoculars by 1st supraciliary [2nd or 3rd loreal so separated]. One subocular intruding only slightly between 6th and 7th labials. Six supraciliaries [6 or 7 supraciliaries], postoculars 4, 6 [4 or 5]. Five temporals between frontoparietal and labials, anterior lower temporal meets 7th and 8th labials. Single nasal meets rostral, supranasal, 1st and 2nd labials, and 2 postnasals. Three loreals [two or three loreals]: 1st small between 2 postnasals, 3rd labial, 2nd loreal and canthal; 2nd loreal large, between 1st loreal, 3rd and 4th labials, 3rd loreal, 1st supraciliary, 1st supraocular and prefrontal. [1st loreal between lower postnasal, 3rd and 4th labials, 2nd loreal, supraciliary, prefrontal and canthal]; 3rd loreal between 2nd loreal, 4th and 5th labials, preocular and 1st supraciliary [2nd loreal has the same contacts]. Small mental two-thirds width of rostral; 8, 7 [6 or 8] infralabials, prominent postmental in contact with labials, 1st and 2nd followed by 4 pairs of chin shields, 1st pair meeting in midline. Transparent area in lower eyelid covered by about 4 vertical scales.

Middorsal scales from posterior part of neck to root of tail with prominent median keel. Keels reduced on tail at about level of hindfeet [keels on tail a little more pronounced]. From occiput to end of tail, dorsal scales have longitudinal striae. Keels and striae fade on lower flank. Scales on underside of body quite smooth. Scales on forelimb and hindlimb with striae and slight keels on dorsal surface only [no keels on scales of limbs]. Soles of feet with swollen soft scales. Vertical ridge-like scale in groove between 3rd and 4th toes and soft fold of skin on proximal posterior face of 3rd toe [this condition of the 3rd and 4th toes is not developed]. Dorsal scales of fingers smooth, dorsal scales of toes striated [no striation on scales of toes].

Forty-one (43) scale rows at midbody [36-40, also confirmed by Boulenger (1885) and Taylor (1956)]; mental to vent 88 scales [85, 90]; occipital to point above vent 91 scales (occiput to base of tail 86) [72-79]; from anal to chest on line joining axillae 55 scales [53, 55]; at level of ankles 20 scale rows around tail [23, 21].

Third digit of forelimb slightly longer than 4th; lamellae 3rd digit: 8, 8 [7 or 8]; lamellae 4th digit 7, 8 [7 or 8]. Length of 4th digit of hindlimb to length of 3rd as 1.2:1; 4th toe lamellae 11, 11.

As indicated, slides were made of scales from various parts of the body; of the *monotropis* only MCZ 37139 had sufficient scales for a parallel set of preparations.

There are numerous scale organs on the prefrontal, frontal, frontoparietal, parietal and occipital scales; there are none on the interparietal [many].

Ten rows of ten dorsal scales (less three missing) had an average of 4.94 [4.71] scale organs per scale. The totals of scale organs for ten longitudinal rows of ten showed a variance of 16.7 per cent; the totals for ten transverse rows of ten showed a variance of 10.6 per cent. This suggests that a transverse or oblique row gives a more reliable count than a longitudinal row. Six of the scales lacked central keels; for the others the central keel divided the scale organs into two groups, mesial and lateral [central keel does not separate two groups]. Counting the scale rows from the vertebral line, the majority of scale organs lie on the lateral side of rows 1 and 2, the mesial side of rows 3 and 4, and all on the mesial side of rows 5 and 6.

Descending the flank the scale organs become reduced in number; on the belly there are none [on belly 2.08 organs/scale].

Three rows of ten scales forwards from the groin had a mean of 3.43 organs/scale [4.8]. On the dorsal tail scales there are very many scale organs, 42–73/scale [9–11/scale], falling to none on the underside [3–4/scale].



Fig. 3. Mesial view, left ramus of lower jaw of *Diploglossus montiserrati* type.

Left dentary bears 20 teeth. Teeth cylindrical; crowns of anterior teeth laterally compressed, crowns of posterior teeth rounded; many of the teeth show signs of wear on the lingual side of the crown. The outer face of the dentary has six foramina. I am indebted to Dr. Robert Hoffstetter for drawing my attention to the existence of a foramen on the inner face of the surangular before the posterior branch of the coronoid in the Cordylidae and some Anguidae. This specimen has two foramina in this position.

The osteoderms show the network of canals in the basal area (buried in the dermis), as described and figured by Hoffstetter (1962) for *D. monotropis*. The distal, epidermis-covered area shows radiating canals. The scale organs lie in the portion of the skin beyond the margin of the osteoderm. It seems unlikely therefore that scrutiny of the osteoderm would give an indication of their presence.

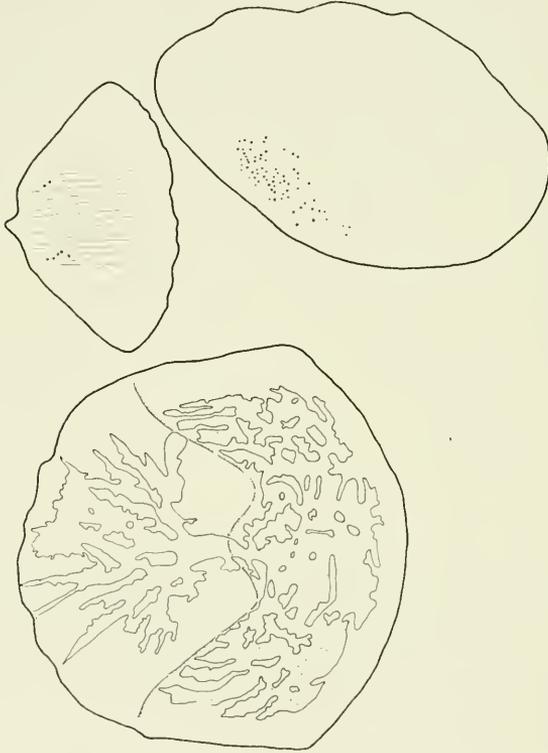


Fig. 4. Lower, middorsal osteoderm; upper left, middorsal scale; upper right, dorsal tail scale: *Diploglossus montisserrati* type.

General coloration medium brown. Top of head uniform brown, upper labials white with a few brown speckles mostly on margins, lower labials and underside of head immaculate. Starting on neck indistinct darker brown lines; across width of 12 dorsal scale rows plain brown; on flanks and onto side of tail speckles

generally covering one or two scales consisting of a dark brown mark followed by white; regenerated portion of tail darker and more uniform brown. Legs with speckles similar to those on flanks. Underside of body immaculate. *D. monotropis* has dark-edged, white crossbands which Boulenger notes may be broken into ocelli on the flanks. Dr. Ernest Williams notes a constant dark streak on the temples of *monotropis* as an additional difference from *montisserrati*.

Dimensions (contorted in preservation): snout to vent *c.* 180 mm, tail (half regenerated) *c.* 165 mm, forelimb 41 mm, hindlimb 45 mm, axilla to groin *c.* 95 mm.

DISCUSSION

We may well ask if the resemblance between *monotropis* and *montisserrati* indicates close relationship. Reference to the table (1959a, p. 13) in my previous paper shows that before the discovery of *montisserrati* the only species to combine the four characters which I hesitatingly regarded as primitive was *monotropis*. The scale organs on the belly, which I did not notice in 1959, may represent an additional primitive character. The only differences which are greater than moderate differences of degree are the color pattern, the lack of scale organs on the interparietal and on the belly, and the very numerous scale organs on the dorsal side of the tail and, perhaps, the dorsal scale count. It is therefore difficult to suppose that the two species are not related and I suggest that it is plausible to assume that, widely separated as they are geographically, they have diverged but little from a common ancestral stock. As I have previously suggested (1959a, p. 11) *monotropis* appears to be related to *fasciatus* and *resplendens* in South America, to *millepunctatus* on lonely Malpelo Island and perhaps to the limbless *Ophiodes*. I have not examined material of *bilobatus* and *lessonae* but it seems possible that these species may be related to the *monotropis* stock with the difference that they have a single prefrontal scale (Boulenger, 1855; Schmidt and Inger, 1951; Taylor, 1956). In connection with this difference it may be noted that the sutures separating the median and lateral prefrontals of *montisserrati* are incomplete. The species of northern Central America and the Greater Antilles differ more markedly from the *monotropis* group. In the Greater Antilles, Jamaica and Hispaniola have a diversity of forms while Cuba and Puerto Rico have only one species each. The Puerto Rican species has not been reported in the Virgin Islands.

It is interesting, therefore, to consider how *montisserrati* may have reached the Leeward Islands. There would seem to be two alternatives: either that *monotropis*-like *Diploglossus* was once widely spread in northern South America and from there reached Montserrat, or that *monotropis*-like stock reached the Greater Antilles from Central America and spread eastward as far as the Leeward Islands.

I regard arrival in the Leeward Islands via the Greater Antilles as unlikely. No forms are known in the Greater Antilles which resemble the *monotropis* group. We would have therefore to suppose that the *monotropis* stock passed through these islands but left no survivors, or that it underwent extensive evolutionary transformation there and gave rise to some of the now dissimilar modern forms yet survived with little change in the Leeward Islands. I have perhaps been too ready to assume in other cases, without detailed examination, that a genus which occurs in the Greater Antilles and the Leeward Islands has spread eastwards from Central America (Underwood, 1963).

I consider the proposition more plausible that the *monotropis* group was once more widely distributed in northern South America. It is a long way from the mainland to Montserrat but the journey does not seem much more improbable than the journey to Malpelo; as there are many intervening islands the journey may not in fact have been made in one stage. As the ocean drift is westwards the take-off point would perhaps be somewhere in the Guianas. That there have been changes in the fauna of the coastal belt of northern South America is very likely. *Phyllodactylus* has a distribution which is interesting in the present connection (Dixon, 1962). It occurs in Barbados, Grenada and Puerto Rico; however, the easternmost record in northern South America is Patos Island in the Gulf of Paria, between Trinidad and Venezuela. The large and conspicuous *Anolis richardii* is common in Tobago, Grenada, and the Grenadines and St. Vincent but none is known in Trinidad or on the mainland (Underwood, 1959b). Evidence of the former occurrence or present survival of the *monotropis* group in the area from the Leeward Islands to the Guianas may yet be discovered. *Diploglossus (lessonae)* does in fact occur in eastern Brazil (Schmidt and Inger, 1951) south of the Amazon.

What is the present status of *D. montisserrati* in Montserrat? Whatever may have been the manner of its arrival, it is now a relict, far removed geographically from relatives. I am inclined to

regard it as a survivor of the pluvial period, which has persisted in a favourable habitat in spite of the recent climatic changes. *Hyla barbudensis*, on the other hand, is an example of a species which was apparently unable to survive the drying of the climate (Auffenberg, 1958).

Although Montserrat is a small island (32½ sq. mi.), it is quite mountainous with peaks high enough (up to 3000 ft.) to precipitate rainfall, and has a good cover of moist forest and a considerable number of small rivers. Woodlands Spring is on the west side of the island and, according to the 1:50,000 survey map (Directorate of Overseas Surveys) it drains into a small stream called Runaway Ghaut.

Mr. Kingsley Howes writes, "This was the second one that I have seen, so they are very rare on the island. The first one I saw was about 25 years ago. . . . They were both seen near fresh water. The first was at sea level near the estuary of a stream, the second at Woodlands Spring, the elevation being 600'. I did not see either of them feeding, but it is possible that the second was feeding on young crayfish which were scurrying around the wet rocks where it was found." The stomach of the specimen in fact appears to be empty. The occurrence of both near fresh water would seem to fit in with the idea that it may be a relict of the pluvial period. The fact that there are many damp situations in the island means that there may be other surviving populations. Taylor describes a specimen of *monotropis* taken "in vegetation growing at the edge of Lake Bonilla . . . Costa Rica."

Most of the reptile stocks of the Leeward and Windward Islands range through several adjacent islands. The *montserratii* stock may well have been more widely distributed in the Leeward Islands and indeed may survive on others besides Montserrat. Survival on the limestone Leeward Islands, from Anguilla to Marie Galante, is unlikely; they are low lying and dry. Some of the volcanic Leeward Islands, from Saba to Basse Terre (Guadeloupe), on the other hand, have some good wet forest on their higher slopes. Montserrat is one of the islands on which mongoose have not been introduced and this may have been a factor in its survival. Both St. Kitts, Nevis and Guadeloupe have mongoose; however, the mongoose may not extend up to the elevation at which the wet forest persists. Saba and St. Eustatius have no mongoose but they have very limited moist forest, in fact, only inside the crater on St. Eustatius. Several collections of bones

have been made in the Leeward Islands and it would not be surprising if the remains of *Diploglossus* were found on islands on which it no longer occurs. For this reason I have figured the lower jaw and an osteoderm.

I owe the specimen on which this paper is based to the generosity of Mr. Kingsley Howes of Woodlands, Montserrat. I am indebted to Dr. Ernest Williams for the loan of the specimens of *monotropis* and for discussion of my manuscript, and to Mr. Benjamin Shreve for the report upon additional specimens of the mainland species.

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B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS.

APRIL 10, 1964

NUMBER 201

FOOD HABITS AND YOUNG STAGES OF NORTH ATLANTIC *ALEPISAURUS* (PISCES, INIOMI).¹

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INTRODUCTION

Other than a few general statements (Clemens and Wilby, 1961:157; Gibbs and Wilimovsky, in press), there is very little information concerning food habits of the lancetfishes, genus *Alepisaurus*. During a recent exploratory fishing cruise (63-4), the U.S. Fish and Wildlife R/V DELAWARE obtained stomach contents from 36 *Alepisaurus jerox* and four *A. brevirostris*, taken by longline at 16 stations from the offing of New England to the Azores. These collections allowed an investigation of the food of *Alepisaurus* across a large portion of the North Atlantic over a relatively short period of time. In addition to the longline stations, four hauls were made with a modified Scharfe midwater trawl (Scharfe, 1960). Since the hauls were made in approximately the same levels as those in which the longlines fished, examination of this material provided some information concerning the selectivity of the lancetfish in its feeding.

The longlines fished from the surface to about 80 fathoms. At most longline stations, sets were made at about 0600 hours and were hauled before 1500. Each midwater haul lasted less than an hour and reached a depth of 10 to 20 fathoms. All hauls were made at night, when vertically migrating animals would be expected to reach the upper limits of their depth ranges. The positions of the longline stations at which *Alepisaurus* were taken and the midwater trawl stations of DELAWARE 63-4 are shown in Figure 1.

Only five *Alepisaurus* smaller than 200 mm SL (standard length) were available to Gibbs (1960) for comparative purposes, and these could not be specifically identified. In the DELAWARE

¹ Contribution No. 1442 from the Woods Hole Oceanographic Institution.

material, *Alepisaurus* was found to prey heavily on its own kind, and 42 young lancetfishes ranging from 50 to 585 mm SL were obtained from stomachs. Series of both species made specific identification of such small specimens possible.

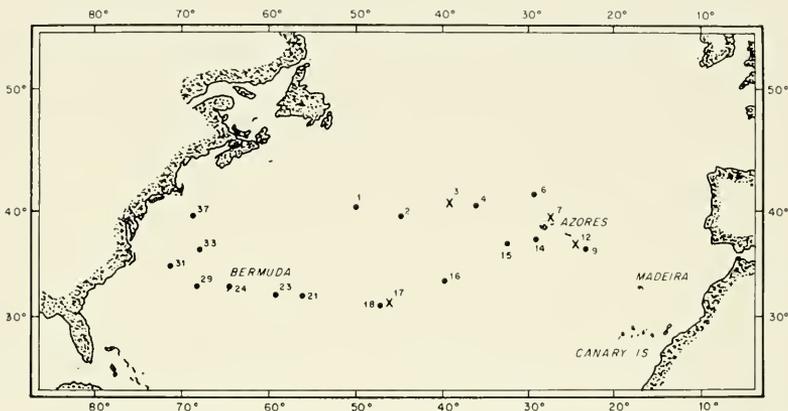


Figure 1. Positions of longline stations at which *Alepisaurus* were taken (●) and midwater trawl stations (X) of DELAWARE 63-4.

ACKNOWLEDGMENTS

Peter C. Wilson and personnel of the Bureau of Commercial Fisheries, Gloucester, made possible the participation in DELAWARE 63-4 by representatives of the Museum of Comparative Zoology, Cambridge, and the Woods Hole Oceanographic Institution. Jonathan L. Treible, representative of the Museum of Comparative Zoology for the duration of the cruise, and Martin R. Bartlett, Woods Hole Oceanographic Institution, made the collections and provided information concerning depths fished by longlines and midwater trawls. Malcolm L. Clarke, National Institute of Oceanography, England, identified tentatively the cephalopods. Daniel M. Cohen, United States National Museum, Washington, D.C., commented on the nomenclature of *Lepidion*. Richard H. Backus, Woods Hole Oceanographic Institution, and Giles W. Mead, Museum of Comparative Zoology, have read and criticized the manuscript. My work was supported by a Woods Hole Oceanographic Institution Summer Fellowship. Half the ship's costs for this cruise were paid for by the National Geographic Society. The material is housed in the Museum of Comparative Zoology.

IDENTIFICATION OF YOUNG STAGES

Two series of *Alepisaurus* were present in the stomach contents. The largest fish in each series was identifiable by characters proposed by Gibbs (1960), notably the shape of the head, the body proportions, and the melanophore structure. The largest *A. brevirostris* was 585 mm SL; the largest *A. ferox* was 267 mm SL.

As Gibbs (1960) observed, marked changes in proportions occur with growth, and the morphometric differences which separate large specimens cannot be used to identify small lancetfishes. However, a distinctive melanophore pattern and the relative position of dorsal and pectoral fins do distinguish the young fishes. Examination of one series, the largest specimens of which were clearly *Alepisaurus brevirostris*, showed melanophores along the midventral surface of the body at all growth stages seen (38 specimens, 49-585 mm SL). These melanophores were absent in the other series (5 specimens, 40-267 mm SL), the largest specimen of which was clearly *A. ferox*. Since *A. ferox* greater than 500 mm SL do have a fine peppering of melanophores on the belly, these spots must appear at some stage in growth between about 270 and 500 mm. The origin of the dorsal fin was in advance of the origin of the pectoral fin in all *A. brevirostris*, whereas the dorsal origin was over or behind the pectoral origin in all *A. ferox*.

Alepisaurus from 260 mm SL down to at least 40 mm SL can be separated as follows:

I. Melanophores present on belly, dorsal origin in advance of pectoral origin, snout profile convex. *Alepisaurus brevirostris* Gibbs

II. Melanophores absent from belly, dorsal origin over or behind pectoral origin, snout profile generally straight (cf. Fig. 2). *Alepisaurus ferox* Lowe

Anal and pectoral fin-ray counts were taken from the young fishes. Many specimens were damaged, hence dorsal counts were impractical. The meristic data (Table 1) show a similar modality to that found by Gibbs (1960).

TABLE 1

Fin-ray count frequencies in young *Alepisaurus*

	Anal rays						Pectoral rays				
	13	14	15	16	17	18	12	13	14	15	16
<i>A. brevirostris</i>	2	13	16	6			2	18	17	1	
<i>A. ferox</i>			1	3		1	1	1	2	1	

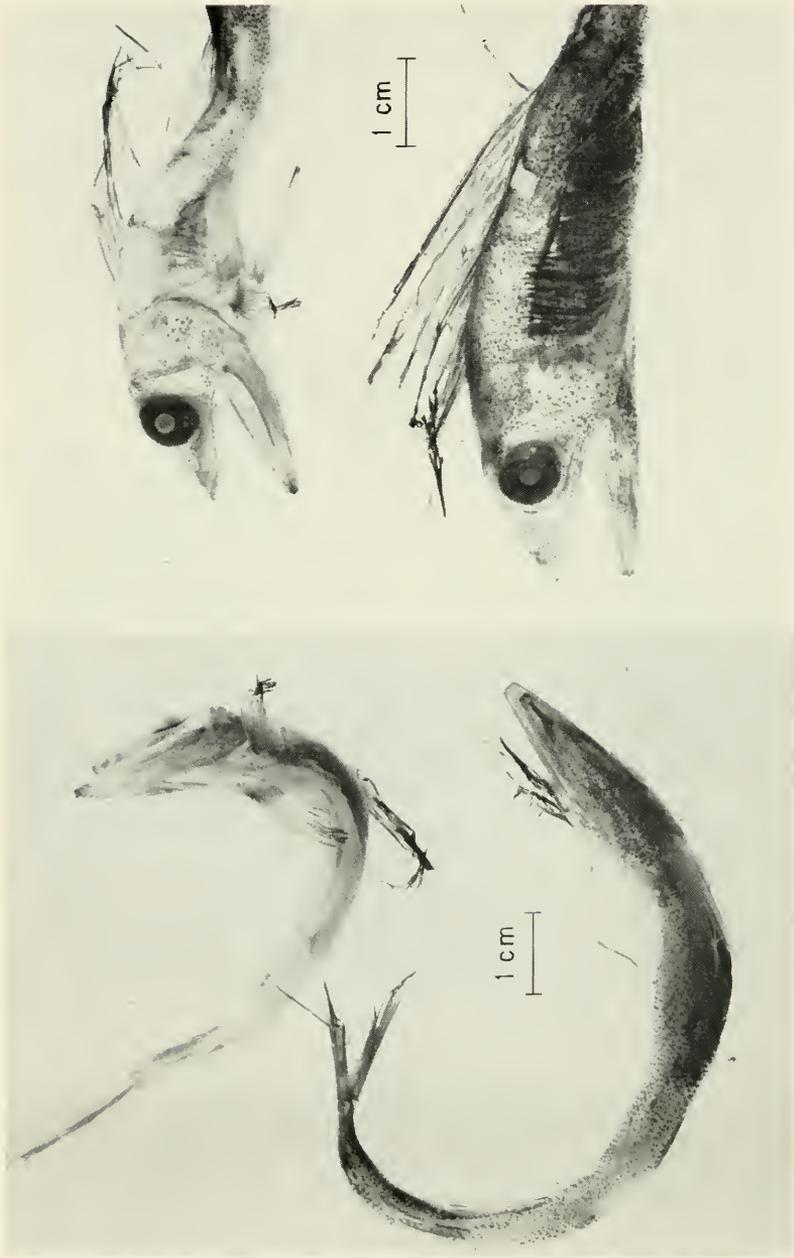


Figure 2. *Alcipisaurus ferax*, above left, has no melanophores on the belly, and, above right, dorsal origin behind pectoral origin and snout profile more or less straight. *A. brevirostris*, below left, has melanophores on the belly, and, below right, dorsal origin before pectoral origin and snout profile convex.

Reported here for the first time is a 40 mm lancetfish, MCZ 42377, taken by Isaacs-Kidd midwater trawl during a shakedown cruise of R/V ANTON BRUUN; 39°10'N, 71°52'W; 1015-1420 hr.; 9 Jan. 1963. The snout of this small fish is curved in profile, but there are no melanophores along the belly and the origin of the dorsal is well behind that of the pectoral. There are 16 rays in the anal fin, and 14 rays in the pectoral. I identify this specimen as *Alepisaurus ferox*, and include it in the above analysis. The 56 mm *Alepisaurus* figured by Maul (1946: 155, fig. 20) is referable to *A. brevirostris* on the basis of head shape and fin positions.

The three specimens of *Alepisaurus brevirostris* from 23°30'W (Table 2, Sta. 9, Coll. 2) constitute an eastward range extension for the species of some 1480 miles. Gibbs and Wilimovsky (in press) report no specimens east of 57°W.

FOOD OF ALEPISAURUS

(Table 2)

Morning longline sets produced far more lancetfish than night sets. Twenty per cent of the longline stations were made at night, but only one of 45 *Alepisaurus* taken was caught on a set which fished primarily during the dark hours. This may indicate that *Alepisaurus* is a day-time feeder, but might also suggest that the bait is not readily seen by the lancetfish at night. In the dark, luminescent animals, such as the hatchetfish *Sternoptyx*, may be more easily detected. No difference, however, was noted between the stomach contents of the night-caught *Alepisaurus* (Sta. 24) and those of fish from morning sets.

Most animals from *Alepisaurus* stomachs were in excellent condition. Few had been digested to any extent. Rofen (in press) suggests that digestion proceeds almost entirely in the intestine of *Alepisaurus*, and that the stomach serves only for storage. This may be a mechanism allowing the lancetfish to dine at opportunity and to digest at leisure.

TABLE 2

Alepisaurus stomach contents, DELAWARE 63-4, 27 April to 7 June 1963. Each collection represents one jar, usually the stomach contents from one fish. In some cases the stomach contents from two or more fish were put in one jar; these appear as single collections with the number of stomachs indicated. The fork length (FL) of the fish from which the stomach contents were obtained is given when known. Number of specimens and range of standard lengths of fishes in righthand column.

Station 1. 40°09'N, 49°54'W. 0645-1510 hr. 27 Apr. 1963

Collection 1, from *A. ferox*:

<i>Chiasmodon niger</i>	(Pisces, Percoidea)	2, 19 & 38 mm
<i>Dirtemus argenteus</i>	(Pisces, Berycomorphi)	1, 14 mm
<i>Urophycis</i> sp.	(Pisces, Anacanthini)	1, 21 mm
<i>Alepisaurus brevirostris</i>	(Pisces, Iniomi)	4, 50-75 mm
<i>Paralepis coregonoides</i>	(Pisces, Iniomi)	2, 41 & 45 mm
<i>Carinaria lamarcki</i>	(Mollusca, Heteropoda)	7
<i>Pterotrachea</i> sp.	(Mollusca, Heteropoda)	10
<i>Phrosina</i> sp.	(Crustacea, Amphipoda)	15
polychaete worm		1

Collection 2, from *A. ferox*:

<i>Schedophilus medusophagus</i>	(Pisces, Stromateoidea)	1, 120 mm
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Collection 3, from *A. ferox*:

<i>Carinaria lamarcki</i>	(Mollusca, Heteropoda)	3
<i>Pterotrachea</i> sp.	(Mollusca, Heteropoda)	39
<i>Phronima</i> sp.	(Crustacea, Amphipoda)	2
<i>Phrosina</i> sp.	(Crustacea, Amphipoda)	1

Collection 4, from *A. ferox*:

<i>Paralepis coregonoides</i>	(Pisces, Iniomi)	2, 48 & 49 mm
<i>Pyrosoma</i> sp.	(Tunicata, Thaliacea)	1
<i>Carinaria lamarcki</i>	(Mollusca, Heteropoda)	21
<i>Pterotrachea</i> sp.	(Mollusca, Heteropoda)	65
<i>Phronima</i> sp.	(Crustacea, Amphipoda)	1
<i>Phrosina</i> sp.	(Crustacea, Amphipoda)	7

Collection 5, from *A. ferox*:

2 small pieces of squid	(Mollusca, Cephalopoda)	
<i>Carinaria lamareki</i>	(Mollusca, Heteropoda)	2
<i>Pterotrachea</i> sp.	(Mollusca, Heteropoda)	31
<i>Brachyscelus</i> sp.	(Crustacea, Amphipoda)	1
<i>Phrosina</i> sp.	(Crustacea, Amphipoda)	16

Collection 6, from *A. ferox*:

<i>Alepisaurus brevirostris</i>	(Pisces, Iniomi)	1, 365 mm
<i>Notolepis rissoi</i>	(Pisces, Iniomi)	1, 89 mm
<i>Paralepis coregonoides</i>	(Pisces, Iniomi)	1, 62 mm
<i>Argonauta</i> sp.	(Mollusca, Cephalopoda)	1
<i>Carinaria lamareki</i>	(Mollusca, Heteropoda)	5
<i>Pterotrachea</i> sp.	(Mollusca, Heteropoda)	6
<i>Phrosina</i> sp.	(Crustacea, Amphipoda)	5
polychaete worm		1

Collection 7, from *A. ferox*:

<i>Alepisaurus brevirostris</i>	(Pisces, Iniomi)	1, 585 mm
<i>Paralepis</i> sp.	(Pisces, Iniomi)	1, 50 mm
<i>Octopodoteuthid?</i>	(Mollusca, Cephalopoda)	1
<i>Carinaria lamarcki</i>	(Mollusca, Heteropoda)	9
<i>Pterotrachea</i> sp.	(Mollusca, Heteropoda)	6
<i>Cavolinia</i> sp.	(Mollusca, Pteropoda)	2
<i>Brachyscelus</i> sp.	(Crustacea, Amphipoda)	20
<i>Phronima</i> sp.	(Crustacea, Amphipoda)	2
<i>Phrosina</i> sp.	(Crustacea, Amphipoda)	106
nemertean		1
polychaete worms		18

Station 2. 39°20'N, 44°50'W. 0650-1430 hr. 29 Apr. 1963

Collection 1, from *A. ferox*:

<i>Brama brama</i>	(Pisces, Percoidea)	2, 34 & 101 mm
<i>Alepisaurus brevirostris</i>	(Pisces, Iniomi)	1, 223 mm
<i>Paralepis coregonoides</i>	(Pisces, Iniomi)	1, 164 mm
<i>Paralepis</i> sp.	(Pisces, Iniomi)	36, 23-60 mm
<i>Sternoptyx diaphana</i>	(Pisces, Stomiatoidea)	1, 34 mm
fish larvae		13
doliolid test	(Tunicata, Thaliacea)	1
octopod	(Mollusca, Cephalopoda)	1
<i>Pterotrachea</i> sp.	(Mollusca, Heteropoda)	2
brachyuran	(Crustacea, Decapoda)	1
<i>Palinurus</i> larva	(Crustacea, Decapoda)	1
<i>Brachyscelus</i> sp.	(Crustacea, Amphipoda)	34
<i>Phronima</i> sp.	(Crustacea, Amphipoda)	2
<i>Phrosina</i> sp.	(Crustacea, Amphipoda)	9

Collection 2, from *A. ferox*:

<i>Lepidion lepidion</i>	(Pisces, Anacanthini)	2, 25 & 45 mm
<i>Alepisaurus brevirostris</i>	(Pisces, Iniomi)	3, 60-295 mm
<i>Notolepis rissoi</i>	(Pisces, Iniomi)	1, 105 mm
<i>Paralepis coregonoides</i>	(Pisces, Iniomi)	5, 30-108 mm
<i>Chiroteuthis</i> sp.	(Mollusca, Cephalopoda)	1 head
Taoniinae	(Mollusca, Cephalopoda)	147
<i>Carinaria lamarcki</i>	(Mollusca, Heteropoda)	5
<i>Pterotrachea</i> sp.	(Mollusca, Heteropoda)	1
brachyuran	(Crustacea, Decapoda)	1
small euphausiids	(Crustacea, Euphausiacea)	4
<i>Brachyscelus</i> sp.	(Crustacea, Amphipoda)	1
<i>Hyperoche</i> sp.	(Crustacea, Amphipoda)	1
<i>Phronima</i> sp.	(Crustacea, Amphipoda)	3
<i>Phrosina</i> sp.	(Crustacea, Amphipoda)	10

Station 4. 40°17'N, 36°07'W. 0630-1435 hr. 1 May 1963

Collection 1, from *A. ferox*:

<i>Carinaria lamarcki</i>	(Mollusca, Heteropoda)	7
<i>Pterotrachea</i> sp.	(Mollusca, Heteropoda)	1
<i>Phrosina</i> sp.	(Crustacea, Amphipoda)	2
<i>Eurydice</i> sp.	(Crustacea, Isopoda)	3

Collection 2, from *A. brevirostris*:

<i>Alepisaurus brevirostris</i>	(Pisces, Iniomi)	1, 64 mm
doliolid test, containing a		
<i>Phronima</i> sp.	(Tunicata, Thaliacea)	1
<i>Carinaria lamarcki</i>	(Mollusca, Heteropoda)	15
<i>Cavolinia</i> sp.	(Mollusca, Pteropoda)	4
<i>Brachyscelus</i> sp.	(Crustacea, Amphipoda)	17
<i>Phronima</i> sp.	(Crustacea, Amphipoda)	3
<i>Phrosina</i> sp.	(Crustacea, Amphipoda)	50
polychaete worms		2

Collection 3, from *A. brevirostris*:

<i>Carinaria lamarcki</i>	(Mollusca, Heteropoda)	17
<i>Pterotrachea</i> sp.	(Mollusca, Heteropoda)	1
<i>Cavolinia</i> sp.	(Mollusca, Pteropoda)	6
<i>Brachyscelus</i> sp.	(Crustacea, Amphipoda)	44
<i>Phronima</i> sp.	(Crustacea, Amphipoda)	2
<i>Phrosina</i> sp.	(Crustacea, Amphipoda)	125
<i>Platyscelus</i> sp.	(Crustacea, Amphipoda)	1
polychaete worm		1

Collection 4, from *A. brevirostris*:

<i>Anotopterus pharao</i>	(Pisces, Iniomi)	1, 277 mm
<i>Alepisaurus brevirostris</i>	(Pisces, Iniomi)	2, 48 & 56 mm
<i>Carinaria lamarcki</i>	(Mollusca, Heteropoda)	ca. 60
<i>Pterotrachea</i> sp.	(Mollusca, Heteropoda)	3
<i>Cavolinia</i> sp.	(Mollusca, Pteropoda)	7
<i>Brachyscelus</i> sp.	(Crustacea, Amphipoda)	69
<i>Phrosina</i> sp.	(Crustacea, Amphipoda)	256
polychaete worm		1

Station 6. 41°20'N, 29°20'W. 1805-1050 hr. 3-4 May 1963

Collection 1, from *A. ferox* 1365 mm FL:

<i>Paralepis coregonoides</i>	(Pisces, Iniomi)	1, 123 mm
<i>Carinaria lamarcki</i>	(Mollusca, Heteropoda)	23
<i>Pterotrachea</i> sp.	(Mollusca, Heteropoda)	12
<i>Phronima</i> sp.	(Crustacea, Amphipoda)	1
<i>Phrosina</i> sp.	(Crustacea, Amphipoda)	9

Station 9. 36°21'N, 23°30'W. 0635-1530 hr. 8 May 1963

Collection 1, from *A. ferox*:

<i>Urophycis</i> sp.	(Pisces, Anacanthini)	1, 9 mm
fish larva		1, 14 mm
<i>Carinaria lamarcki</i>	(Mollusca, Heteropoda)	1
<i>Pterotrachea</i> sp.	(Mollusca, Heteropoda)	29
<i>Brachyseclus</i> sp.	(Crustacea, Amphipoda)	1
<i>Phrosina</i> sp.	(Crustacea, Amphipoda)	2

Collection 2, from *A. ferox*:

<i>Lophius piscatorius</i>	(Pisces, Pediculati)	2, 40 & 48 mm
<i>Cubiceps gracilis</i>	(Pisces, Stromateoidea)	1, 65 mm
<i>Schedophilus medusophagus</i>	(Pisces, Stromateoidea)	1, ca. 60 mm
<i>Alepisaurus brevirostris</i>	(Pisces, Iniomi)	3, 69-178 mm
<i>Sternoptyx diaphana</i>	(Pisces, Stomiatoidea)	2, 24 & 27 mm
fish larvae		8
doliolid tests, one containing a <i>Phronima</i>		5
unident. squids, 4 spp.	(Mollusca, Cephalopoda)	4
<i>Carinaria lamarcki</i>	(Mollusca, Heteropoda)	9
<i>Pterotrachea</i> sp.	(Mollusca, Heteropoda)	220
<i>Phronima</i> sp.	(Crustacea, Amphipoda)	5
<i>Phrosina</i> sp.	(Crustacea, Amphipoda)	5

Station 14. 37°25'N, 29°10'W. 0610-1335 hr. 16 May 1963

Collection 1, from *A. ferox* 1585 mm FL:

<i>Schedophilus medusophagus</i>	(Pisces, Stromateoidea)	3, 33-40 mm
<i>Paralepis coregonoides</i>	(Pisces, Iniomi)	1, 129 mm
<i>Carinaria lamarcki</i>	(Mollusca, Heteropoda)	11
<i>Pterotrachea</i> sp.	(Mollusca, Heteropoda)	6

Station 15. 36°55'N, 32°32'W. 0400-1110 hr. 17 May 1963

Collection 1, from *A. ferox* 1437 mm FL:

<i>Lophius piscatorius</i>	(Pisces, Pediculati)	2, 62 & 80 mm
<i>Schedophilus medusophagus</i>	(Pisces, Stromateoidea)	1, 35 mm
<i>Alepisaurus brevirostris</i>	(Pisces, Iniomi)	1, 98 mm
<i>Sternoptyx diaphana</i>	(Pisces, Stomiatoidea)	3, 28-30 mm
doliolid test	(Tunicata, Thaliacea)	1
<i>Argonauta</i> sp.	(Mollusca, Cephalopoda)	3
<i>Phronima</i> sp.	(Crustacea, Amphipoda)	1
<i>Phrosina</i> sp.	(Crustacea, Amphipoda)	1

Collection 2, from *A. ferox* 1342 mm FL:

<i>Paralepis atlantica</i>	(Pisces, Iniomi)	1, 98 mm
<i>Sternoptyx diaphana</i>	(Pisces, Stomiatoidea)	1, 28 mm
doliolid test	(Tunicata, Thaliacea)	1
Taoniinae	(Mollusca, Cephalopoda)	1
<i>Phronima</i> sp.	(Crustacea, Amphipoda)	1
<i>Phrosina</i> sp.	(Crustacea, Amphipoda)	24
<i>Platyscelus</i> sp.	(Crustacea, Amphipoda)	2
nemerteans		18
polychaete worm		1

Station 16. 33°20'N, 39°50'W. 0410-1110 hr. 19 May 1963

Collection 1, from *A. ferox* 1265 mm FL:

<i>Cubiceps gracilis</i>	(Pisces, Stromateoidea)	2, 76 & 83 mm
<i>Alepisaurus brevirostris</i>	(Pisces, Iniomi)	7, 71-439 mm
<i>Macroparalepis affine</i>	(Pisces, Iniomi)	2, 64 & 114 mm
<i>Sternoptyx diaphana</i>	(Pisces, Stomiatoidea)	21, 8-31 mm
fish larvae		17
doliolid tests	(Tunicata, Thaliacea)	29
salps	(Tunicata, Thaliacea)	146
<i>Argonauta</i> sp.	(Mollusca, Cephalopoda)	2
<i>Japetella</i> sp.	(Mollusca, Cephalopoda)	7
unident. squids	(Mollusca, Cephalopoda)	2
<i>Carinaria lamarecki</i>	(Mollusca, Heteropoda)	2
<i>Pterotrachca</i> sp.	(Mollusca, Heteropoda)	remnants
<i>Cavolinia</i> sp.	(Mollusca, Pteropoda)	15
<i>Limacina</i> sp.	(Mollusca, Pteropoda)	3
<i>Brachyscelus</i> sp.	(Crustacea, Amphipoda)	36
<i>Phronima</i> sp.	(Crustacea, Amphipoda)	32
<i>Phrosina</i> sp.	(Crustacea, Amphipoda)	14
<i>Platyscelus</i> sp.	(Crustacea, Amphipoda)	42
polychaete worms		5

Collection 2, from *A. ferox* 1292 mm FL:

<i>Alepisaurus brevirostris</i>	(Pisces, Iniomi)	2, 113 & 124 mm
<i>Alepisaurus ferox</i>	(Pisces, Iniomi)	1, 267 mm
<i>Carinaria lamarecki</i>	(Mollusca, Heteropoda)	1
<i>Phrosina</i> sp.	(Crustacea, Amphipoda)	1
<i>Lanceola</i> sp.	(Crustacea, Isopoda)	1

Collection 3, from *A. ferox* 1325 mm FL:

<i>Alepisaurus brevirostris</i>	(Pisces, Iniomi)	1, 486 mm
<i>Paralepis atlantica</i>	(Pisces, Iniomi)	1, 84 mm
<i>Sternoptyx diaphana</i>	(Pisces, Stomiatoidea)	1, 22 mm
nemerteans		15

Collection 4, from *A. ferox*:

<i>Alepisaurus brevirostris</i>	(Pisces, Iniomi)	1, 437 mm
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Station 18. 31°00'N, 47°05'W. 0555-1320 hr. 21 May 1963

Collection 1, from *A. ferox* 1166 mm FL:

<i>Diplospinus multistriatus</i>	(Pisces, Scombroidea)	4, ca. 30 mm
<i>Cubiciceps gracilis</i>	(Pisces, Stromateoidea)	1, 84 mm
<i>Alepisaurus brevirostris</i>	(Pisces, Iniomi)	1, 154 mm
<i>Alepisaurus ferox</i>	(Pisces, Iniomi)	1, 91 mm
<i>Paralepis atlantica</i>	(Pisces, Iniomi)	1, 96 mm
<i>Paralepis elongata</i>	(Pisces, Iniomi)	5, 101-162 mm
<i>Sternoptyx diaphana</i>	(Pisces, Stomiatoidea)	9, 18-30 mm
fish larvae		35
<i>Pyrosoma</i> sp.	(Tunicata, Thaliacea)	1
<i>Abraliopsis</i> sp.	(Mollusca, Cephalopoda)	2

Station 21. 32°00'N, 56°10'W. 0605-1320 hr. 24 May 1963

Collection 1, from *A. ferox* 1068 mm FL:

<i>Brama brama</i>	(Pisces, Percoidea)	2, 37 & 55 mm
<i>Alepisaurus brevirostris</i>	(Pisces, Iniomi)	1, 463 mm
<i>Paralepis</i> sp.	(Pisces, Iniomi)	1, 75 mm
<i>Sternoptyx diaphana</i>	(Pisces, Stomiatoidea)	11, 21-32 mm
<i>Onychoteuthis</i> sp.	(Mollusca, Cephalopoda)	1
<i>Carinaria lamarecki</i>	(Mollusca, Heteropoda)	1
<i>Cavolinia</i> sp.	(Mollusca, Pteropoda)	1
<i>Phrosina</i> sp.	(Crustacea, Amphipoda)	1

Collection 2, from 3 *A. ferox* 941-1043 mm FL:

<i>Bothus</i> sp.	(Pisces, Heterosomata)	1, 19 mm
<i>Diplospinus multistriatus</i>	(Pisces, Scombroidea)	7, 20-163 mm
<i>Alepisaurus brevirostris</i>	(Pisces, Iniomi)	1, 81 mm
<i>Alepisaurus ferox</i>	(Pisces, Iniomi)	2, 82 & 131 mm
<i>Paralepis coregonoides</i>	(Pisces, Iniomi)	7, 68-99 mm
<i>Lobianchia doleini</i>	(Pisces, Iniomi)	1, 31 mm
<i>Sternoptyx diaphana</i>	(Pisces, Stomiatoidea)	5, 20-27 mm
fish larvae		7
doliolid tests	(Tunicata, Thaliacea)	4
salps	(Tunicata, Thaliacea)	2
<i>Argonauta</i> sp.	(Mollusca, Cephalopoda)	4
<i>Japetella</i> sp.	(Mollusca, Cephalopoda)	2
<i>Carinaria lamarecki</i>	(Mollusca, Heteropoda)	3
brachyuran	(Crustacea, Decapoda)	1
<i>Brachyscelus</i> sp.	(Crustacea, Amphipoda)	1
<i>Phronima</i> sp.	(Crustacea, Amphipoda)	4
<i>Phrosina</i> sp.	(Crustacea, Amphipoda)	3

<i>Lanceola</i> sp.	(Crustacea, Isopoda)	1
nemertean		1
polychaete worms		15

Station 23. 32°05'N, 59°10'W. 0605-1340 hr. 25 May 1963

Collection 1, from 4 *A. ferox* 772-1276 mm FL:

<i>Diplospinus multistriatus</i>	(Pisces, Scombroidea)	14, 27-131 mm
<i>Anoplogaster cornuta</i>	(Pisces, Berycomorphi)	1, 11 mm
<i>Regalecus glesne</i>	(Pisces, Allotriognathi)	1, 160 mm
leptocephalus larvae	(Pisces, Apodes)	5, ca. 60 mm
<i>Alepisaurus brevirostris</i>	(Pisces, Iniomi)	5, 82-383 mm
<i>Paralepis atlantica</i>	(Pisces, Iniomi)	2, 76 & 100 mm
<i>Paralepis coregonoides</i>	(Pisces, Iniomi)	5, 87-ca. 110 mm
<i>Paralepis elongata</i>	(Pisces, Iniomi)	2, 135 & 153 mm
<i>Sternoptyx diaphana</i>	(Pisces, Stomiatoidea)	12, 15-27 mm
bits of <i>Pyrosoma</i> test	(Tunicata, Thaliacea)	
united. squids	(Mollusca, Cephalopoda)	2
<i>Carinaria lamarki</i>	(Mollusca, Heteropoda)	2
<i>Pterotrachea</i> sp.	(Mollusca, Heteropoda)	1
<i>Brachyseclus</i> sp.	(Crustacea, Amphipoda)	3
<i>Phronima</i> sp.	(Crustacea, Amphipoda)	1
<i>Phrosina</i> sp.	(Crustacea, Amphipoda)	26
<i>Platyseclus</i> sp.	(Crustacea, Amphipoda)	1
polychaete worms		15

Station 24. 32°45'N, 64°36'W. 1855-0825 hr. 26-27 May 1963

Collection 1, from *A. ferox* 1146 mm FL:

<i>Anoplogaster cornuta</i>	(Pisces, Berycomorphi)	1, 45 mm
<i>Paralepis elongata</i>	(Pisces, Iniomi)	2, 127 & 138 mm
<i>Sternoptyx diaphana</i>	(Pisces, Stomiatoidea)	2, 27 & 30 mm
<i>Octopodoteuthis</i> sp.	(Mollusca, Cephalopoda)	1
<i>Pholidoteuthis</i> sp.	(Mollusca, Cephalopoda)	1
polychaete worm		1

Station 29. 32°50'N, 68°15'W. 0610-1340 hr. 1 June 1963

Collection 1, from *A. ferox* 1028 mm FL:

<i>Diplospinus multistriatus</i>	(Pisces, Scombroidea)	1, 116 mm
<i>Sternoptyx diaphana</i>	(Pisces, Stomiatoidea)	2, 20 & 22 mm
doliolid test	(Tunicata, Thaliacea)	1
<i>Phronima</i> sp.	(Crustacea, Amphipoda)	1
<i>Phrosina</i> sp.	(Crustacea, Amphipoda)	1
polychaete worms		3

Station 31. 34°45'N, 71°15'W. 0610-1515 hr. 2 June 1963

Collection 1, from 5 *A. ferox* 1039-1254 mm FL:

<i>Diplospinus multistriatus</i>	(Pisces, Scombroidea)	1, 131 mm
<i>Brama brama</i>	(Pisces, Percoidea)	2, 40 & 95 mm
<i>Anoplogaster cornuta</i>	(Pisces, Berycomorphi)	1, 75 mm
<i>Alepisaurus brevirostris</i>	(Pisces, Iniomi)	2, 124 & 131 mm
<i>Macroparalepis affine</i>	(Pisces, Iniomi)	1, 150 mm
<i>Paralepis atlantica</i>	(Pisces, Iniomi)	5, 93-119 mm
<i>Paralepis coregonoides</i>	(Pisces, Iniomi)	14, 79-120 mm
<i>Paralepis elongata</i>	(Pisces, Iniomi)	2, 61 & 125 mm
<i>Argyroplecus aculeatus</i>	(Pisces, Stomiatoidea)	1, 32 mm
<i>Sternoptyx diaphana</i>	(Pisces, Stomiatoidea)	6, 14-29 mm

Station 33. 36°27'N, 67°50'W. 0610-1505 hr. 3 June 1963

Collection 1, from *A. ferox* 811 mm FL:

<i>Diplospinus multistriatus</i>	(Pisces, Scombroidea)	5, 61-194 mm
<i>Paralepis coregonoides</i>	(Pisces, Iniomi)	3, 67-106 mm
<i>Sternoptyx diaphana</i>	(Pisces, Stomiatoidea)	3, 20-29 mm
<i>Pterotrachea</i> sp.	(Mollusca, Heteropoda)	2
<i>Phrosina</i> sp.	(Crustacea, Amphipoda)	2
polychaete worms		2

Station 37. 39°23'N, 68°33'W. 0620-1445 hr. 7 June 1963

Collection 1, from *A. brevirostris* 778 mm FL:

Tetraodontidae	(Pisces, Plectognathi)	1, 16 mm
<i>Helicolenus dactylopterus</i>	(Pisces, Scleroparei)	2, 24 & 25 mm
<i>Lepidion lepidion</i>	(Pisces, Anacanthini)	2, 42 & 42 mm
<i>Syngnathus pelagicus</i>	(Pisces, Solenichthyes)	1, 113 mm
<i>Macroparalepis affine</i>	(Pisces, Iniomi)	1, 138 mm
Ommastrephidae	(Mollusca, Cephalopoda)	2
Taoniinae	(Mollusca, Cephalopoda)	6
<i>Brachyscelus</i> sp.	(Crustacea, Amphipoda)	3
<i>Phronima</i> sp.	(Crustacea, Amphipoda)	1
<i>Phrosina</i> sp.	(Crustacea, Amphipoda)	2

With regard to the size of its prey, *Alepisaurus* practices no discrimination. Adapted for swallowing large prey (Marshall, 1955:330), it will also readily devour small creatures. A 1265 mm *A. ferox* (Sta. 16, Coll. 1) had eaten seven *A. brevirostris* ranging from 71 to 439 mm in standard length; another *A. ferox* (Sta. 1, Coll. 7) contained a 585 mm *A. brevirostris* in addition to 106 hyperiid amphipods, each about 20 mm long.

Lancetfish stomachs most commonly contained hyperiid amphipods, heteropods, paralepidids, *Sternoptyx*, and other *Alepisaurus*. At least one of these groups was found at every station, and three or more occurred simultaneously in 66 per cent of the collections. Of the 32 collections, amphipods occurred in 78 per cent, heteropods in 72 per cent, paralepidids in 59 per cent, *Alepisaurus* in 56 per cent, and *Sternoptyx* in 44 per cent. Since these animals do occur so regularly in the stomachs, they must habitually frequent the same depths as does *Alepisaurus*.

Stomach contents reflected local abundances. Heteropods occurred in 17 out of 19 (89%) of the stomachs from stations 1 through 15, and they were also a major constituent of the midwater hauls. Heteropods were found in only 6 out of 13 (46%) of the stomachs from stations 16 through 37. In contrast, *Sternoptyx* had been eaten by 77 per cent of the fish from stations 16 through 37, but by only 44 per cent of the fish from stations 1 through 15. On the southerly leg of the cruise, fishes predominated both in stomach contents and in the midwater haul.

Myctophid fishes were notably absent from most stomach contents. Only one was found, a 31 mm *Lobianchia dofleini* (Sta. 21, Coll. 2). None occurred in the fish from station 9, although a one-hour midwater trawl at station 12 took 101 myctophids of a dozen species. The commonness of these small fishes in midwater hauls makes their absence from *Alepisaurus* stomachs particularly puzzling. Myctophids are noted vertical migrators (Marshall, 1960). If *Alepisaurus* does not migrate extensively, and if its principal depth differs from the day and night levels of myctophids, the duration of the lancetfish's encounter with myctophids would be brief during any diurnal cycle, and consumption of them therefore low.

Completely absent from the stomach contents were the characteristic middle-depth fishes *Gonostoma*, *Stomias*, and *Chauliodus*. These fishes are distributed mainly between 200 and 1500 meters (Haffner, 1952; Marshall, 1960). Their absence from *Alepisaurus* stomachs, and the presence of primarily epipelagic fishes such as *Cubiceps*, *Brama*, and *Paralepis elongata* strengthens the belief (Gibbs and Wilimovsky, in press) that the lancetfish frequents the upper layers.

Little difference was noted between food of *Alepisaurus ferox* and *A. brevirostris*. *A. brevirostris* may favor invertebrates, particularly the hyperiid amphipod *Phrosina*. All *A. brevirostris* stomachs contained these amphipods, but only 75 per cent of those from *A. ferox* did. There were 256 amphipods in an *A. brevirostris*

from Station 4 (Coll. 4), and only two in the *A. ferox* from the same station (Coll. 1). The maximum number of *Phrosina* from a single *A. ferox* was 106, and the average number per fish was 9.3. The maximum number of *Phrosina* from a single *A. brevirostris* was 256; 108.3 was the average. Fishes were more common in *A. ferox* stomachs. *Sternoptyx* and paralepidids occurred in 50 and 64 per cent, respectively, of *A. ferox* stomachs, but were found in 0 and 25 per cent, respectively, of the *A. brevirostris* stomachs. Since stomach contents were obtained from only four *A. brevirostris*, and since three came from one station, these comparisons are inconclusive.

Rarely encountered fishes found in the stomach contents were *Anotopterus pharao* (Sta. 4, Coll. 4), *Regalecus glesne* (Sta. 23, Coll. 1), and four pelagic young of *Lophius piscatorius* (Sta. 9, Coll. 2; Sta. 15, Coll. 1).

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B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS.

APRIL 10, 1964

NUMBER 202

THE BLIND SNAKES (*TYPHLOPS*) OF HAITI WITH DESCRIPTIONS OF THREE NEW SPECIES¹

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When the Herpetology of Hispaniola (Cochran, 1941) was published only 24 specimens of *Typhlops* were available from the entire island. Recent collecting (1950-1962) in Haiti has produced 93 specimens of blind snakes from that country alone, most of them now in the Museum of Comparative Zoology.

Part of the field work was made possible by the following grants to the Museum of Comparative Zoology: National Science Foundation Grants NSF 16066, NSF 5634, and one from the American Philosophical Society. The six specimens from Gonave Island were obtained by Philip S. Humphrey collecting for the Yale Peabody Museum and the University of Florida. A description of the various expeditions is given in Williams *et al.*, 1963.

I wish to express my appreciation to Ernest E. Williams who was responsible for getting this material together and making it possible for me to study it. Also I wish to thank Doris M. Cochran for permission to study the type of *Typhlops sulcatus*. Miss A. G. C. Grandison supplied counts and descriptive notes on four specimens in the British Museum. Nicholas Strekalovsky made the drawings of the new species herein described.

The following abbreviations are used to designate the collections where these specimens are deposited: AMNH, American Museum of Natural History; CM, Carnegie Museum; MCZ, Museum of Comparative Zoology; UF, University of Florida Museum; USNM, United States National Museum; YPM, Yale Peabody Museum.

¹Notes on Hispaniolan herpetology no. 10.

Examination of this material discloses that in addition to the two species previously known from Haiti, *lumbricalis* and *pusillus*, there are three forms new to science. All of the five species represented in this collection have the following characters in common: relatively narrow strap-like rostrals; completely divided nasals; preocular contacting the third upper labial only; scale rows either 20-20-20 or 20-20-18; at least one pair of enlarged parietal scales; four upper labials; three lower labials; and clearly visible eyes. With this great similarity they also show distinctive differences in the number of middorsal scale rows, number of preoculars, shape and size of ocular, shape of head, and color.

In number of middorsal scales these snakes may be divided into two distinct groups: those with a relatively low number (240-330), two species, and those with over 385, three species. The three new forms are all in the group with the high number of middorsal scales. Two of these are further distinguished by having very small pointed heads.

*TYPHLOPS CAPITULATUS*¹ sp. nov.

Figure 1

Holotype: MCZ 62636. From Manneville, Haiti, at the northwest end of Lake Saumâtre. Collected by A. S. Rand and J. Lazell, 10 August 1960.

Paratype: MCZ 69006. From the same locality as the type. Collected by E. E. Williams and A. S. Rand, 13-14 August 1959.

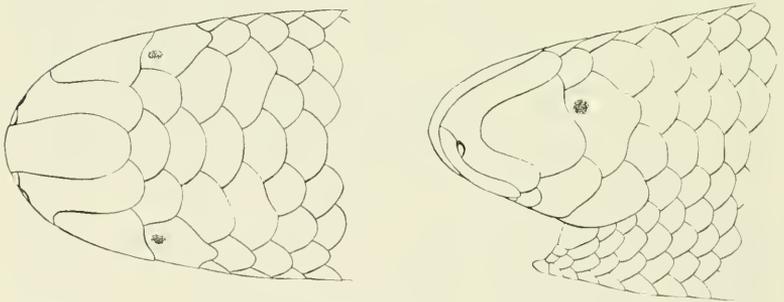


FIG. 1. *Typhlops capitulatus* sp. nov. Type MCZ 62636. From Manneville, Haiti. Dorsal and lateral views.

¹From the Latin "having a small head."

Diagnosis: A slender small-headed species of *Typhlops* characterized by the following combination of characters: high number of dorsal scales, 385-400; scale rows 20-20-20; dorsal color extending on to venter, a white anal spot; preocular almost triangular; head small and pointed; ocular almost as wide as high.

Description: Sides of head tapering from about the level of the seventh middorsal scale. Rostral narrow, its width one-third that of the head, not extending to a line connecting the eyes; nasals completely divided by a suture that extends from the second upper labial to the rostral; preocular almost triangular, approximately as high as wide and in contact with the third upper labial, its anterior edge curved but not elongated. Ocular broad, but little higher than wide, its posterior edge strongly convex (Fig. 1). Two pairs of enlarged parietal scales; two postoculars on each side. Eye small, scale rows around body 20-20-20, dorsal scales from rostral to caudal spine about 400.

Color: Light brown above, somewhat paler below although pigmented, venter with scattered white scales, anal region and underside of tail white, dorsal color fades gradually on head to entirely unpigmented snout.

Size: Total length 205 mm, head width at level of eyes 2.7 mm, diameter at midbody 4 mm, tail slightly longer than wide.

Variation: MCZ 69006 is a very small specimen, total length 93 mm, and is pale brown above and below although the characteristic pattern of pigmentation can be seen with magnification. This specimen has about 385 dorsal scales from rostral to spine. In detail of head scutellation it agrees with the type.

Remarks: This species is most closely related to the species on Gonave Island, described below, from which it may be distinguished by the shape of the preocular.

TYPHLOPS GONAVENSIS sp. nov.

Figure 2

Holotype: YPM 3003. From Point à Raquette, on the south shore of Gonave Island, Haiti. Collected by Philip S. Humphrey and Sarita Van Vleck, 9 April 1959.

Paratypes: YPM 3004, and UF A943. With the same data as the holotype.

Diagnosis: A slender small-headed species of *Typhlops* characterized by the following combination of characters: high number of dorsal scales, 409-423; scale rows 20-20-20; dorsal color

extending on to venter, a white anal spot; may be distinguished from *capitulatus* which it most closely resembles by the distinctive shape of the preocular which is wider than high and narrowest anteriorly.

Description: Sides of head tapering from about the level of the seventh middorsal scale. Rostral narrow, its width one-third that of the head, not extending to the level of the eyes; nasals completely divided by a suture that extends from the second upper labial to the rostral; preocular wider than high, narrowest anteriorly (Fig. 2), in contact with the third upper labial; ocular small but little higher than wide, its posterior edge strongly convex; two pairs of enlarged parietals; two postoculars on each side; eye small; scale rows around body, 20-20-20; middorsal scales from rostral to spine about 418.

Color in preservative: Dark purplish brown above, somewhat paler below but heavily pigmented with an irregular white area in anal region. Dorsal color fades gradually on head to unpigmented snout. Color in life (from notes by Sarita Van Vleek): Reddish brown inferiorly, grading to burnt umber on tail, venter purplish gray anteriorly becoming pale gray-brown posteriorly.

Size: Total length 189 mm, tail 4.2 mm; head width at level of eyes 2.7 mm; diameter at midbody 4 mm; tail slightly longer than wide.

Remarks: This species is most closely related to *capitulatus* on the mainland of Hispaniola and apparently has differentiated from that species following isolation on Gonave Island. It is easily recognized by the peculiar shape of the preocular. These two species have the smallest and the most pointed heads of any of the known Antillean *Typhlops*.

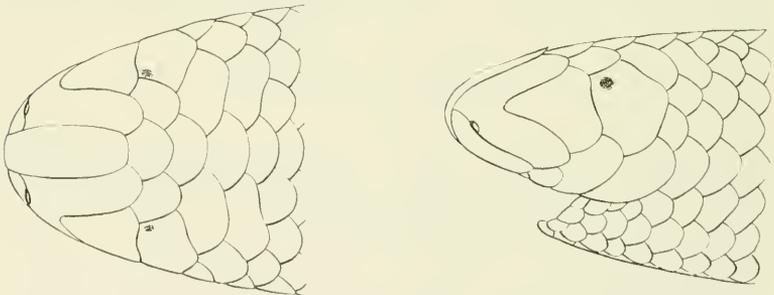


FIG. 2. *Typhlops gonavensis* sp. nov. Type YPM 3003. From Point à Raquette, Gonave Island. Dorsal and lateral views.

TYPHLOPS HAITIENSIS sp. nov.

Figure 3

Holotype: MCZ 62635. From Manneville, Haiti. Collected by A. S. Rand and J. Lazell, 10 August 1960.

Paratypes (14): MCZ 69007-12, from Manneville, Haiti. Collected by E. E. Williams and A. S. Rand, 13-14 August 1959. USNM 117273-74, 117276, from Trou Caiman, Haiti. Collected by A. Curtiss, 18 February 1943. CM 38804-8, from Manneville, Haiti. Collected by George Whiteman, 1963. Manneville is near the northwest end of Lake Saumâtre, on the north edge of the Cul de Sac Plain; Trou Caiman is a small freshwater lake just west of Manneville.

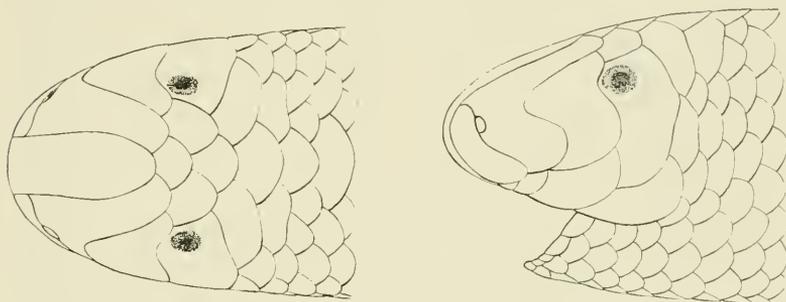


FIG. 3. *Typhlops haitiensis* sp. nov. Type MCZ 62635. From Manneville, Haiti. Dorsal and lateral views.

Diagnosis: A species of *Typhlops* characterized by a high number of dorsal scales, 400-452; scale rows 20-20-20; dorsal color extending on to venter, white anal spot; preocular higher than long, in contact with the third upper labial; ocular narrow, more than twice as high as wide; head broadly rounded as seen from above.

Description: Snout, as viewed from above, truncate and broadly rounded, not tapering; rostral width about one-fourth the width of the head, rostral extending to the level of the eyes; nostrils lateral; nasals completely separated by a suture extending from the second upper labial to the rostral. The preocular higher than wide in contact with the third upper labial only (Fig. 3). One pair of enlarged strap-like parietals each as wide as two body scales; a single postocular; eye large and conspicuous. Scale rows around body 20-20-20, dorsal scales from rostral to tail spine about 435.

Color: The head scales have dark brown centers and relatively wide light margins giving the top of the head a striped appearance; dorsal brown color extends on to the venter where it is interrupted by irregular light areas along the midventral line. The dorsal scales are dark brown with light margins. The light margins are aligned giving the effect of fine light longitudinal lines.

Size: Total length 240 mm, tail 5 mm, width of head at level of eyes 3.5 mm, diameter at midbody 5 mm, tail slightly longer than wide.

Variation: The 14 paratypes agree in details of head scutellation, and in having 20-20-20 scale rows. The number of dorsal scales in this series varies from 400 to 452. The number of enlarged parietal scales also varies. All have one pair of greatly enlarged strap-like scales; some have a second pair equally enlarged, while others show a graded change from this condition to where the second pair is not distinguishable from the body scales. All have a single postocular. The color varies from dark to light brown in the large specimens. The three smallest specimens are very pale above and below, but under magnification it can be seen that the dorsal pigment extends on to the venter in the same pattern observed in the larger specimens. The extent of the light areas on the venter varies considerably; the three specimens from Trou Caiman have little or no brown pigment on the venter, while MCZ 69012 has the venter almost entirely pigmented.

TYPHILOPS PUSILLUS Barbour

The 27 specimens examined from the mainland of Hispaniola agree with those reported by Cochran (1941) except that in this series all have two postoculars between the fourth upper labial and the parietal.

The greatest variation is shown by the three specimens from Gonave Island. These agree with the mainland forms in possessing divided preoculars, two postoculars and in other details of head scutellation. They differ from the mainland specimens in having a lower number of dorsal scales (258-268 compared with 285-319 for the specimens from Bombardopolis on the northwest peninsula). They also differ in color as they are brown above and pale below and in this respect resemble *lumbricalis*.

TYPHILOPS LUMBRICALIS (Linnaeus)

This species has the most extensive range of any of the Antillean *Typhlops*. It has been found on Hispaniola, Cuba, several islands in the Bahamas, and in British Guiana, South America. Throughout this range, it is remarkably consistent in characters: scale rows 20-20-18, rarely 20-18-18; usually one pair of enlarged parietals and usually two postoculars. The middorsal scales range from 240-320 (Legler, 1959).

The established lack of variation in the number of scale rows in various parts of its extensive range makes it very surprising to find a population of this species on the southwest peninsula of Haiti that is highly variable.

There are 41 specimens of *lumbricalis* at hand from the southwest peninsula, representing several localities from Miragoane to Jeremie, and one specimen from Grand Cayemite Island. In number of rows of scales around the body they vary as follows: 22-20-20 (2), 20-20-20 (27), 20-20-18 (12). The number of enlarged parietals also varies: 1L-1R (14), 1L-2R (11), 2L-1R (5), 2L-2R (10). All but one have two postoculars on each side. The exception has the upper postocular on each side fused to the parietal. The number of middorsal scales ranges from 273-324, average 301. Although this is within the known range of variation for *lumbricalis*, it is higher than for most specimens of that species from other parts of Hispaniola. The shape and arrangement of the head scales is the same as in other populations. The color pattern is also the same. Although the number of rows of scales is both high and variable, this population can not be distinguished from *lumbricalis* by any character or combination of characters, and it appears to be one variable population rather than a mixture of two or more forms.

In addition to the specimens from the southwest peninsula, there are five specimens from Port-au-Prince and Manneville. These have the scales in 20-20-18 rows, middorsal scales ranging from 261 to 290, and are typical *lumbricalis*.

Grant (1956) discusses four specimens of *lumbricalis*, three from Eaux Gaillées and one from Port-au-Prince. The number of middorsal scales ranges from 257 to 275 and indicates that these are *lumbricalis* as currently defined. There are also four specimens of *lumbricalis* in the British Museum from Haiti, two from Pont Beudet and two from Hinche. Miss A. G. Grandison supplied the counts for these and the middorsal scales

range from 260-294 — well within the range of variation for *lumbricalis*. The average number of dorsal scales for all 13 specimens from Haiti outside the southwest peninsula is 279 with a range of 257-294.

DISCUSSION

The five species now known from Haiti are similar in having a maximum of 20 scale rows, preocular in contact with the third upper labial only, and a relatively narrow rostral. Yet with this apparent similarity the five forms represent three distinct phyletic lines of *Typhlops*.

1. The group including *lumbricalis* and *pusillus* is distinguished by having a low number of middorsal scales, 240-330. These two forms on Hispaniola are readily separated from each other by the presence of a single preocular in *lumbricalis* and by a divided preocular in *pusillus*.
2. A slender, small-headed group with a high number of middorsal scales, 385-423; this includes two species, *gonavensis* on Gonave Island, and *capitulatus* on the mainland. These are the most distinctive *Typhlops* in the area as no other species known from the Antilles has such a small head. The two forms are obviously closely related and are probably insular populations of what was originally one form. The two may be distinguished from each other by the shape of the preocular.
3. The third group is represented by one species, *haitiensis*. Like the small-headed forms it has a very high number of middorsal scales (400-454) but unlike the species of that group it has a broadly rounded truncate snout, as well as a distinctively shaped preocular and ocular. Of the five species known from Haiti it is the only one that typically has a single postocular. The others have two postoculars with one occurring as an uncommon variant.

These three different groups do not seem to be closely related to each other. The distributional data, although limited, seem to support the concept that only unrelated forms can occur sympatrically, and even then probably by occupying different ecological niches. For example, *lumbricalis* and *pusillus* appear very similar in body proportions and scutellation, and differ in the number of preoculars. A divided preocular is also known as a rare variant in *lumbricalis* (Legler, 1959).

Probably *pusillus* was derived from *lumbricalis* at sometime when Hispaniola was a series of islands.

Today *pusillus* occurs on the northwest peninsula and ranges across the northern part of the island at least as far as the southern shore of Bahia de Samana. Cochran (1941) reported one specimen from Sanchez and I have examined four from Samana (AMNH 50353-56).

The range of *lumbricalis* includes all of the southwest peninsula and extends eastward along the southern coast where it is known from Barahona (Noble and Hassler, 1933)¹ and San Pedro de Macoris. On the northern coast it is known as far westward as Puerto Plata. The range of the two species overlap on the northeast coast. Whether they are ecologically separated in this area of overlap can not be determined from the available data. At Manneville, the one locality where three species have been found, each species represents a different group.

In view of the large number of *Typhlops* in collections from the northwest peninsula and all of them *pusillus*, it would appear that *lumbricalis* does not occur there. The opposite is true of the southwest peninsula where extensive collecting has revealed only *lumbricalis*.

TYPHLOPS SULCATUS Cope

The finding on Haiti of species with a high number of dorsal scales raised the question of what relationship these forms might have with *sulcatus* on nearby Navassa Island, the only other *Typhlops* known from the Antilles with both 20 scale rows and a high (397) number of dorsal scales. As no other specimens of *sulcatus* have been collected since Cope (1868) described it on the basis of one specimen, the type was examined.

As the type appears today, it is a specimen that was preserved just prior to shedding; in fact, the old head shields have been shed (probably after preservation), and the new head shields are represented by soft raised areas outlined by deep sulci that mark the position of the original sutures. The extensions of the nasal sutures from the nostril to rostral are little more than faint lines but sufficient to indicate that this species does have completely divided nasals. Since Cope (1868) also

¹The specimen with 385 middorsal scales from Alta Vela Island reported as *lumbricalis* by Noble and Hassler (1933) is not that species as currently defined. A preliminary examination discloses this specimen as more closely related to *sulcatus* than it is to the mainland forms.

described this specimen as having completely divided nasals he may have seen it with the nasal plates in place when the sutures might have been more distinct. Other characters of this specimen are: very long parietals extending down the posterior edge of the oculars to well below the level of the eyes, and a single postocular; both of these characters are well shown by Cochran (1941, p. 310, fig. 88). As stated by Cope the body is more slender than that of *lumbricalis*; it is also distinguished from that species by the high number of middorsal scales. From the species on Haiti with middorsal scales over 385, it is distinguished by the shape and size of the ocular and preocular, and by the very long parietals.

This specimen has the snout tapered in front of the eyes very much like *monensis* but not at all like the narrow-headed forms on Haiti which have the entire head tapered from well back of the eyes. Until such time as more specimens are available it seems best to recognize *sulcatus* as a distinct species.

The other characters for this species mentioned in the literature, trilobate snout and incomplete nasal sutures, are conditions that are associated with shedding (Richmond, 1961). The extension of the nasal suture from nostril to rostral is very faint on most specimens of small *Typhlops* and difficult to see at best. As the nasal plate thickens, prior to shedding, the nasal suture from labial to nostril becomes more conspicuous while the suture from nostril to rostral becomes fainter and may actually disappear as a suture although its presence can usually be detected as a fine dark line crossing an otherwise smooth area of the nasal plate. Also associated with shedding are the deep sulci representing the sutures between the other head scales.

Since *sulcatus* is known from only one specimen, and that one shedding, it is little wonder that it has been variously described as having complete nasal sutures (Cope, 1868), incomplete nasal sutures (Cochran, 1924, 1941), and complete on one side and incomplete on the other (Legler, 1959).

TYPHLOPS

Key to the forms occurring in Haiti

- A. Preocular divided *pusillus*
- AA. Preocular single B
- B. Ocular narrow and high, over twice as high as wide, posterior edge of ocular almost straight, preocular higher than wide (400-460 dorsal scales) (Fig. 3) *haitiensis*

- BB. Ocular wide, but little higher than wide, posterior edge strongly convex, preocular as wide or wider than high C
 C. Venter unpigmented, same color as underside of tail, less than 330 dorsal scales, head rounded *lumbricalis*
 CC. Dorsal dark color extending on to venter, underside of tail and anal area white, 380-430 dorsal scales, head tapering D
 D. Preocular longer than high, anterior angle acute (Fig. 2) *gonavensis*
 DD. Preocular almost triangular, anterior angle rounded (Fig. 1) *capitulatus*

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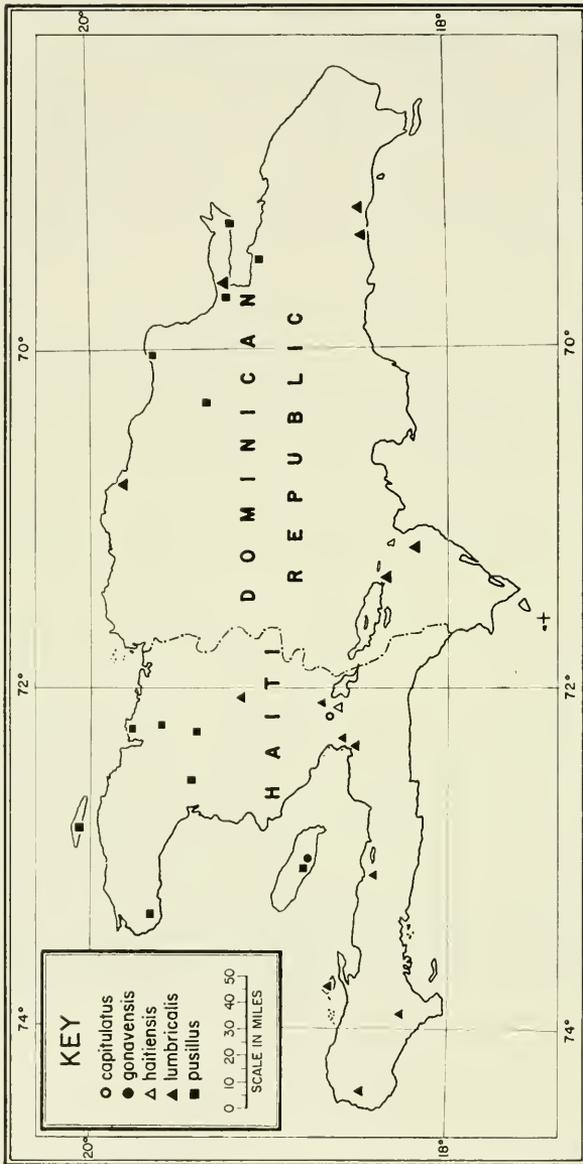


FIG. 4. Distribution of *Typhlops* in Haiti, including published records from Cochran (1941) for *pusillus* and *lumbricalis*. The cross (+) at lower center of the map indicates the island of Alta Vela from which the problematical specimen resembling *sulcatatus* is derived.

B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS.

APRIL 10, 1964

NUMBER 203

A NEW CAPROMYID RODENT FROM THE QUATERNARY OF HISPANIOLA

BY CLAYTON E. RAY¹

U. S. National Museum

During the early part of 1963, Mr. Robert Allen and I conducted field work on several Caribbean islands under the joint auspices of the Museum of Comparative Zoology at Harvard College and the Florida State Museum, supported in part by National Science Foundation grants GB 178 and G 16066. Our primary objective was the collection of vertebrates, both Recent and fossil. The period from 17 March through 4 April was spent in the Dominican Republic, during which time we received the cordial cooperation of Prof. Eugenio de Jesús Marcano F. and Ing. Emile de Boyrie Moya, Universidad Autonoma de Santo Domingo. The cave on the north flank of the Sierra de Neiba, from which *Antilloagale marcanoï* Patterson 1962 was obtained in 1958, was revisited on 31 March through 2 April with the specific objective of securing supplementary material of this form. Although we had little success in this, meager evidence of two additional taxa was obtained: a single metatarsal of a tiny species of *Acratocnus* (Hooijer and Ray, in press), and a single cheek-tooth (MCZ 7675) of a large caviomorph rodent, described below. These specimens derive from the same thin reddish brown cave earth in the first chamber, from which the 1958 collections were obtained (see Patterson, 1962). This deposit contains a moderately rich accumulation of well-preserved remains (including skulls) of the common Hispaniolan caviomorphs, among which are interspersed a few fragments and isolated elements of other taxa, including *Solenodon*, *Nesophontes*, bats, and birds.

¹ Published by permission of the Secretary of the Smithsonian Institution.

Through the courtesy of the various curators in charge, I have had at my disposal the rich collections of fossil and Recent eavio-morph rodents in the American Museum of Natural History, the Museum of Comparative Zoology (MCZ), and the U. S. National Museum (USNM). Comparison with relevant genera in these collections shows that the single tooth is that of a capromyid having its closest affinities with *Plagiodontia*,² but referable to none of the described species of that genus (Johnson, 1948). The peculiarities of the tooth are sufficiently striking to provide adequate basis for characterizing the species which it represents. It is probable that the species will require a new genus for its accommodation when it is better known, but it may be assigned with question to *Plagiodontia* pending discovery of additional material. The find provides yet another example of the novelties that reward exploration in Hispaniola, the least known, paleontologically, of the Greater Antilles.

RODENTIA

CAPROMYIDAE

PLAGIODONTIA? ARAEUM³ sp. nov.

Type: MCZ no. 7675, isolated left upper cheektooth, almost certainly the fourth (deciduous) premolar; damaged slightly along the posterolabial wall; the only known specimen of the species.

Horizon and locality: Late Pleistocene or Recent; first chamber of unnamed cave 2 kilometers SE of Rancho de La Guardia, Municipio de Hondo Valle, Provincia de San Rafael, República Dominicana. The coordinates of Rancho de La Guardia as given in Gazetteer no. 33 of the United States Board on Geographic Names are 18°43'N, 71°39'W.

Diagnosis: Differing from the upper cheekteeth of all other members of the genus *Plagiodontia* in its absolutely greater maximum diameter of occlusal surface and in its extreme antero-lingual-posterolabial compression (to which the specific name alludes).

²It might be suspected on the basis of size and general structure that the specimen is an upper cheektooth (as yet unknown) of *Quemisia*. However, the walls of each reentrant fold in the upper cheekteeth of *Quemisia* would undoubtedly be tightly appressed as they are in the lower cheekteeth. Though the folds in MCZ 7675 are narrow, their walls are not appressed (Fig. 1).

³ἀραιόγυ· narrow.

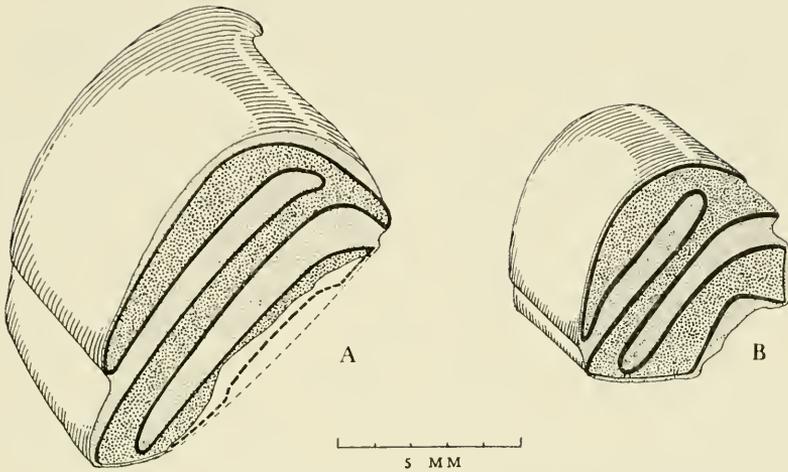


Figure 1. Occlusal views of (A) MCZ 7675, left DP⁴ of *Plagiodontia aracam*, the holotype, and (B) MCZ 35314, right DP⁴ (reversed) of *P. hylacum*. Fine stippling represents cementum; coarse stippling, dentine. Drawn by Sue Hirschfeld under NSF GB 178.

Description: Anterior margin of tooth strongly convex as in DP⁴ of *Plagiodontia*, not flattened as in M¹-M³; incipient anterolabial fold absent, as in all *Plagiodontia*, excepting *P. acdium* (Johnson, 1948); reëntrant folds relatively long and narrow, parallel-sided; lingual reëntrant with slight posterad flexure at internal extremity, not observed in other *Plagiodontia*; labial reëntrant with concomitant flexure near its mouth; posterolabial concavity in enamel wall shallow in comparison to other species; longitudinal axis of tooth curved (convex anterolingually) as in upper cheekteeth of other *Plagiodontia*.

Measurements: All measurements of DP⁴ are given in mm in the following table. Anterolingual-posterolabial diameter of occlusal surface in MCZ 7675 is estimated owing to damage along posterolabial wall of crown.

	<i>P. aracum</i> MCZ 7675	<i>P. ipmaeum</i> USNM 254376, right DP ⁴	<i>P. hylaeum</i> MCZ 35314, right DP ⁴
Maximum diameter of occlusal surface (A)	11.0	8.2	6.8
Anterolingual-posterolabial diameter of occlusal surface (B)	5.2	6.7	5.0
Ratio of B/A	.47	.82	.74
Maximum diameter of crown perpendicular to longitudinal axis (C)	10.7	7.6	6.8
Minimum diameter of crown perpendicular to longitudinal axis (D)	5.0	5.6	4.1
Ratio of D/C	.47	.74	.60
Height of crown perpendicular to occlusal plane	15.0	19.5	12.4

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B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS.

MAY 15, 1964

NUMBER 204

THE STATUS OF *PSEUDOGEEKKO SHEBAE* AND OBSERVATIONS ON THE GECKOS OF THE SOLOMON ISLANDS

BY WALTER C. BROWN¹

INTRODUCTION

Brown and Tanner (1949) referred a unique specimen (Brigham Young University [BYU], No. 7002) of a previously undescribed geckonid lizard from Guadalcanal in the Solomon Islands to the new species *shebae* in the genus *Pseudogeckko* Taylor (1922), thus establishing the second species known for the genus and extending the range to include a second peripheral group of islands, analogous in position to the Philippines. At that time we had not had the opportunity of examining any material of the type species of the genus, the Philippine species *Pseudogeckko compressicorpus*.

New material has now provided the opportunity to reassess the relationships of *P. shebae* and to redefine its differences from the other small geckos of the Solomon Islands. Dr. Ernest Williams, Museum of Comparative Zoology, recently called my attention to the difficulty of identifying certain specimens, which, on the basis of descriptions in the literature, were apparently referable either to *Lepidodactylus guppyi* or *Pseudogeckko shebae*. The series of specimens in question (Museum of Comparative Zoology, Nos. 64152, 65862, 67122, 67124, 74517-19, and Stanford University, No. 23720) were collected by Mr. Fred Parker on Bougainville Island, Solomon Islands, during 1961-62. These have provided the point of departure for the present paper.

This study is part of the author's investigations on the herpetofaunas of the Islands of the Pacific area, supported by

¹ Division of Systematic Biology, Stanford University and Menlo College, Menlo Park, California.

a grant from the National Science Foundation. Illustrations were prepared by Mr. Walter Zawojcki, Stanford Research Institute.

THE RELATIONSHIPS OF THE GENUS *PSEUDOGEEKKO*

Taylor (1922, p. 103), in erecting the genus *Pseudogekko*, suggested that it might have its closest affinities with *Thecadactylus* (I assume *T. australis* = *Pseudothecadactylus australis*: Brongersma, 1936, p. 136). There is reason, however, to believe that the closeness of this relationship is doubtful. Recently, five specimens of *Pseudogekko compressicarpus* became available: Stanford University Nos. 23548-49, from Zamboanga, Mindanao Island, and 23654-55 from Bohol Island, and Museum of Comparative Zoology No. 44130, the latter collected by Taylor at Saub, Mindanao, and never previously reported. An examination of the foot structure of these specimens indicates probable close affinities with three other Oriental-Pacific genera (*Lepidodactylus*, *Gekko* and *Luperosaurus*), which also belong to the subfamily Gekkoninae as defined by Underwood (1954).

The six Oriental-Pacific genera, *Gekko*, *Hemiphyllodactylus*, *Lepidodactylus*, *Luperosaurus*, *Pseudogekko* and *Pseudothecadactylus*¹, all belong to that group with moderately to strongly dilated digits, with the distal joint relatively short, compressed, and arising from the tip or near the tip of the dilated part.

If digital structure alone is considered, these six genera fall into four sections. *Hemiphyllodactylus* is rather sharply distinguished by the greatly reduced first digit and the fact that the distal compressed phalanx is not attached all the way to the tip of the dilated portion, as pointed out by Stejneger (1899) and Smith (1933). *Pseudothecadactylus* forms a second section distinguished by the double series of lamellae which are widely separated distally. As they are presently understood, *Gekko* and *Luperosaurus* fall into a third section which may be distinguished from *Lepidodactylus* and *Pseudogekko* on the basis of the lamellae being entire throughout the length of the digit. In general the species of the genus *Gekko* are larger than are the species in the other genera, and the species of *Luperosaurus* exhibit more extensive webbing. However, a critical study of

¹ *Pseudothecadactylus* confined to the islands of Torres Straits and Australia is not properly Oriental-Pacific but is here considered because of Taylor's belief in its relationship to *Pseudogekko*.

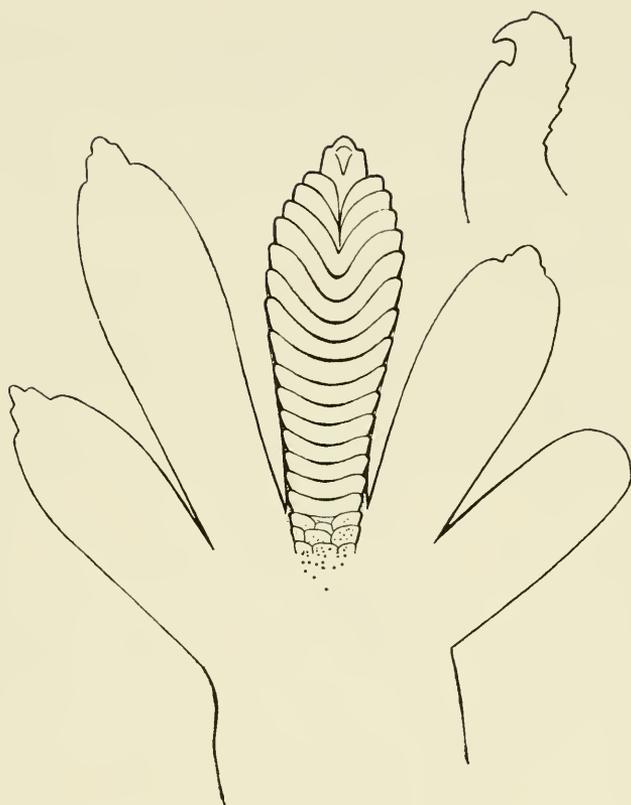


Figure 1. *Pseudogekko compressicorpus*.

all known species in these last four genera and consideration of other characters than digital structure will be necessary before the generic limits and relationships can be clearly understood.

This is borne out by the difficulties which have at times arisen in assigning certain species to one or the other of these genera. Thus Boulenger (1885a, p. 162) included in *Lepidodactylus* three species later placed in *Hemiphyllodactylus* by Stejneger (1899, pp. 788, 799) and Smith (1933, p. 15). Again, Boulenger (1885b, p. 473), in describing *Gekko pumilus*, noted that the species was very like a *Lepidodactylus* in many characters, being placed in *Gekko* on the basis of the undivided lamellae. Examination of one specimen of *pumilus* (MCZ 69216) suggests that

it may be more closely related to *Luperosaurus* with reduced webbing and skin folds. Taylor (1915, p. 96), on first describing *compressicorpus*, placed it in the genus *Luperosaurus* but later (1922) separated this species from *Luperosaurus* and erected

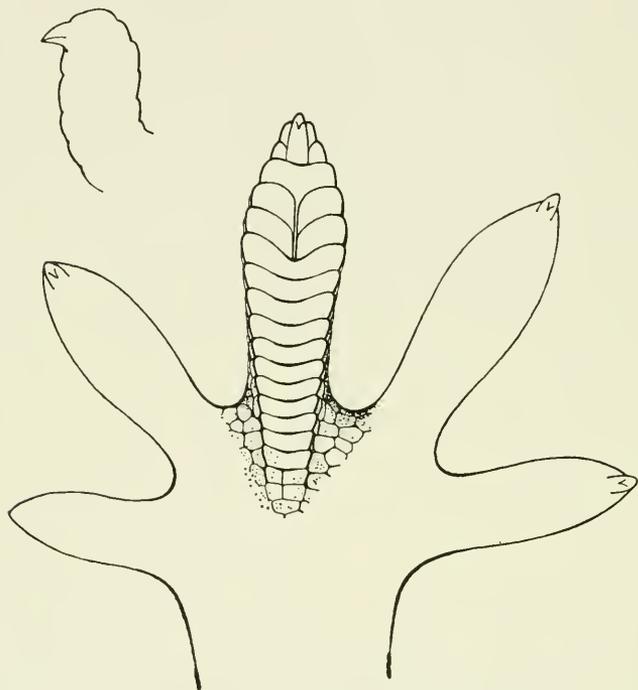


Figure 2. *Pseudogekko shebae*.

the genus *Pseudogekko* for it. Again, an examination of the paratype of *Luperosaurus macgregori* Stejneger (Stanford University No. 6263, a hatchling measuring 23.5 mm from snout to vent) reveals that the sub-terminal lamellae are divided in the midline, and hence that this specimen should be referred to *Lepidodactylus* species as that genus is presently understood. (The assignment of *macgregori* to the genus *Luperosaurus* is thus placed in doubt and the type should be re-examined in this light.)

DISTINGUISHING CHARACTERS OF
PSEUDOGEKKO SHEBAE AND
LEPIDODACTYLUS GUPPYI

Pseudogekko would appear to be distinguished from *Lepidodactylus* primarily on the basis of the more slender habitus and the more narrowly but uniformly dilated digits. Both *P. shebae* and *P. compressicarpus* are more slender in body and exhibit less broadly dilated digits (Fig. 1) than most of the several species of *Lepidodactylus* which I have had the opportunity of examining. If the ratio "breadth of head: snout-vent length" is used as a measure of habitus, the range for *Pseudogekko shebae* and *Pseudogekko compressicarpus*, based on the few adult specimens available, is from about 14-16 per cent; for five species of *Lepidodactylus* (*christiana*, *lugubris*, *aureolineatus*, *planicaudus* and *guppyi*) the range is 18-21 per cent.



Figure 3. *Lepidodactylus guppyi*.

(*Lepidodactylus brevipes* from the Philippines is an exception with respect to both of these characters and is closer to *Pseudogekko*. A careful study of this species will probably show that it should be placed with *P. shebae* and *compressicarpus*.)

The differences in foot structure of *Lepidodactylus guppyi* and *Pseudogekko compressicarpus* are illustrated in Figures 1 and 3. The condition of the terminal lamella—divided or entire—is not a generic character, since it is divided in *Pseudogekko compressicarpus* and *Lepidodactylus lugubris* and entire in *Pseudogekko shebae* and *Lepidodactylus guppyi*.

The number of preanal and femoral pores in males and the size of the head scales, as illustrated by the number of scales between the eyes in the mid-orbital plane, will help to distinguish *Pseudogekko shebae* from *Lepidodactylus guppyi* (Table 1).

In addition to *L. guppyi* and *P. shebae*, members of the *lugubris-woodfordi* species complex occur also in the Solomon Islands. Individuals of this species or group of species, however, are readily distinguished from *Lepidodactylus guppyi* and *Pseudogekko shebae* on the basis of the divided terminal lamella on all toes but the first. This scale is undivided on all toes on specimens of *L. guppyi* and *P. shebae*.

SUMMARY

The Oriental-Pacific geckonid lizards of the genera *Gekko*, *Lepidodactylus*, *Luperosaurus* and *Pseudogekko* represent categories which probably include closely related groups of species but, as they are presently understood, are not sharply and clearly delimited from each other. Two additional genera, *Hemiphyllodactylus* and *Pseudothecadactylus*, although they probably represent lines of evolution distinct for a longer period of time, have by some authors been regarded as very closely related to these four genera.

Superficial resemblances between species and the lack of sharp lines of demarcation between the genera not infrequently have made difficult the proper generic assignment of some of the species and even the determination of the species to which isolated individuals belong. A case in point is the identification of specimens of *Pseudogekko shebae* and *Lepidodactylus guppyi*, both known from the Solomon Islands. Their distinguishing characteristics and present generic assignment have been briefly discussed in the present paper.

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Table 1

Frequency of lamellar, pore and certain body-scale counts in the available samples of *Pseudogekko shebae* and *Lepidodactylus guppyi*.

	Third-toe lamellae (hind limb)	Prenal and femoral pores	No. Freq.	Number of scales across the head at mid-orbital plane	No. Freq.	Snout-vent length of mature males (in mm)
<i>Pseudogekko shebae</i>						
BYU 7002	11	1	32	1	22-23	36.2 N=1
<i>Lepidodactylus guppyi</i>						
MCZ 49224,	11	1	35	1	32	44.4-51.0 N=6
49494-95,	12	1	38	1	33	
64152,65862,	13	4	40	3	34	
67122,67124,	14	4	41	1	35	
74517-19	15	1	42	2	36	
					38	

B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS.

JULY 15, 1964

NUMBER 205

REDESCRIPTION OF *AMPHISBAENA DUBIA* MÜLLER (AMPHISBAENIA: REPTILIA)¹

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This note provides a standardized (Gans and Alexander, 1962) redescription of *Amphisbaena dubia* Müller, 1924, and adds many new records for the species, extending its range from São Paulo into Paraná and Santa Catarina. I am grateful to Mr. W. C. A. Bokermann for the gift of two specimens. The following curators of institutions (referred to in abbreviations throughout) placed me in their debt by loan of material: Miss Alice G. C. Grandison of the British Museum (Natural History), London (BM); Drs. Paulo E. Vanzolini and A. Stanley Rand of the Departamento de Zoologia, São Paulo, S. P., Brazil (DZ); Dr. Ernest E. Williams of the Museum of Comparative Zoology (MCZ); Dr. Konrad Klemmer of the Senckenbergischen Naturforschenden Gesellschaft, Frankfurt a. M., Germany (SMF); Dr. Joseph Eiselt of the Naturhistorischen Museums zu Wien, Austria (VM); and Dr. Heinz Wermuth [formerly] of the Zoologischen Museums der Universität, Berlin, Germany (ZMU). Specimens in the Gans collection are referred to by the letters CG. Dr. Virginia Cummings figured the specimens and Miss Charlyn Rhodes contributed technical assistance. The over-all project owes its support to Grant NSF G-21819 from the National Science Foundation.

¹Notes on amphisbaenids, 12.

AMPHISBAENA DUBIA MÜLLER

Amphisbaena dubia Müller, 1924, p. 86. Terra typica: "Piracicaba, Staat São Paulo, Brasilien." HOLOTYPE: ZMU 26394.

[Not=*A. dubia* Rathke, 1863; cf. Gans, 1961, p. 220; China, 1963, p. 197.]

Diagnosis: A medium sized form of *Amphisbaena* without major fusions of head shields; with one or more pairs of large parietals; with a blunt-tipped cylindrical tail without autotomy constriction or autotomy; and with two clear round precloacal pores in males and none [or two very faint indications only] in females. Specimens have 213 to 231 body annuli; 13 to 17 caudal annuli; 13 to 16 (generally 14 or 16) dorsal and 16 to 19 (generally 16 or 18) ventral segments to a midbody annulus; and two rows of postgenials and no postmalars. The color of preserved specimens is a light brown faintly countershaded. Segments bear a light brown circular spot.

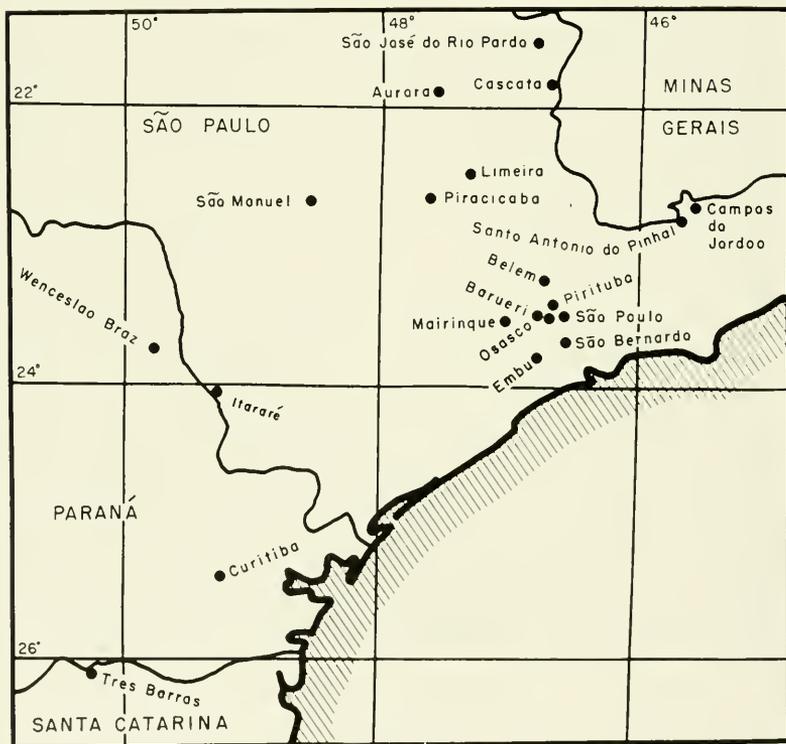


Fig. 1. *Amphisbaena dubia*. Sketch map showing localities mentioned in text.

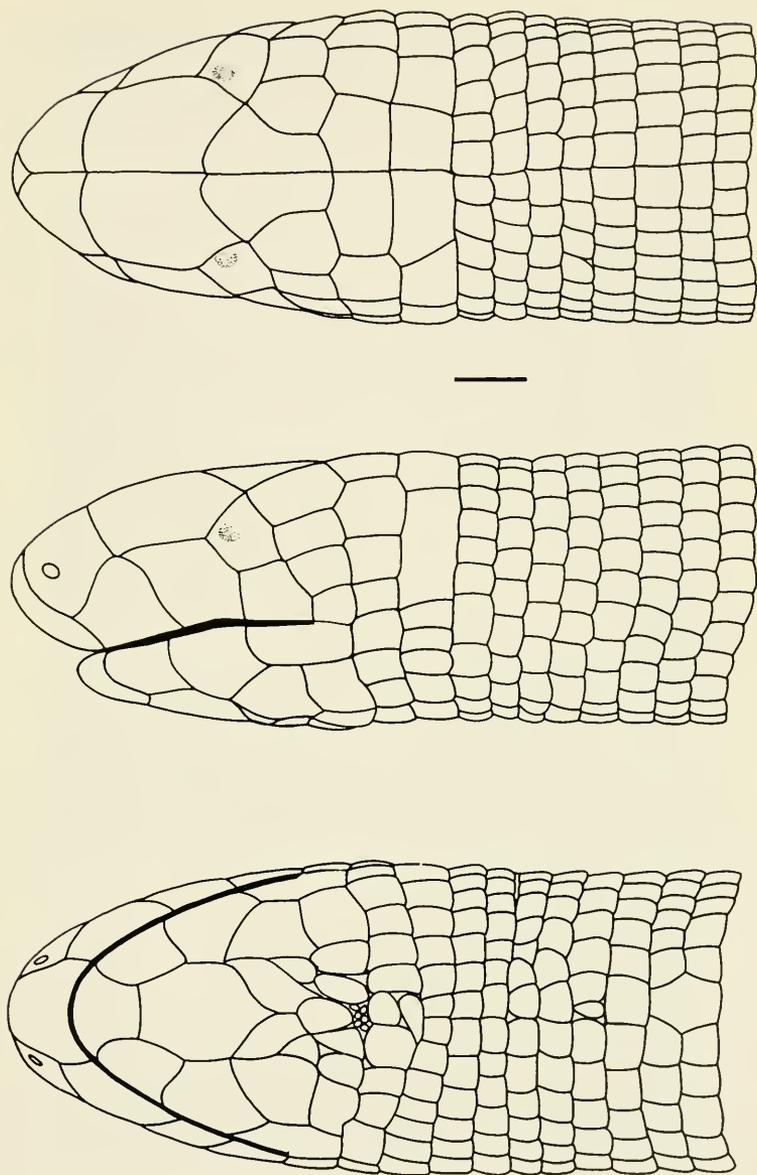


Fig. 2. *Amphisbaena dubia*. Dorsal, lateral and ventral views of the head of the holotype, ZMU 26394. The line equals 1 mm to scale. (V. Cummings, del.).

Discussion: The holotype was available for examination and its assignment poses no problems. The specimen is slightly faded, but otherwise in excellent condition.

The name *A. dubia* of Rathke (1863, p. 128), a senior homonym of *A. dubia* Müller, refers to *Amphisbaena fuliginosa* ssp. (cf. Gans, 1961, p. 220) and has been suppressed under Opinion 664 (China, 1963, p. 197).

The examination of the British Museum specimen confirms Vanzolini's (1949) statement that Boulenger (1885) had included an individual of *A. dubia* in the series upon which he based his concept of *A. vermicularis* Wagler.

It is interesting that the samples show no geographic variation.

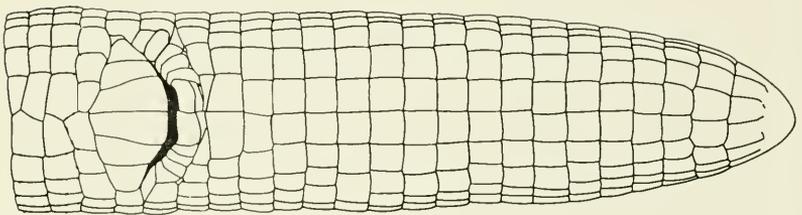


Fig. 3. *Amphisbaena dubia*. Ventral view of cloaca and tail of the holotype. The line equals 1 mm to scale. (V. Cummings, del.).

Description: Figure 2 shows views of the head, Figure 3 the ventral surface of the cloaca and tail, and 4, 5, and 6 photographic details of the coloration and other aspects of the specimens. Figure 7 gives a scatter diagram of tail versus snout-vent length. Meristic data are listed in the table.

This is a medium sized species of *Amphisbaena*, of a light tan color in preservative with faint countershading. The pigment is evenly distributed across the segments and appears to fade out ventrally. The dorsal midbody segments show a light circular spot in the center of each segment.

The head segmentation is characterized by lack of major fusions. An azygous rostral barely visible in dorsal view is followed by four or five pairs of enlarged cephalic shields in contact along the dorsal midline. The nostrils pierce the first pair (nasals). The second pair (prefrontals) are the largest segments of the head. There are two and one-half or three supra- and two and

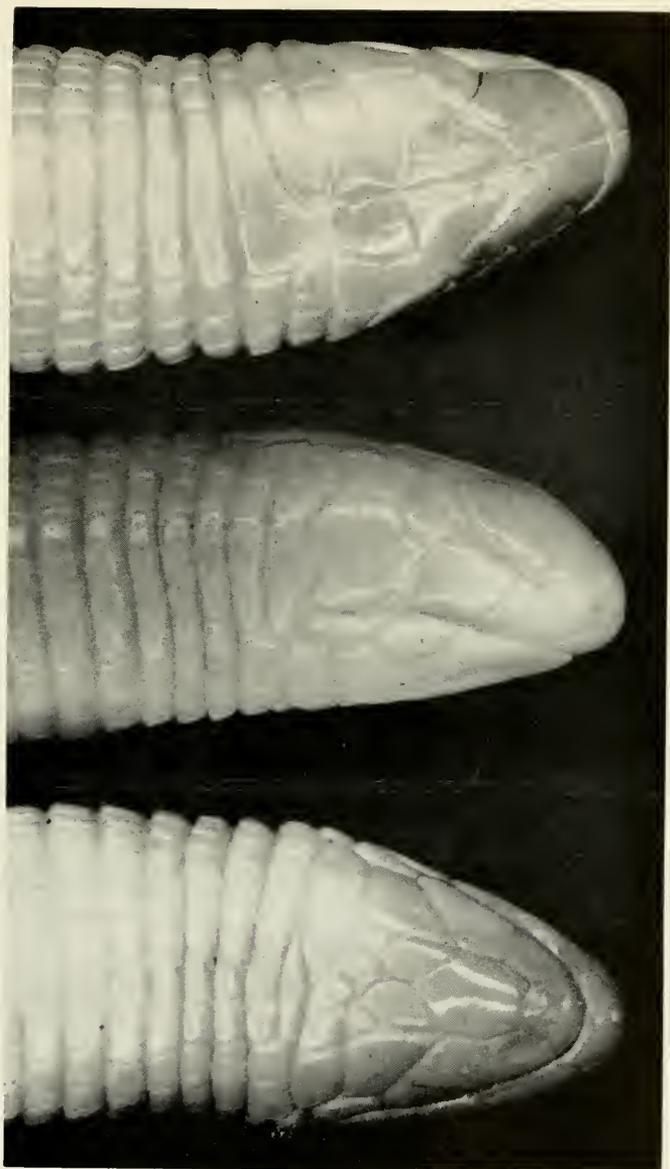


Fig. 4. *Amphisbaena dubia*. Dorsal, lateral and ventral views of SMF 11813 from Curitiba, Paraná.

one-half (or three) infralabials with the third infralabial extending considerably beyond the angulus oris. The supralabials are large, the second largest and the first next in size. The first two sutures incline anteriorly at an angle of approximately 45° , the last ascends the snout almost vertically. The angulus oris lies anterior to the suture between frontals and parietals. The ocular is quadrangular.

The mental is of approximately the same size as the first infralabials. The second infralabials are clearly the largest in the row, while the postmental is the largest segment on the lower jaw. Posteriorly its tip is inserted between the two large, tear-drop shaped first postgenials which in some specimens keep the postmental from even point-contact with the malars. The second postgenials are irregular. Occasionally a segment from this row extends forward to contact the postmental. The row back of the malars is counted as the first body annulus since it falls posterior to the angular oris: there are thus no postmalars.

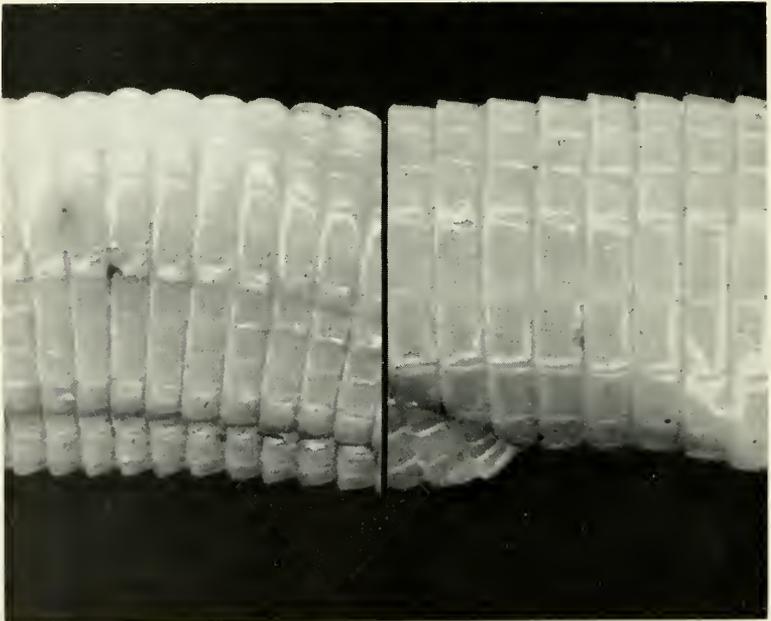


Fig. 5. *Amphisbaena dubia*. Dorsal (left) and ventral (right) views of the holotype, ZMU 26394, at midbody to show size of segments. The pigment has faded too much to be discernible.

Dorsally, the first body annulus curves anteriorly, becoming wider to form the segments of the temporal-postocular row and abut to the lateral edges of the frontals. In a few specimens there is a splitting of this row giving a semblance of a dorsal intercalated half-annulus. The second row includes the relatively large first parietals as its dorsalmost segments. The second parietals are ordinarily not elongate and their anterior and posterior sutures generally run in parallel, at right angles to the long axis of the trunk. Enlargement, if present, occurs



Fig. 6 *Amphisbaena dubia*. Dorsal, lateral and ventral views of tail of male specimen (CG 2093). Note clearly marked precloacal pores which are absent in females (cf. Fig. 3).

mainly by broadening (or fusion) of the middorsal segments into a pair of second parietals.

The head is relatively blunt, flattened slightly dorsoventrally and oval in cross-section. The lower jaw is but slightly shorter than the upper. The temporal muscles are only faintly indicated by swelling in these presumably adult specimens. The nuchal region is very faintly constricted.



The cloacal region is characterized by two small round pre-cloacal pores in males and none or at best a very faint indication in females. Five to eight pre-cloacal and nine to 15 post-cloacal segments fringe the cloacal slit. There is no autotomy annulus and the species appears incapable of autotomy. Caudal annuli number 13 to 17. The tail is wider than high in cross-section with a tendency toward ventral flattening. The distal half is faintly swollen and finally tapers very rapidly toward a faint vertical ridge on its tip.

The lateral sulci are clearly marked, starting after the first fifth of the body length and proceeding to the level of the cloaca. At midbody each of them is as wide or wider than one of the adjacent segments, and filled with broken segments and diagonal folding lines that enter the inter-annular sutures at an angle that generally cuts off the corners of the bordering segments. The dorsal and ventral sulci are indicated only by alignment of the intersegmental sutures.

The dorsal segments of a midbody annulus are approximately one and one-half times as long as wide, while the midventral segments range between one and a quarter to one and three-quarters times as wide as long.

Habits: The Curitiba specimen contained three elongate eggs each encased in a very thin leathery shell. The posterior and best formed one measured approximately 9×17 mm *in situ*.

Range: Eastern portions of the states of São Paulo, Paraná, and northern Santa Catarina, Brazil.

Distribution records: BRAZIL: _____, (Boulenger, 1885; Vanzolini, 1949); BM 1961.2023. *São Paulo:* "Inland" _____, MCZ 20655-20657; VM 12335-4. São José do Rio Pardo, DZ 6442. Cascata, DZ 6432. Aurora, DZ 6439. Limeira, DZ 6436. Piracicaba, (Müller, 1924); ZMU 26394 (holotype). São Manoel do Paraíso (=São Manuel), DZ 1266, 1266B, 6520. Santo Antonio do Pinhal, DZ 6440. Belem, DZ 2425. Pirituba, DZ 6438. São Paulo, DZ 7053, 7676. Osaseo, DZ 7054. Barueri, CG 2092-2093. Mairinque, DZ 6433. São Bernardo do Campo, DZ 1284. Embu (=Embu Guaçu), DZ 6461. Itararé, DZ 6443. *Paraná:* Wenceslao Braz, DZ 6667. Curitiba, SMF 11813. *Santa Catarina:* Tres Barras, DZ 6437.

Data for specimens of Amphisbaena dubia Müller

Collection and number	Sex	A N U L I		SEGMENTS		Labials	Chin	Cloacal	Length
		Body+Lat.+Tail	Dors.+Vent.	Dors.+Vent.	Supra+Infra				
BM 1961.2023	♂	223+3+15	14+16-17	3+2-1/2	2-4-(7)	2-6-13	205+17		
MCZ 20655	♀	224+3+13	15+18	3+2-1/2	2-3-(7)	2F-6-12	268+21		
MCZ 20656	♀	226+3+15	14+18	3+2-1/2	2-3-(7)	2F-6-12	287+25		
MCZ 20657	?	218+3+15	14+18	3+2-1/2	2-3-(8)	2-6-13	175+16		
VM 12335-4	♂	213+3+14	14+18	2-1/2+2-1/2	2-3-(7)	2-8-11	247+21		
DZ 6442	-	216+3+14	14+14	3+2-1/2	3-(11)-(7)	3-8-11	228+118		
DZ 6432	-	222+3+13	14+16	3+2-1/2	2-3-(8)	2-8-10	235+118		
DZ 6439	-	213+3+14	14-5+16	2-1/2+2-1/2	2-3-(7)	2-8-12	263+24		
DZ 6436	-	218+3+14	14+16	2-1/2+2-1/2	2-----	2-6-12	213+18		
ZMU 26394	♀	221+3+17	14+16	3+2-1/2	2-3-(7)	0-6-12	139+14		
DZ 1266	-	214+3+14	13-4+16	3+2-1/2	2-4-(8)	2-6-15	227+20		
DZ 6520	-	214+3+14	14+16	3+2-1/2	2-3-(6)	2F-6-11	250+21		
DZ 6440	-	223+4+16	16+18	3+2-1/2	3-4-(7)	2-6-12	217+19		
DZ 2425	-	223+3+15	16+17-18	3+2-1/2	2-4-(8)	2F-6-11	262+22		
DZ 6438	-	221+4+15	14+17-18	3+2-1/2	2-3-(7)	2F-6-11	217+18		
DZ 7053	-	219+3+13	14+16	2-1/2+2-1/2	2-3-(7)	2-8-10	252+19		
DZ 7676	-	224+4+15	14+18	2-1/2+2-1/2	2-3-(7)	2-8-10	247+22		
DZ 7054	-	227+3+14	14+16-18	2-1/2+2-1/2	3-3-(7)	2F-6-10	243+21		
CG 2092	♀	216+3+14	14+18-19	3+2-1/2	2-3-(7)	0-7-10	239+20		
CG 2093	♂	226+3+14	14+17-18	2-1/2+2-1/2	2-3-(7)	2-6-11	207+19		
DZ 6433	-	219+3/4+15	15-16+18	3+2-1/2	2-3-(8)	2F-8-10	251+22		
DZ 1284	-	216+3+14	14+16	3+2-1/2	2-4-(7)	2F-5-10	149+13		
DZ 6461	-	227+3+14	14+18	3+2-1/2	2-4-(8)	2-6-14	247+22		
DZ 6443	-	228+4+16	14-15+16	3+2-1/2	2-3-(6)	2-10-14	210+18		
DZ 6667	-	231+3/4+15	14-15+15-16	-----	2-3-(7)	3-5---	278+24		
SMF 11813	♀	213+3+15	14+16	3+3	2-3-(6)	2F-6-12	254+21		
DZ 6437	-	225+3+15	14-15+18	3+2-1/2	2-3-(8)	2-7-9	261+20		

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B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS.

JULY 15, 1964

NUMBER 206

THE AÏSTOPOD AMPHIBIANS SURVEYED

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INTRODUCTION

In 1874 the Committee on the Structure and Classification of the Labyrinthodonts submitted to the British Association for the Advancement of Science a new and comprehensive classification of the known Paleozoic amphibians. L. C. Miall, as secretary, is usually cited as the author of the several new group names which were published in the committee's report in 1875. Among these new taxa was the Aïstopoda, proposed to include two genera of limbless, snake-like amphibians from the Coal Measures of Ireland which committee-member T. H. Huxley had described in 1866 and 1867. These genera, *Dolichosoma* and *Ophiderpeton*, were included in a single family until 1908 when Hugo Schwarz established a separate family for *Ophiderpeton*. Originally classed as a suborder of the order Labyrinthodontia, the Aïstopoda are now recognized as an order of the subclass Lepospondyli.

Knowledge of the group was soon expanded through the work of E. D. Cope and Anton Fritsch; both families proved to be represented by identical or near-identical genera in the mid-Pennsylvanian cannel coals of Ohio and Bohemia. More recently J. T. Gregory and the Turnbills have described a slightly older member of the *Dolichosoma* group from the Mazon Creek nodules of Illinois. The oldest known aïstopod was found in the Lower Mississippian of Scotland by Thomas Stock; the youngest is represented by material from early Permian fissure deposits in Oklahoma, first reported by Gregory, Peabody and Price and currently being described by McGinnis.

All the existing specimens of aïstopods are imperfect or fragmentary — only two complete skeletons are known — and most of the early descriptions were based on unprepared specimens. In

these circumstances it is not surprising that the various nominal genera have been bandied about by taxonomists and confused with unrelated types of snake-like amphibians, or that the grouping of these genera in families or even in a single order has sometimes been questioned (e.g. by Romer, 1950A, p. 629).

Difficulties in identifying from the literature my own collections of aïstopods and other amphibians from Linton, Ohio, led me to examine Cope's type specimens from that locality at the American Museum of Natural History. A number of these specimens (but none of the aïstopods) had been acid-etched by A. S. Romer in the course of his faunal revision (1930D); the rest had never been prepared. Worse yet, many of them proved to be decomposing or disintegrating as a result of pyrite disease. To prevent the loss of this important collection I was authorized by curators G. G. Simpson and E. H. Colbert to undertake a salvage program. Accordingly, the decomposed bone and pyrite were dissolved away with hydrochloric acid and the remaining blocks of coal-shale, after thorough washing and drying, were reinforced with cellulose cement. Thus prepared, the specimens are preserved as high-fidelity molds of the skeletons. Red latex casts from these molds reproduce the originals in minute detail (Baird, 1955).

SPECIMENS EXAMINED

Stock's Mississippian "*Ophiderpeton*" and specimens of *Ophiderpeton brownriggii*, *O. granulosum* and *Phlegethontia mazonensis* at the Museum of Comparative Zoology (MCZ), as well as latex casts of the Turnbills' *Phlegethontia mazonensis* and a suite of galvanotypes of Fritsch's Bohemian specimens, have been available for comparison with the American Museum (AMNH) types and my own collections which are housed chiefly at Harvard and Princeton. A specimen of *Phlegethontia linearis* collected by Thomas Stock in 1888¹ was loaned for preparation and study by the United States National Museum.

ACKNOWLEDGMENTS

I am pleasantly indebted to Drs. Simpson and Colbert and Mrs. Rachel H. Nichols for making available the Cope-Newberry collection, to Dr. Alfred S. Romer for the freedom of the Museum of Comparative Zoology's collections and great library, to Drs. C.

¹ Notes will be found on page 13, following the text.

Lewis Gazin and Peter P. Vaughn for the loan of National Museum material, and to Dr. William D. Turnbull for supplying latex casts of his Braidwood *Phlegethontia*. My good friend Robert W. Morris deserves especial thanks for guiding me to the Linton locality in 1950 and introducing me to the pleasures of Pennsylvanian herpetology. Two of my eight collecting trips were financed by the National Science Foundation and the W. B. Scott Fund of Princeton University, whose support is gratefully acknowledged. Dr. Joseph T. Gregory and Miss Helen J. McGinnis have helpfully criticized the manuscript; Miss McGinnis, furthermore, has generously made available her unpublished monograph on *Phlegethontia*.

SURVEY OF THE AĪSTOPODA

Our discussion of the ordinal characters of the AĪstopoda had best be prefaced by a table of the known members with their source localities and stratigraphic ages. It should be noted that nearly every describer has acted on the time-honored principle of "new locality, new species" even though he was seldom able to compare his new species with a prepared specimen or an adequate description of any previously described species. On the other hand, the faunal similarities between the Westphalian coal-swamp faunas of Illinois, Ohio, Pennsylvania, Nova Scotia, the British Isles and Bohemia — similarities which current studies (Baird, 1963) show to be even closer than Westoll (1944A, p. 106) indicated — should lead us to expect identical genera with closely related if not identical species.

To determine specific differences in the fragmentary and variously preserved material at hand will be difficult at best. For present purposes, then, I have reluctantly followed prior authors in allowing each local fauna its indigenous nominal species, but I have recognized only one species per genus in each fauna. The latter restriction follows W. D. Matthew's principle that "in a collection of unified origin . . . congeneric animals will generally be of a single species, or, if they are of more than one species, the discontinuity between the groups will be large and evident. In such a collection, then, in the absence of fairly obvious discontinuity, the variation within a genus should usually be taken as intraspecific." (Simpson *in* Matthew and Paula Couto, 1959, p. 51.) Thus the list which follows is essentially a record of generic distribution with the species of each genus arranged in approximate order of geologic age.²

Class AMPHIBIA

Subclass LEPOSPONDYLI

Order AĪSTOPODA Miall, 1875A

Family uncertain.

"*Ophiderpeton*" of Stock, 1882B. Wardie, near Edinburgh, Scotland. Lower Oil-Shale Group, Calciferous Sandstone Series, Lower Carboniferous (early Mississippian).

Family Ophiderpetontidae Schwarz, 1908B. [Syn.: Steenisauridae Huene, 1948G.]

Ophiderpeton Huxley in Etheridge, 1866A.³ [Syn.: *Oestocephalus* Cope, 1868J; *Thyrsideium* Cope, 1875D;⁴ *Steenisaurus* Kuhn, 1938A.⁵]

O. brownriggii Huxley in Wright and Huxley, 1866A (type species). Jarrow Colliery, Castlecomer, Co. Kilkenny, Ireland. Leinster Coals, late Westphalian B (early Mid-Pennsylvanian).

O. nanum Hancock and Atthey, 1868A. Newsham, Northumberland, England. Low Main Coal, late Westphalian B (early Mid-Pennsylvanian).

O. granulatum Fritsch, 1880 (1883A). Nýřany (Nürschan), Plzěn Basin, Bohemia, Czechoslovakia. Gaskohl, late Westphalian D (Mid-Pennsylvanian).

O. cf. amphiuminum (this paper). I. F. Mansfield mine, Cannelton, Beaver Co., Pennsylvania. Roof shale of Upper Kittanning Coal, Allegheny Group, late Westphalian D (Mid-Pennsylvanian).

O. amphiuminum (Cope), 1868J. Linton, Jefferson Co., Ohio. Canneloid shale below Upper Freeport Coal, Allegheny Group, late Westphalian D (late Mid-Pennsylvanian).

O. vicinum Fritsch, 1880 (1883A). Kounova, Kladno-Slaný-Rakovník Basin, Bohemia, Czechoslovakia. Late Stephanian (late Pennsylvanian).⁶

Family Phlegethontiidae Cope, 1875D. [Syn.: Dolichosomatidae Lydekker, 1890A, a superfluous substitute name proposed to include Cope's Phlegethontiidae and Molgophidae.]

Dolichosoma Huxley, 1867B.

D. emersoni Huxley, 1867B (type species). Jarrow Colliery, Castlecomer, Co. Kilkenny, Ireland. Leinster Coals, late Westphalian B (early Mid-Pennsylvanian). The specimen on which this genus was founded is obscured by a film of

matrix: until it is prepared we have no basis for distinguishing *Dolichosoma* from *Phlegethontia*, with which it may well be congeneric.

Phlegethontia Cope, 1871L.

P. mazonensis Gregory, 1948C. Mazon Creek, Grundy Co., and Braidwood, Will Co., Illinois. Francis Creek Shale above Morris (No. 2) Coal, Carbondale Formation, Westphalian C-D boundary (Mid-Pennsylvanian).⁷

P. [*Dolichosoma*] *longissima* (Fritsch, 1875A), new comb. Nýřany, Plzeň Basin, Bohemia, Czechoslovakia. Gaskohl,

late Westphalian D (Mid-Pennsylvanian). The close similarity of this species to its near-contemporaries in America bespeaks a common genus. To group the four species together as *Phlegethontia* seems more realistic than to segregate the Bohemian form as a species of the little-known genus *Dolichosoma*. If future work on *Dolichosoma* should confirm Fritsch's generic assignment, all the species of *Phlegethontia* would have to be transferred to that genus.⁸

P. linearis Cope, 1871L (type species). Linton, Jefferson Co., Ohio. Canneloid shale below Upper Freeport Coal, Allegheny Group, late Westphalian D (late Mid-Pennsylvanian). The type and only specimen of *P. serpens* Cope, 1871L, differs from *P. linearis* chiefly in its much larger size; its specific distinctness is very doubtful.

P. new species, McGinnis MS, 1964. Quarry 6 miles north of Fort Sill, Comanche Co., Oklahoma. Fissure filling correlative with Arroyo Formation, Clear Fork Group, Autunian (early Permian). (Gregory, Peabody and Price, 1956, p. 3: "an aistopod.")⁹

ORDINAL CHARACTERS

Reserving for future discussion the undescribed Mississippian genus, we may examine the ordinal characteristics of the AĪstopoda as they appear in *Ophiderpeton* and *Phlegethontia*. In deference to Miss McGinnis' forthcoming paper on the skeletal morphology of *Phlegethontia*, detailed osteological descriptions will be omitted here. The skull structure of *Phlegethontia* is adequately known from the descriptions by Fritsch, Gregory and the Turnbolls; that of *Ophiderpeton* has been interpreted by Steen on the basis of rather unsatisfactory specimens. Detailed comparisons between the skulls of these genera must therefore wait until the

excellent type skull of *Ophiderpeton amphiuminum* (AMNH 6857) can be fully prepared and analyzed.

Different as the two genera are in skull and jaw configuration, in the more fundamental characters of the postcranial skeleton and skin they show many similarities—similarities beyond their common lepospondyl heritage of holospondylous, amphicoelous vertebrae (Fig. 1). Among these characters in common are the following:

1. *Body long and snake-like.* Vertebral counts are possible in a few specimens of aïstopods:

<i>Ophiderpeton brownriggii</i> (type), posterior part missing	c. 60
<i>O. granulorum</i> (type of <i>O. persuadens</i>), complete juvenile	100+
<i>Phlegethontia linearis</i> (type), at least two loops missing	c. 206
<i>P. longissima</i> (type); Fritsch estimated 200+ in life	150
<i>P. mazonensis</i> (Braidwood specimen), complete juvenile	c. 140

Number of vertebrae would appear to be a function of age in *Phlegethontia*. At least 230 must have been present in a presumably adult individual such as the type specimen of *P. linearis*. Cervical, dorsal and caudal vertebrae are differentiated.

2. *Vertebrae with low, blade-like neural spines, transverse processes formed by parapophyses, hypapophysal flanges on the caudals, and foramina for the spinal nerves.* The neural spine extends the full length of the vertebra, bifurcating where it merges with the posterior margin of the neural arch. (The artificial lack of neural spines on Miss Steen's plasticene squeezes of *Ophiderpeton amphiuminum* caused her to doubt their existence, but spines are well developed in this species and in *O. granulorum*.)

The transverse process, which arises from the centrum and articulates with the capitulum of the rib, is accordingly interpreted as a parapophysis. Transverse processes of the cervical vertebrae slant posteroventrally; those of the long dorsal series gradually change direction from posterolateral to lateral to anterolateral, while those of the caudals slant anterolaterally.

In the caudal vertebrae a pair of hypapophysal processes form flanges which run the length of the centrum and fence the haemal canal. Basapophysal processes may be present on the dorsal centra but are feebly developed at best.

In *Phlegethontia* a foramen for the spinal nerve occurs below the anterior end of the posterior zygapophysis or slightly further forward, behind the transverse process. This foramen appears to be present also in *Ophiderpeton* although it is generally obscured by dorsoventral compression or concealed by the dermal armor in the specimens at hand. Small foramina for the spinal nerves

are clearly visible in a series of caudals (MCZ 2165) from Linton which are attributed to *Ophiderpeton amphiuminum* on the basis of the associated osteoderms. Intravertebral nerve foramina are not present in the Microsauria and Nectridea from Linton.

3. *Relatively straight, unicipital, tetra-radiate ribs.* Their proximal ends are K-shaped, the "tuberculum" (better termed the costal process) and the shaft forming the upright of the K, the capitulum forming the upper arm, and a pointed posteromedial process (the "ventraler Fortsatz" of Fritsch) forming the lower arm. The costal process, which in *Ophiderpeton* has a cupped head like the capitulum, appears to be a displaced tuberculum which has lost its vertebral articulation. In *Ophiderpeton* the shaft and posteromedial process are stout and stiletto-like; in *Phlegethontia* the shaft is slender and flexible and the posteromedial process is absent or weakly developed, perhaps in part because of retarded ossification.

In articulated skeletons (which have usually been dorso-ventrally compressed) the ribs typically lie with their shafts parallel to the column; the capitulum articulates with the transverse process while the costal process lies above or beside the overlapping shafts of the preceding ribs. In this manner three ribs overlap in *Ophiderpeton*, four in *Phlegethontia*. Gregory (1948C, p. 652) has interpreted the costal process ("tuberculum") as articulating with the transverse process in *P. mazonensis*, but this is definitely not the case in the specimens of *Phlegethontia* from Braidwood, Linton and Nýřany, nor in *Ophiderpeton*—if it were, the ribs would have to project laterally in a manner reminiscent of *Draco volans*! In life the ribs were probably aligned nearly parallel to the body axis with their distal ends not greatly depressed from the horizontal. In *Phlegethontia* the anterior dorsal ribs curved a little around the thoracic cavity, but in *Ophiderpeton* all the ribs were straight. Short dorsal and ventral muscles from the vertebrae presumably inserted on the costal process and posteromedial process, respectively, functioning to move the rib on the fulcrum of its capitulum.

4. *Hyoid shaped like a shallowly curved sickle.* This element, clearly seen in the three local populations of *Phlegethontia*,¹⁰ was first identified in *Ophiderpeton* by Fritsch (1901A, p. 88) but has not been mentioned in subsequent discussions of that genus. Preparation reveals its presence in the type specimen of *O. amphiuminum* (AMNH 6857). Gregory (1948C, p. 648) very plausibly interprets the sickle-shaped hyoid as the first ceratobranchial.

5. *Limbs and girdles absent.* In none of the aïstopod material is there anything which can be interpreted as the rudiment of a pectoral or pelvic girdle. The elements which Steen (1913A, p. 876) identified (but did not illustrate) as the "clavicle and cleithrum" in a British Museum specimen of *Ophiderpeton ammonium* are very probably the hyoids.

6. *Ventral armor of needle-shaped gastralia arranged en chevron.* *Ophiderpeton* has a stout thoraco-abdominal sheathing of fusiform osteoderms which are packed together in a herringbone pattern, the apex of the chevrons pointing forward. In the cervical region the spicules become smaller and grade into minute wheat-shaped ossicles which cover the gular area. This arrangement appears to be the primitive condition in the Aïstopoda and compares closely with that found in Paleozoic labyrinthodonts and reptiles. In contrast, the ventral armor of the specialized genus *Phlegethontia* is reduced to a short series of widely spaced, thread-like gastralia in the anterior thoracic region.

As dorsal armor does not occur in the Phlegethontiidae it is not listed here as an ordinal characteristic, although it may well prove to be typical of the less highly specialized Aïstopoda. In *Ophiderpeton* the cheeks and the dorsal surfaces of trunk and tail are sheathed with oat- or pebble-shaped osteoderms (Fig. 1 C), and a similar dermal covering can be seen in the oldest known representative of the order, Stock's Mississippian aïstopod from Scotland (discussed below).

DISCUSSION

The foregoing tabulation of characteristics will, I trust, serve to establish the unity of the order Aïstopoda and provide some basis for a discussion of its history and affinities. In contrast to the other lepospondyl groups of the Pennsylvanian coal-swamps, most of which make their first appearance—full-fledged but of unknown ancestry—in Westphalian time, the aïstopods have an ancient pedigree. The oldest known member of this group is indeed the oldest known lepospondyl, and until the discovery of the late Devonian ichthyostegids in Greenland it was the oldest known amphibian of any sort.

The unique skeleton of this eo-aïstopod (MCZ 2185) was collected by Thomas Stock in the Wardie shales of the Calciferous Sandstone Series of Scotland; its age in American terms is early Mississippian. Although mentioned in a paper by its collector (Stock, 1882B) the specimen remains unprepared and undescribed.

A long, sausage-shaped concretion of dense ironstone encloses the pyritized skeleton and promises formidable difficulties to the preparator. Fractures in the frontal plane at various levels, however, reveal aïstopod characteristics: an elongate, apparently limbless body armored with pebble-like dorsal osteoderms and needle-like gastralia; vertebrae with hourglass-shaped centra and long, low neural spines; and sharp, straight-shafted ribs. The bulbous, well-ossified calvarium recalls that of *Phlegethontia*. Although the proper classification of this genus must await preparation and detailed anatomical study, we may say that canny Thom Stock hit close to the mark in labeling it "*Ophiderpeton*."

From the remarkable specialization already achieved by early Mississippian time we must infer that the history of the Aïstopoda carries well back into the Devonian. Here the total absence of limbs and girdles in all known aïstopods provokes speculation. Did the group originate from a tetrapod ancestor, or directly from some crossopterygian fish through the suppression of the fins? We have no proof either way. But the many features which aïstopods share with the limbed lepospondyls, most obviously their basic skull structure and the division of the body into neck, trunk and tail, make it extremely unlikely that the forefather of the group was anything but a tetrapod.

Affinities of the Aïstopoda, as mentioned earlier, have been much debated. In surveying the literature we will do well to restrict our attention to those commentators who have had first-hand knowledge of the specimens.

J. T. Gregory in 1948 assigned *Phlegethontia* to the "*Dolichosomatidae*" and classed this family with the Ophiderpetontidae as the suborder Aïstopoda of the order Microsauria. Influenced by the reptilian features of *Phlegethontia* and by the belief that *Cephalerpeton* is a microsauro (which it is not) as well as a captorhinoid reptile (which it is), he placed the orders Microsauria and Captorhinomorpha together in the infraclass Captorhina of the subclass Eureptilia. In 1950, however, he conceded that the order Aïstopoda should probably be assigned to the amphibian subclass Lepospondyli. Gregory's 1948 paper convincingly demonstrated that the similarities of the Aïstopoda to the Lysorophidae, Apoda and Amphisbaenidae are the result of convergence in animals of similar ecotype, and that these groups are only remotely related.

The Turnbills in 1955 pointed out that Lydekker's family name Dolichosomatidae is objectively synonymous with Cope's earlier name Phlegethontiidae; they assigned *Dolichosoma* to the latter

family. They also noted without comment that both Lydekker and Schwarz had included the Molgophidae in the Aïstopoda.¹¹ Stressing that the postcranial skeleton has more fundamental significance than the skull, they applied the same classification—class Amphibia, subclass Lepospondyli, order Aïstopoda—used in this paper.

Gregory, Peabody and Price (1956) carefully compared the vertebral structure of the various lepospondyl groups and concluded that the "Aïstopoda are a highly specialized limbless group of great antiquity [which] may provisionally be regarded as an early offshoot of the neotridian stock."

Basing his observations in part on my preparations and the undescribed Mississippian aïstopod, Williams (1959) emphasized the antiquity of the typical lepospondylous centrum which he homologized (quite rightly, in my opinion) with the pleurocentrum of other ancient tetrapods and the centrum of the living amphibians. Rejecting the theory that lepospondyls had an independent derivation from the crossopterygian fishes, he observed that "if then the lepospondyls are to be derived from the ichthyostegalian, rhachitomes, or anthracosaurs, the pleurocentral centrum speaks for anthracosaur affinities."

Without questioning the morphological theory on which Williams' hypothesis of anthracosaur affinities is based, I would like to point out some uncomfortable facts. The oldest true reptile which is adequately known, *Cephalerpeton*, is of mid-Pennsylvanian age and has composite vertebrae in which the relative sizes of pleurocentrum and hypocentrum (=intercentrum) are the same as in Permo-Carboniferous mammal-like reptiles and the living *Sphenodon*. In the same swamp with *Cephalerpeton* lived *Diplovertebron* [*Eusauropleura*], a form in which the hypocentrum is much larger in proportion to the pleurocentrum; this genus may reasonably be taken as a morphological ancestor of the Seymouriamorpha from which the true reptiles are believed to be derived. *Diplovertebron*, however, is so similar to the embolomere labyrinthodonts in its skull and appendicular skeleton that it must be classed as an amphibian—an anthracosaur. Amphibians with similar vertebral proportions coexisted with true embolomeres at least as far back as late Mississippian time, so the common ancestry of the diplovertebrontids and embolomeres can hardly be dated later than the middle Mississippian. That the ancestors of the reptiles had a relatively large hypocentrum, and that reduction of the hypocentrum characterized the transition from amphibians to reptiles, can hardly be doubted. Derivation of

this proto-reptilian vertebral structure from the ichthyostegid pattern of late Devonian time is quite undocumented but presents no great theoretical difficulties; the ichthyostegalian vertebra in turn is readily derivable from that of crossopterygian fishes such as *Eusthenopteron*.

In striking contrast to this plausible sequence of morphological stages stands the oldest known lepospondyl, Stock's early Mississippian aĭstopod. Its vertebrae are holospondylous without any trace of an ossified hypocentrum or of laterally paired pleurocentra like those of the ichthyostegalians and crossopterygians. In vertebral form this co-lepospondyl appears to be much further removed from the anthracosaur-reptile lineage than that lineage is from the rhachitome-stereospondyl line. Indeed, the evidence now available suggests rather that the dominance of the pleurocentrum evolved in convergent fashion in the lepospondyls and anthracosaurs. Thus in my opinion the evidence for lepospondyl-anthracosaur affinities is too tenuous, and the point of supposed common origin too remote in time, to justify speculation.

Relationships of the Aĭstopoda to other lepospondylous amphibians are almost equally difficult to determine. The urodeles and anurans (Lissamphibia) need not be considered here, for their persistent four-leggedness and their relatively recent pedigree testify that any connection between Lissamphibia and Aĭstopoda must be indirect, by way of one of the Paleozoic lepospondyl groups. The apodans (Gymnophiona), though similarly devoid of limbs and girdles, show features of the scales and vertebrae which ally them rather with the microsaur.

Among Paleozoic lepospondyls the Neetridea (let us use the correct spelling if only for the sake of novelty) display similarities in vertebral structure which have led Gregory, Peabody and Price (1956) to consider them as distantly related to the aĭstopods. This hypothesis is the most plausible one yet advanced. But it should be emphasized that all known neetrideans had intervertebral spinal nerves and well-developed (though sometimes diminutive) appendicular skeletons, including the sculptured clavicles and interclavicle which characterize Paleozoic amphibians in general. Aĭstopods had intravertebral spinal nerves and lacked limbs and girdles, apparently since early Mississippian time. Thus if these two groups had a common ancestor it must be sought in Devonian rocks—rocks in which amphibians of any kind are extremely rare. Until pertinent fossils can be found and described, therefore, the affinities of the Aĭstopoda must remain in doubt.

The foregoing discussion will have served its purpose if it stimulates further research by clarifying the nature of this peculiar group of amphibians and pointing up some of the many unanswered questions concerning them. Perhaps it is too much to hope that anything can remedy the common but unfortunate tendency to omit the diaeresis and pronounce the name as "ACE-topod" or "ICE-topod." Like the proverbial politician, the aïstopods should be happy to be called by any name so long as they are recognized in print.

OPHIDERPETON FROM CANNELTON, PENNSYLVANIA

Seven associated vertebrae (PU 17293) which recently came to light in the Princeton paleobotanical collections provide a new horizon and locality record for the genus *Ophiderpeton*. This specimen, collected by I. F. Mansfield in 1877, comes from the richly fossiliferous roofing shale of the Upper Kittanning Coal, a member of the Allegheny Group and late Westphalian D (Middle Pennsylvanian) in age. The source locality is Mansfield's mine near Cannelton in Darlington Township, Beaver County, Pennsylvania. This is the first lepospondylous amphibian to be recorded from Cannelton.

Much of the bone has flaked away and little remains but the neural arches and spines. Absence of the diagnostic ribs and gastralia makes generic identification difficult, as the neural arches of *Ophiderpeton* and *Phlegethontia* appear very similar when crushed. Dimensions of the vertebrae fall within the range of the pene-contemporaneous *O. amphiuminum*, but they are also compatible with the exceptionally large *Phlegethontia* specimen named *P. serpens* by Cope. The most diagnostic feature available seems to be the medial notch in the posterior border of the neural arch: this is deep in the Cannelton aïstopod and *Ophiderpeton amphiuminum* but shallow in *Phlegethontia*. As *Ophiderpeton* is common in the Linton fauna while only one *Phlegethontia* specimen of equivalent size is known, statistical probabilities also favor assignment of the Cannelton aïstopod to *Ophiderpeton*. Although the difference in age between the Linton and Cannelton deposits makes a specific difference possible, in default of morphological evidence the specimen may best be designated *Ophiderpeton* cf. *amphiuminum* (Cope).

SUMMARY

The order Aĭstopoda is a natural group of snake-like lepospondylous amphibians which inhabited the Paleozoic coal-swamps of Europe and North America. Two families, each essentially monotypic, are distinguished: the Ophiderpetontidae of the early middle to late Pennsylvanian and the more highly specialized Phlegethontiidae of the early Pennsylvanian to early Permian. The oldest known lepospondyl, an undescribed aĭstopod from the early Mississippian of Scotland, is of uncertain family position.

Pending detailed comparison of the skulls, ordinal characteristics may be found in the postcranial skeleton: (1) body long and snake-like, reaching a vertebral count of about 230; (2) holo-spondylous, amphicoelous vertebrae with low, blade-like neural spines, transverse processes formed by parapophyses, hypapophyseal flanges on the caudals, and foramina for the spinal nerves; (3) relatively straight, unicipital, tetradial ribs; (4) sickle-shaped hyoids; (5) limbs and girdles entirely lacking; (6) ventral armor of needle-shaped gastralia arranged *en chevron*, and (except in phlegethontiids) dorsal armor of pebble-shaped osteoderms.

The remarkable specialization already achieved by the early Mississippian implies an origin well back in Devonian time; a tetrapod ancestry rather than direct derivation from the cross-terygian fishes is indicated. Relationships of the order are obscure. A proposed connection with the anthracosaur-reptile lineage is controverted by the available evidence, and among lepospondyl groups only the Neetridea show even distant affinities with the Aĭstopoda.

NOTES

¹The man who actually collected the superb skeletons of Linton amphibians which the U. S. National Museum acquired from R. D. Lacey, and which Moodie (1909B) attempted to describe, has not previously been identified. Circumstantial evidence points to Thomas Stock of Edinburgh whose great collection of Scottish Carboniferous fishes and amphibians was purchased by the Museum of Comparative Zoology in 1883. In the MCZ archives is a letter from Stock to Alexander Agassiz, sent from Wellsville, Ohio (the town just north of Linton) on April 30, 1888, which states in part: "I am staying about here . . . collecting the Linton fishes and labyrinthodonts. . . . I have been very successful with the rare group of Carboniferous labyrinthodonts and have already several nice ones that I should think would

be a valuable addition to your collection." Unfortunately for Harvard, Agassiz declined to buy Stock's collection. Evidently it was sold to Laccoe, for several of the Laccoe specimens from Linton bear stickers inscribed "Stock #--."

² Current stratigraphic practice, followed in this paper, places the Mazon Creek fauna close to the Westphalian C-D boundary or in earliest Westphalian D and assigns the Cannelton fauna to late Westphalian D; the Linton fauna is very late Westphalian D. However, recent paleobotanical work by Cridland, Morris and Baxter (1963, p. 63) implies that the Francis Creek Shale (Mazon Creek fauna) is only slightly older than the Upper Freeport Coal (Linton fauna) but considerably younger than the Kittanning Coal Group (Cannelton fauna).

³ Names of the Jarrow amphibians are usually cited as of Huxley, 1867. However, *Ophiderpeton* and four other genera were first validly published in January of 1866 by Etheridge, who credited their authorship to Huxley. Generic descriptions were provided although no species were named. As a *genus coelebs* (i.e. without named species) is valid under the International Rules of Zoological Nomenclature, the genus *Ophiderpeton* properly dates from January, 1866; its type species was first described in April of that year by Huxley in a paper by Wright and Huxley. *Dolichosoma emersoni* was not described until 1867.

⁴ Preparation of the type specimen (AMNH 6900) of the type species *Thyrsideum fasciculare* Cope confirms Romer's (1930D) identification of it as *Ophiderpeton amphiuminum*. I mention this fact in order to resolve Mille, Dechaseaux's doubts (1955, p. 278) about the identity of *Thyrsideum*.

⁵ *Steenisaurus* was proposed by Oskar Kulm (1938A, p. 51) in a footnote to *Ophiderpeton granulatum* Fritsch: "*Ophiderpeton* Fritsch non Huxley (teste Steen) = *Steenisaurus* nov. nom." Steen's publications do not suggest any such generic distinction, nor do the specimens document it.

⁶ The specimen figured by Schwarz (1908B, figs. 1-4) under the name *Ophiderpeton vicinum* is apparently from Nýřany. Because of the difference in age I prefer to assign the late Westphalian material from Nýřany to *O. granulatum* and restrict the name *O. vicinum* to late Stephanian material from Kounová.

⁷ A specimen (USNM 4313) which was assigned to *Phlegethontia mazonensis* by Gregory (1950A, p. 867) proves on preparation to be *Cocytinus*, the first record of a lysorophid microsaur in the Mazon Creek fauna.

⁸ *Dolichosoma scutiferum* Fritsch, 1901A, is here synonymized with *Phlegethontia longissima*. The type of "*Dolichosoma*" *angustatum* Fritsch is a neotridan skull roof from which the postfrontal and postorbital bones have been displaced during fossilization: its proper name is *Sauroplorea* [*Urocordylus*] *scalaris* (Fritsch).

⁹ Two supposed aïstopods from Europe require some comment here. *Palacosiren beinerti* Geinitz, 1861A, based on vertebrae from the Upper Rotliegende of Olivětín (Oelberg bei Braunau), Bohemia, has been interpreted as a gigantic aïstopod by Fritsch (1883A, p. 125). So far as one can

judge from Geinitz and Deichmüller's lithograph (1882A, pl. 9) the centra are hourglass-shaped only externally: they lack the funnel-like amphicoely which characterizes the Aïstopoda. Until preparation and restudy of this specimen reveal its affinities it remains *incertae sedis*.

The imprint of a small skeleton from the late Stephanian or early Autunian of La Machine, Nièvre, France, has been tentatively identified as an aïstopod by Thevenin (1910A, p. 39). Its preservation is so poor that little more than the gross morphology can be made out. The skeleton looks more lysorophid than aïstopod to me, but this suggestion must be tempered by the fact that lysorophids are known at present only from North America. Until further material is available the affinities of Thevenin's animal must be left *sub judice*.

¹⁰ The element in *Phleggethoutia longissima* ("*Dolichosoma scutiferum*") which Fritsch (1901A, p. 88) called a grill-bar and Steen (1938, p. 226) called a rib is readily identifiable with the hyoid in *P. linearis* and *P. mazonensis*. Structures identified by Fritsch as gill-rays and shown forming external gill-tufts in his well-known reconstruction are actually gastralria, as Steen has pointed out.

¹¹ Preparation of type specimens from Linton makes it abundantly clear that the Pennsylvanian genera *Molgophis*, *Cocytinus* and *Lysorophus* and the Permian species commonly assigned to *Lysorophus* form a closely-knit family of microsaurian affinities. Although the family name Molgophidae Cope 1875 has priority, I prefer to retain, at least for the present, the more familiar name Lysorophidae Williston 1908. Whether *Lysorophus* Cope 1877 is generically distinct from *Molgophis* Cope 1868 remains to be determined.

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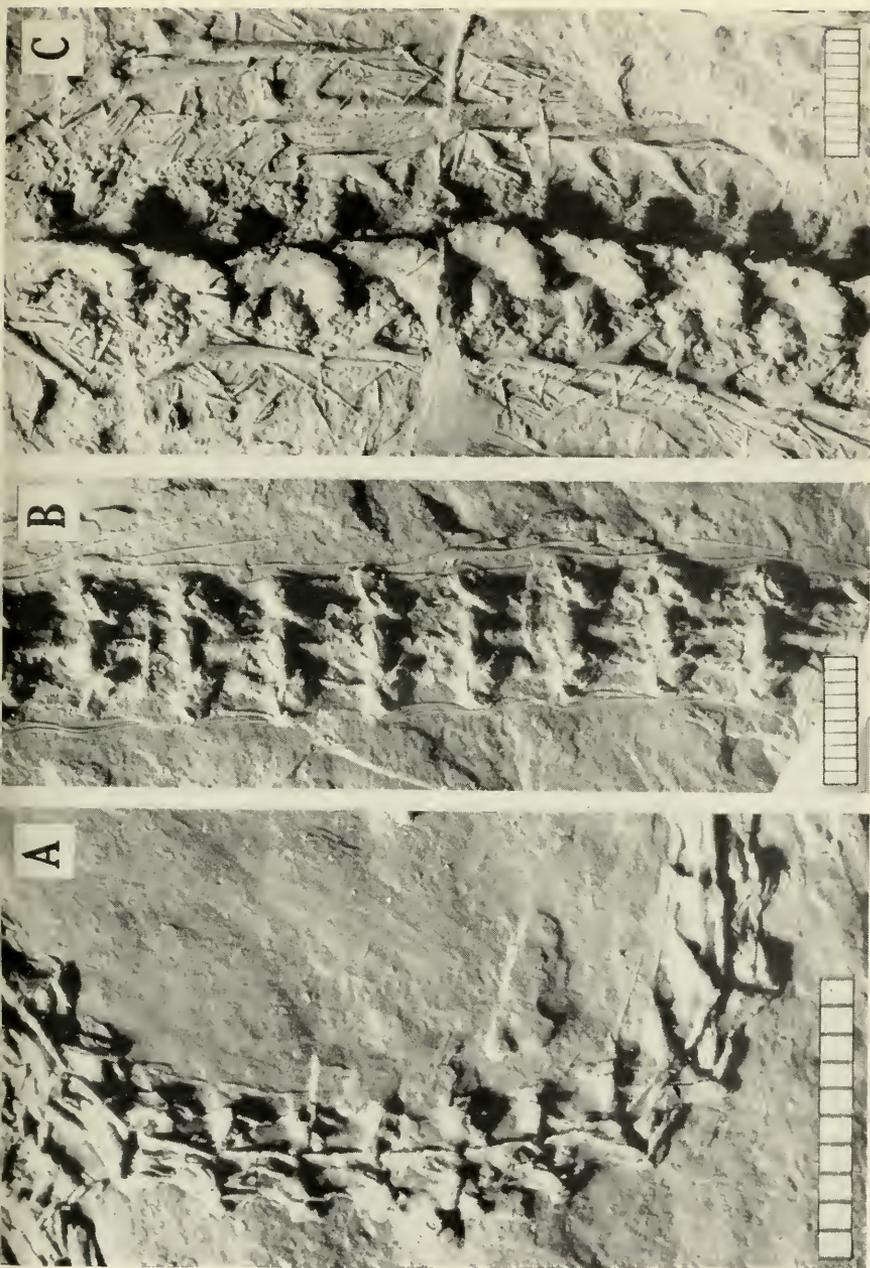


Fig. 1. Aistopod dorsal vertebrae. A, *Philegethonlia linearis* (type specimen, AMNH 6966) in dorsal view. B, *P. linearis* (type of *P. serpens*, AMNH 6899) in ventral view. C, *Ophiderpeton amphiumum* (MCZ 2128, Leo Lesquereux coll.) in dorsal view. Photographs of red latex casts; scales in millimeters.

B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS.

JULY 28, 1964

NUMBER 207

NOTES ON THE HORSESHOE BATS *HIPPOSIDEROS CAFFER*, *RUBER* AND *BEATUS*

BY BARBARA LAWRENCE

INTRODUCTION

Attempts to identify a small series of *Hipposideros*, collected in the Belgian Congo by Alvin Novick in 1956, have made necessary a re-examination of the distribution and specific characters of *caffer*, *ruber* and *beatus*. This has brought to light some new characters of the nasal swellings and of the nose leaves, and emphasizes the importance of the nasal region in general for showing specific differences.

HIPPOSIDEROS RUBER CENTRALIS ANDERSEN

Study of a series of six males and five females from Kivu Forest, Ituri Province, has led to a re-examination of the *caffer-ruber* group in the Museum of Comparative Zoology collections in the light of Verschuren's and Aellen's recent discussions of these small hipposiderids. The group is admittedly a confusing one. It is the more so because as competent a worker as Andersen (1906, pp. 281-282) interpreted his findings as evidence of a complicated distribution pattern which brought together in a single area different subspecies of the species *caffer*. Subsequently Hollister (1918, pp. 85-87) pointed out that two clearly distinct species, *ruber* and *caffer*, occur together in East Africa. Our material amply confirms this; we even have specimens of *ruber* and *caffer* taken in the same basement. This situation was apparently not clear to Aellen (1952, p. 76) when he followed Hollister in synonymizing *centralis* with *ruber*, although he failed to give *ruber* full specific status, considering it instead a subspecies of *caffer*. In addition he extended the range of what he called *caffer ruber* clear across the Congo to the Cameroons, whence

he recognized three other races of *caffer*. Such a distribution pattern evidently did not satisfy him and subsequently (Perret and Aellen, 1956:435; Aellen, 1957:198) he stated that the whole *caffer* complex was in need of revision, though he did not further discuss the relation of *ruber* to *centralis*.

Verschuren (1957, pp. 346-374), although he deals with a limited area, seems to have understood the situation better and it is significant that much of his work was based on field studies of the live bats. Aside from *H. beatus* which is easily distinct, he recognizes two species: *caffer centralis*, a forest form which readily adapts to life in houses, and *nanus* which is more characteristically a savannah form. According to him, the latter were far less numerous than the former and the two were only found together in one cave in heavily wooded savannah country.

Verschuren's distinction between *nanus* and *centralis* is good and on a subspecific level our material agrees well with his. On a specific level, the evidence at hand for considering *centralis* a race of *caffer* rather than of *ruber* is not convincing. Length of tooth row, width across the molars at M³, and the relation of zygomatic to mastoid width, while useful as key characters, are not good indicators of specific relationships. Careful examination of series of the *caffer-ruber* and *beatus* groups from a number of localities in a belt across central Africa suggests very strongly that modifications of the nasal structures both internal and external are the best index to specific relationships. This is perhaps not surprising. Since hipposiderids make their sounds through their noses, small variations in the relative size of the different parts of the nasal swellings and the septa which incompletely divide them should be important. Before final decision can be made on the classification of this group, the functional significance of these morphological differences needs to be much better understood.

As far as the material studied is concerned, attempts to separate *ruber* and *caffer* show that, whereas most of the differences between the two species are of size not proportion, there is a real difference of kind in the compartments of the nasal swellings. In all forms, in dorsal view (strongly illuminated from below), three pairs of compartments are visible: 1. anterior, more or less dorsal and lateral to the external nares; 2. medial, between one and the olfactory part of the brain; and 3. posterolateral to the others, and the largest. Variation in size of these is a good diagnostic character. When *caffer* is viewed from above,

the relatively very small size of compartment two and the somewhat larger size of three are sufficient to distinguish it from *ruber*. No doubt sections and other more detailed studies would show further differences in this region.

Present knowledge of the small hipposiderids, excluding *beatus*, of east and central Africa can then be summarized as follows. In the savannah country of eastern Africa two species, *ruber* and *caffer*, occur together, of similar proportions externally and cranially, but conspicuously different in size. They may be further distinguished by the proportions of the nasal compartments. Near topotypes of *ruber* from Kilosa in southern Tanganyika and specimens from Mtimbuka south of Lake Nyasa resemble each other closely, while to the north a series from Mt. Elgon is somewhat intermediate towards a more western race.

This western race has the skull as long as, but slightly narrower than, typical *ruber* and small nasals which give it the appearance of a large *caffer*. The proportions of the nasal compartments, however, are of the *ruber* type. The specimens at hand from the Ituri Forest, two from Rutshuru and one from Avakubi all belong to this western form, as does probably a specimen from Ulkerewe Island. Whether the name *centralis* is available for this western race or whether Hollister is correct in synonymizing *centralis* with *ruber*, cannot be determined until the type series is re-examined. Since the type locality of *centralis*, Entebbe, Uganda, lies west of Mt. Elgon whence we have intermediate specimens, it seems advisable for the time being to continue to use *centralis* for the Congo race.

As for the specific status of *centralis*, the structure of the nasal compartments and apparent intergrading with *ruber* are evidence of a closer relationship with this form than with *caffer*. This is in accord with Andersen's (1906, p. 281) subdivisions of *caffer*, except that his group 2, "*H. c. centralis*" (= *ruber*), is raised to specific rank and two subspecies of this, *ruber ruber* and *ruber centralis*, are recognized.

There also occurs in central Africa a bat with *caffer*-like nasal compartments but of nearly the same size as *centralis*. We have one specimen from Beni of this apparent race of *caffer* which we take to be *nanus* and probably the same as the series so identified by Verschuren. The sympatric occurrence of representatives of two rather similar species of small *Hipposideros* recognized by Hollister in East Africa seems to be typical of the Congo region as well.

Verschuren's habitat notes for *caffer centralis* (= *ruber centralis*) and *nanus* (= *caffer nanus*) suggest that *caffer* may be typically a savannah form which has spread west where suitable country is to be found, while *ruber*, a forest form, has moved into dry country fairly extensively, possibly because of its adaptability to roosting in buildings.

HIPPOSIDEROS BEATUS MAXIMUS VERSCHUREN

Two males, collected at Mabali, agree with Verschuren's (1957, p. 364) description in being larger than *beatus* from the Cameroons, and extend the range of *b. maximus* considerably to the southwest. Until Verschuren published his account of the bats of Garamba, it had generally been accepted that *nanus* was a small relative of *beatus* and represented this species in the northeastern Belgian Congo. Actually, as Verschuren has said (1957, pp. 370-72), the eastern relative of *beatus* is a larger not a smaller race and *nanus* is quite a different animal. As stated above, it is very likely a form of *caffer*.

With the discovery of this larger race, Andersen's (1906, p. 275) characters of tooth row and zygomatic arch no longer hold for the species. One of the specimens of *beatus maximus* from Mabali is almost identical in zygomatic-mastoid proportions with a similar-sized *guineensis*, a member of the *caffer-ruber* group, from Metet, while length of upper cheek teeth and width across the tooth rows taken outside M^3 are exactly the same in both. As for the supposedly shorter tibia of *beatus*, the typical race is smaller than *guineensis* and so has a conspicuously shorter tibia. In the larger *b. maximus*, the tibia is only slightly shorter and the ratio of length of tibia to length of forearm while usually less than in *guineensis* occasionally shows no difference.

A search for better diagnostic characters to separate the *caffer-ruber* races from *beatus* again has shown the importance of the nasal region. Cranially, these differences are hard to measure though they are apparent enough to the eye. In *beatus* the rostrum bulks larger in proportion to the cranium with the width across the nasal swellings relatively greater in proportion to their total length. In spite of this, the inflation of the nasal region is less than in the *caffer-ruber* group. In particular, compartment three is relatively small as seen both in dorsal and in side view.

Externally, width of nasals is usually reflected in width of nose leaf. While this character is often of subspecific value, specific relationships are better shown by differences in details of structure of nose leaves than by absolute size. Here again

we find *beatus* sharply distinct from the *ruber-caffer* group. In *beatus*, the center of the horseshoe is shallower, and associated with this general difference are a number of particular characteristics. The septum slopes rather evenly inward to a point between the nostrils, whereas in *caffer* and *ruber* it has a very marked lumpy projection midway of its length, internal to which it makes a sharp angle where it meets the face between the nostrils. The nostrils themselves are less deep set and the pits ventral to them are shallower in *beatus* than in *caffer* and *ruber*. Further, in *beatus*, the two lateral accessory leaflets are of nearly equal length with a small warty growth dorsal to the end of the inner one, while in *caffer* and *ruber* the inner accessory leaflet is longer than the outer and the wart lies posterior rather than dorsal to its end. Verschuren's figures (1957, figs. 137, 141, and 146) show well the differences in septum between the two groups, while the pale rim around the nostrils seems to be associated with their shallowness in *beatus*. The difference which he figures in surface of the sella is harder to see in alcoholic specimens and the development of the medial thickening is not a character which separates all the *caffer-ruber* group from *beatus*. Other external characters which help to confirm the distinct position of *beatus* are the average more distal attachment of the wing membrane and less funnel-shaped ears.

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B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS.

NOVEMBER 12, 1964

NUMBER 208

THREE NEW SPECIES OF FROGS (LEPTODACTYLIDAE, *ELEUTHERODACTYLUS*) FROM HISPANIOLA

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Among specimens collected during the summer of 1962 in southwestern Haiti are representatives of two undescribed species of *Eleutherodactylus*, both of which belong to the *ricordi* group. A third new species from the República Dominicana was taken during the summer of 1963; the affinities of this third species are distinctly with species from Haiti, and it is appropriate to describe the three new forms in a single paper. In Hispaniola, I have had the capable assistance of Miss Patricia A. Heinlein, and Messrs. Ronald F. Klimkowski, Dennis R. Paulson, David C. Leber and Richard Thomas. For significant comparative material I wish to thank Dr. Doris M. Cochran, United States National Museum (USNM), and Dr. Ernest E. Williams, Museum of Comparative Zoology (MCZ), whose assistance in these studies is very deeply appreciated. The illustrations are the work of Mr. Leber, and I wish to thank him and the above mentioned persons for their assistance in the field. The types have been given to the Museum of Comparative Zoology. Paratypes of the new forms have been deposited in the American Museum of Natural History (AMNH) and the Museum of Natural History, University of Kansas (KU); material in my own collection is designated as the Albert Schwartz Field Series (ASFS).

In July 1962, during a stay at Camp Perrin in Haiti, Mr. Leber took an especially interesting and rather large frog from a nearby cave during a diurnal visit. Nocturnal visits to the cave resulted in the taking of no more specimens of this frog, so that

it is represented only by one individual. Although I am reluctant to describe a new species of *Eleutherodactylus* on such limited material, the species is so distinctive that I have no hesitancy in naming it as

ELEUTHERODACTYLUS COUNOUSPEUS new species

Figure 1

Holotype: MCZ 43199, an adult male, from Grotte de Counou Bois, 1 mile (1.6 km) southwest of Camp Perrin, Dépt. du Sud, Haiti, taken 30 July 1962 by David C. Leber. Original number X3266.

Diagnosis: An *Eleutherodactylus* of the *ricordi* group characterized by a combination of large size (snout-vent length 48 mm), large digital discs, a greenish yellow dorsal ground color with black markings consisting primarily of a dark interocular bar, a dark postocular V, and a scapular cross, a heavily mottled throat, and lacking inguinal glands.

Description of type: An adult male, with the following measurements (in millimeters): snout-vent length, 48.0; head length, 18.5; head width, 17.2; diameter of tympanum, 3.1; diameter of eye, 7.1; naris to anterior corner of eye, 6.4; femur, 21.3;

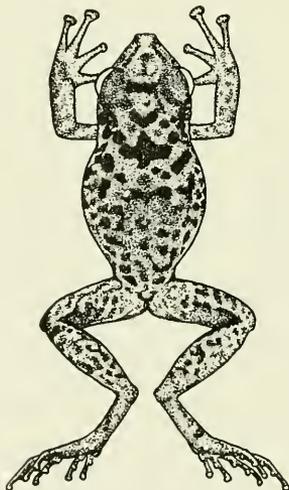


Fig. 1. *Eleutherodactylus counouspeus*, new species, type, MCZ 43199, snout-vent length 48.0 mm.

tibia, 22.5; fourth toe, 18.1. Head slightly narrower than distance from snout to posterior border of tympanum; snout decidedly truncate with nares prominent at anterior end of canthus rostralis; diameter of eye greater than distance from naris to anterior corner of eye; diameter of tympanum about one-half diameter of eye, distance from tympanum to eye about one-third diameter of tympanum; tympanum oval, the vertical diameter slightly greater than the horizontal. Interorbital distance 5.5, less than diameter of eye. Digital discs present and well developed, those on fingers three and four distinctly larger than those on digits one and two, disc of finger three the largest and equal to about three-quarters size of tympanum. Fingers long and slender, unwebbed, 3-4-2-1 in order of decreasing length; subarticular tubercles prominent, gray. Toes moderately long, with vestigial webs, 4-3-5-2-1 in order of decreasing length; subarticular tubercles prominent, gray. Heels touch when femora held at right angles to body axis. Inguinal glands absent. Dorsum smooth; upper eyelids with low rounded tubercles. Throat slightly granular, belly smooth; abdominal disc poorly developed but lateral margins of disc fairly conspicuous. Dorsal surfaces of forelimbs smooth, of hindlimbs granular, especially on dorsal surfaces of crura. Posterior face of thighs with many small, juxtaposed rounded granules. Tongue small, entire, free behind, its greatest width equal to about one-half that of floor of mouth. Vomerine teeth in two short, almost straight series, beginning well within the inner margins of the choanae and separated from the choanae by a distance equal to about three times the diameter of a choana, the two series separated from each other by a distance equal to the diameter of a choana.

Coloration of type: Dorsal ground color in life greenish yellow (slightly brighter than Pl. 21L1 of Maerz and Paul, 1950), with dorsal black markings as follows: a black interocular bar, a black median postocular V, a black scapular cross with a rounded black spot anterior and lateral to the side "arms" of the cross, a rather linear blotch on the sides posterior to the forearm insertion, and the balance of the dorsum and sides with lighter and irregular obfuscations of dark (Fig. 1). Fore- and hindlimbs diffusely spotted with dark with no apparent banding or barring; concealed surfaces pale purplish gray overlaid with brown suffusions. Throat yellowish green, heavily mottled with brownish; belly pinkish with admixture of yellow-green, and suffused with brown stippling; underside of crura rather heavily

marbled with brown. Lores yellow-green with an indistinct darker canthal line. Iris bronzy in life, with a reddish pupillary ring.

Comparisons: No other Hispaniolan members of the *ricordi* group reach the size of *counouspeus* except *E. schmidti* Noble and its races *rucillensis* Cochran and *limbensis* Lynn, and possibly *E. femurlevis* Cochran. The webbed feet in *E. schmidti*, along with the entirely different color pattern and the reddish-orange venter will distinguish it from *counouspeus*. *E. schmidti* is known only from the Cordillera Central and the Cordillera Septentrional in the República Dominicana and from the area about Limbé in Haiti and is thus not sympatric with *counouspeus*. I have not examined the type and apparently only specimen of *femurlevis*, which has a snout-vent length of 42 mm (Cochran, 1941:62); however, the detailed description of the pattern as well as the photograph of the specimen (*ibid.*, pl. 10 C) indicate that there is little similarity between it and *counouspeus*. *E. femurlevis* has a pale, wide, interocular bar banded narrowly anteriorly with brown, a brown loreal spot, pale gray crossbands on the legs, immaculate venter — none of which corresponds to the pattern of *counouspeus*. The photograph of the type does not show a conspicuously large-eyed frog, and the legs appear shorter and the discs much less enlarged. It has seemed most pertinent to compare these two species not only because of some similarity in size but also because they both occur in the same general region on the southwestern Haitian peninsula, *femurlevis* having been described from Desbarrière, on the north and east foothills of the Massif de la Hotte.

Observations: The type of *E. counouspeus* was taken by Mr. Leber as it actively hopped about on rocks about fifty feet back from the entrance of the Grotte de Counou Bois in the morning. No other specimens were secured on a later visit and no voice was heard which might be associated with this species; *E. pictissimus* was taken fairly abundantly in the same cave.

In general habitus, *E. counouspeus* resembles *E. zcus* from Cuba; both are rather long-legged, large-eyed species with large digital discs. The pattern of the two is vaguely similar although they are not at all comparable in coloration. Since both are petricolous and/or cavernicolous forms, I feel that these similarities are due to convergence and do not show relationships. In Antillean *Eleutherodactylus* there is often a remarkable

similarity in pattern and coloration between unrelated forms which are petricolous (Schwartz, 1960:41-42).

A second new species of the *ricordi* group from the western portion of the Tiburon Peninsula is named in honor of Dennis R. Paulson who helped collect the type series and whose interest and diligence in field work in the West Indies deserves special mention:

ELEUTHERODACTYLUS PAULSONI new species

Figure 2

Holotype: MCZ 43200, a gravid female, from 4.5 miles (7.2 km) northwest of Les Cayes, Dépt. du Sud, Haiti, one of a series taken 7 August 1962 by David C. Leber and Dennis R. Paulson. Original number X3796.

Paratypes: ASFS X3797-98, AMNH 71987-89, same data as type; ASFS X2799, Camp Perrin, Dépt. du Sud, Haiti, 23 July 1962, collected by a native; MCZ 43201, Grotte de Counou Bois, 1 mi. (1.6 km) SW Camp Perrin, Dépt. du Sud, 26 July 1962, Lucien Rigaud; KU 79811, 4 km (6.4 km) NW Les Cayes, Dépt. du Sud, Haiti, 7 August 1962, D. C. Leber; MCZ 33825, Place Negre, near Jérémie, Dépt. du Sud, Haiti, Lue and George Whiteman, 11 December 1960.

Diagnosis: A species of *Eleutherodactylus* of the *ricordi* group characterized by a combination of rather small size (females snout-vent length to 26 mm), very small digital discs, a dorsal



Fig. 2. *Eleutherodactylus paulsoni*, new species, type, MCZ 43200, snout-vent length 25.4 mm.

pattern of dark brown marbling with a pair of buffy dorso-lateral stripes, scattered dorsal pinkish warts, without red or orange on the hindlimbs, and with inguinal glands.

Description of type: A gravid female with the following measurements (in millimeters): snout-vent length, 25.4; head length, 10.5; head width, 10.0; diameter of tympanum, 2.1; diameter of eye, 3.6; naris to anterior corner of eye, 3.0; femur, 11.9; tibia, 13.5; fourth toe, 11.5. Head slightly narrower than distance from snout to posterior border of tympanum; snout truncate with nares prominent at anterior end of canthus rostralis; diameter of eye slightly longer than distance from naris to anterior corner of eye; diameter of tympanum greater than one-half diameter of eye, distance from tympanum to eye equal to about one-half diameter of tympanum. Fingers rather long and slender, unwebbed, 3-4-2-1 in order of decreasing length; subarticular tubercles prominent, gray. Toes moderately long, with vestigial webs, 4-3-5-2-1 in order of decreasing length; subarticular tubercles prominent, gray. Heels overlap when femora held at right angles to body axis. Inguinal glands present. Dorsal surface, including eyelids, snout, and upper surfaces of all limbs heavily rugose; a raised median dorsal line. Throat and belly smooth; abdominal discs poorly developed. Posterior and ventral surfaces of thighs with many large, conspicuous juxtaposed granules. Tongue rather small, entire, free behind, its greatest width equal to about one-half that of floor of mouth. Vomerine teeth in two rather long, slightly bowed, series, beginning at outer margin of choanae and separated from the choanae by a distance equal to one-half the diameter of a choana, the two series separated from each other by the same distance.

Coloration of type: Dorsal ground color in life brown, with a rather irregularly marbled darker brown pattern, a dark brown interocular bar preceded by a paler tan snout, much marbled with dark brown. Scattered conspicuous warts from the level of the eyes onto the lower back, pinkish in life and strongly contrasting with the dark ground color. Dorsolateral stripes indistinct and buffy, almost completely obscured in the preserved specimen by dark pigment. Dorsal ground color distinctly more reddish posteriorly than anteriorly. Antebrachia with about three obscure crossbars, brachium marbled dark; hindlimbs very obscurely crossbarred and dotted with paler, their concealed surfaces dark brown, with some lighter stippling

medially. Belly immaculate opalescent whitish; throat with large to small discrete dots and stipples; underside of antebrachia clouded with brown; underside of thighs and crura rather heavily marbled and clouded with brown.

Variation: Five adult females (including the type) have the following measurements: snout-vent length, 24.0 (21.5-25.8); head length, 9.6 (8.3-10.6); head width, 9.1 (8.1-10.1); tympanum, 2.0 (1.9-2.1); eye, 3.5 (3.2-3.8); naris to eye, 2.8 (2.4-3.2); femur, 11.3 (10.0-13.6); tibia, 12.3 (11.3-13.9); fourth toe, 10.7 (9.8-12.2). A single adult male paratype measures: snout-vent length, 22.1; head length, 8.8; head width, 7.8; tympanum, 1.9; eye, 3.3; naris to eye, 2.3; femur 10.4; tibia, 11.4; fourth toe, 10.7. Females reach a larger size than males; interestingly, the largest female (MCZ 33825) is from the north side of the Massif de la Hotte. The condition of this specimen is such that it is not readily compared with specimens from the south side of the Massif, but superficially it seems identical except for its slightly larger size. It is, of course, possible that such northern frogs may be found to be racially distinct from southern frogs.

In color and pattern, the series shows variation principally in the distinctness of the dorsolateral stripes. When present, they are boldly outlined in dark brown and extend from the posterior portion of the upper eyelid to the groin. The brown dorsum with a more reddish (chestnut) tinge posteriorly was noted for all fresh material; the pinkish warts are likewise a characteristic feature. The dorsolateral stripes vary from buffy to reddish; the interocular bar can be either tan or light buffy. The belly varied from white to translucent gray. The degree of throat spotting varies considerably, with the type showing the mean condition; in some specimens the dots form almost a complex dark brown reticulum and in others they are larger and more uniform than in the type, but nonetheless discrete. All specimens, even the smallest juvenile (snout-vent 11.5), have the throat marked with dark spots.

Comparisons: Shreve and Williams (1963:331) referred to a single specimen (MCZ 33825) under their discussion of *E. fureyensis* saying that "a single specimen from the vicinity of Jeremie . . . somewhat resembles this species and may be the La Hotte region representative." The specimen referred to is here designated as a paratype of *E. paulsoni*. Their comment, however, points out the comparison which it is most necessary

to make — that between *paulsoni* and *furcyensis*: In coloration and pattern these two species are quite different. *E. furcyensis* has prominently banded crura and thighs, and lacks dorso-lateral lines. The anterior and posterior faces of the thighs are red (Pl. 4D11) in *furcyensis* (these same areas are dark in *paulsoni*) and there is additionally a faint orange wash in the groin. Female *furcyensis* have the throat slightly purplish, flecked with black, whereas male *furcyensis* have the belly pale yellow; neither of these features occurs in *paulsoni*. *Furcyensis* has a dark brown dorsum with a pair of pale orange-buff reversed parentheses, not a pair of dorsolateral lines. The two species do resemble each other in the throat spotting, which is a variable but always present feature in *furcyensis*, although no specimens at hand have the throat with a dark reticulum.

Structurally, the two species differ in that *paulsoni* has inguinal glands and *furcyensis* lacks them. In comparably sized specimens, the discs of *furcyensis* are larger than those of *paulsoni*. The differences in coloration and pattern are so striking as to preclude the possibility that these two forms are related on a subspecific level.

In size, *furcyensis* exceeds *paulsoni* in both sexes (largest female *furcyensis* snout-vent, 37.0; largest male, 28.0), although the small series of *paulsoni* makes comparison difficult. At least fourteen adult female *furcyensis* have higher values in all measurements taken.

The remaining *ricordi* group members in Hispaniola are: *glandulifer*, *darlingtoni*, *weinlandi*, *rufifemoralis*, *schmidti*, *femurlevis*, *pictissimus*, *leoncei* and *counouspeus* (list principally from Shreve and Williams but with some interpolations of my own). Of these species, *schmidti* and *counouspeus* are known to lack glands. These two forms are likewise much larger than *paulsoni*, are differently patterned, and *schmidti* has webbed feet. Of the forms with glands, *paulsoni* is exceeded in size by *glandulifer*, *darlingtoni*, *weinlandi*, *pictissimus*, and *leoncei*. None of these larger species have patterns which are in any way comparable to that of *paulsoni*, although the dorsum of *weinlandi* with its anteriorly and posteriorly differing dorsal ground colors is vaguely similar. *E. darlingtoni* has large digital discs, whereas *leoncei*, *weinlandi* and *pictissimus* have small digital discs. I have not examined specimens of either *femurlevis* or *rufifemoralis*; the latter is however much smaller than *paulsoni* (largest recorded snout-vent length 18) and is much

differently patterned. *E. femurlevis*, on the other hand, is much larger (snout-vent 42) and again with a different pattern.

Observations: The type and paratopotypes were taken in leaf litter under large trees along the bank of an intermittent river (Rivière de la Grande Ravine du Sud); the adjoining area was thorn scrub. Another was taken at the cave entrance of the Grotte de Counou Bois, and a single individual from 4 km NW Les Cayes was taken on the ground among dead leaves in grass about 2 m high. At the type locality of *paulsoni*, *E. pictissimus* was the commonest frog encountered.

Shreve and Williams (1963:338-9) discussed the Hispaniolan and Cuban components of the *dimidiatus* and *varleyi* groups. To the former they assigned the Cuban species *albipes*, *dimidiatus*, and *emiliae* and the Hispaniolan *jugans*, and to the latter the Cuban *varleyi* and *cubanus* (which has customarily been placed in the *dimidiatus* group) as well as *E. phyzelus* Schwartz which I consider a synonym of *E. varleyi* Dunn. I concur in these assignments. Shreve and Williams also consider *E. ventrilineatus* a member of the *dimidiatus* group (although it is peripheral) in spite of its short vomerine series (*dimidiatus* group members are characterized by long vomerine series). *E. ventrilineatus* is so obviously related to *E. jugans* that, except for the vomerine series, one might be inclined to regard them as conspecific. Thus, on Hispaniola, *jugans* and *ventrilineatus* are the only known members of the *dimidiatus* group. Both are restricted to higher elevations in the mountains of the south island, *jugans* in the Massif de La Selle, *ventrilineatus* in the Massif de la Hotte.

A small series of a third Hispaniolan species belonging to this assemblage was taken by Richard Thomas in the Sierra de Neiba in the República Dominicana; since this form is the first recorded from the north island (and has thus "crossed" the Cul de Sac-Valle de Neiba plain), I propose that it be named, from the Greek word for "transgressor,"

ELEUTHERODACTYLUS PARABATES new species

Figures 3, 4

Holotype: MCZ 43202, a gravid female, from 20 km southwest of Hondo Valle, 5950 feet (1800 m), Independencia Province, República Dominicana, taken 11 August 1963 by Richard Thomas. Original number V366.

Paratypes: ASFS V365, V367-70, same data as type.

Diagnosis: An *Eleutherodactylus*, related to *E. ventrilineatus* Shreve, with short vomerine series but differing from both *ventrilineatus* and *jugans* in smaller size, in the presence of digital discs, in ventral pattern, and in relative size of tympanum.

Description of type: A gravid female with the following measurements (in millimeters): snout-vent length, 24.1; head length, 8.6; head width, 8.8; diameter of tympanum, 1.7; diameter of eye, 2.7; naris to anterior corner of eye, 2.4; femur, 8.6; tibia, 9.8; fourth toe, 9.3; tympanum/tibia ratio 16.8. Head slightly broader than distance from snout to posterior border of tympanum; snout rather pointed with nares conspicuous at anterior end of canthus rostralis; diameter of eye greater than distance from naris to anterior corner of eye; diameter of tympanum greater than one-half diameter of eye; distance from tympanum to eye equal to about three-quarters diameter of tympanum. Interorbital distance 3.2 mm, greater than diameter of eye. Digital discs present and moderately well developed, those on fingers three and four larger than those on digits one and two, disc on finger three the largest and equal to about one-half size of tympanum. Fingers rather short, unwebbed, 3-4-2-1 in order of decreasing length; subarticular tubercles



Fig. 3. *Eleutherodactylus parabates*, new species, type, MCZ 43202, snout-vent length 24.1 mm.

fairly prominent, gray. Toes moderately long, unwebbed, 4-3-5-2-1 in order of decreasing length; subarticular tubercles prominent, gray. Heels overlap slightly when femora are held at right angles to body axis. Inguinal glands absent. Dorsum smooth. Throat and belly smooth; abdominal disc not prominent with only the pectoral fold moderately conspicuous. Dorsal surface of forelimbs smooth, of thighs smooth, but dorsal surface of crura studded with a few scattered low tubercles. Posterior face of thighs with many low rounded juxtaposed granules. Tongue rather large, ovate, entire, free behind, its greatest width equal to slightly more than half of floor of mouth. Vomerine teeth in two short transverse patches, beginning at the midlevel of the choanae and separated from the choanae by a distance equal to about two and one-half times the diameter of a choana, the two series separated from each other by a distance equal to twice the diameter of a choana.

Coloration of type: Dorsal ground color brown in a longitudinal band from snout to groin, enclosing a median tan dorsal line from snout to above vent, where it divides, each branch proceeding across the posterior of the thigh to behind knee; dorsal band separated from darker brown sides by a faint tan dorsolateral stripe which begins at the eye and proceeds to near the groin (Fig. 3). Sides darker brown. A tan canthal

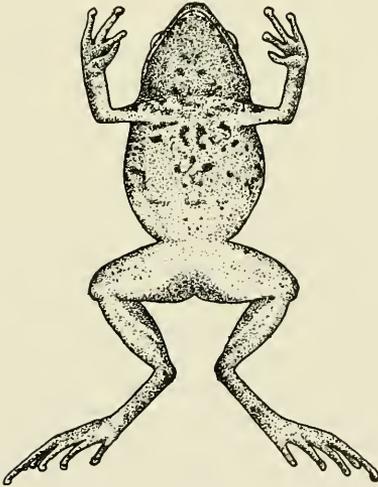


Fig. 4. *Eleutherodactylus parabates*, new species, ventral view, type, MCZ 43202.

line above a dark brown stripe which continues posteriorly as a supratympanic stripe to above the forelimb insertion; lores and cheek brownish, lips mottled. Dorsal surface of forelimbs brown, brachia slightly paler, antebrachia with remnants of two or three crossbars. Dorsal surface of hindlimbs dark brown, as are concealed surfaces, with a vague remnant of one darker crossbar on the crura; a darker brown postanal triangle present. Throat and belly yellowish tan, heavily mottled with brown; the mottling consists of dots of varying intensities, with the large dots generally darker, the smaller lighter, giving an irregularly mottled appearance (Fig. 4). Undersurface of all limbs mottled with brown, heaviest on crura and pes.

Variation: Four gravid females (including the type) have the following measurements (means followed by ranges) and ratios: snout-vent length, 23.8 (22.3-24.3); head length, 8.6 (8.0-8.9); head width, 8.9 (8.5-9.4); tympanum, 1.6 (1.5-1.7); eye, 2.7 (2.6-2.8); naris to eye, 2.1 (1.9-2.4); femur, 8.6 (8.3-9.0); tibia, 9.6 (9.3-9.8); fourth toe, 9.2 (9.0-9.3); tympanum/tibia ratio, 16.5 (15.6-17.3); tibia/snout-vent length, 40.3 (38.3-43.0). A single adult male measures: snout-vent length, 17.6; head length, 6.2; head width, 6.7; tympanum, 1.0; eye, 2.0; naris to eye, 1.5; femur, 6.7; tibia, 7.3; fourth toe, 7.2; tympanum/tibia ratio, 13.7; tibia/snout-vent length, 41.5.

In life the dorsal ground color of the entire series was like that of the type; however, only one other paratype has the median dorsal line. In this specimen the dorsal band is somewhat lighter than the type and there is conspicuous deposition of dark pigment adjacent to the median line and laterally along the region of the dorsolateral line, so that the dorsal band is rather conspicuously cut off from the sides, and the median line is also set off from the dorsal band. The four specimens which lack the median line also seem to lack a dorsal band. In these there is a dark interocular bar setting off a paler (more grayish) snout, and the sides are vaguely barred posteriorly. These specimens also have a single dark antebrachial bar and a single crural bar with a faint indication of a thigh crossbar as well. Even the smallest juvenile (snout-vent 11.0) shows the dark ventral mottling of the type, which is also a standard feature of the balance of the series. One female paratype additionally has a pair of tan scapular spots, each accompanied by a more laterally placed darker brown spot.

Comparisons: Only two known Hispaniolan species of *Eleutherodactylus* are comparable to *E. parabates* in squatly habitus — *E. jugans* and *E. ventrilineatus*. From both of these, *parabates* differs in possessing digital discs. From *jugans*, *parabates* differs as well in having a short vomerine series. I have not seen either *jugans* or *ventrilineatus* in life, and preserved specimens are all rather old and discolored. However, specimens of *ventrilineatus* lack a middorsal line, which occurs in *parabates*. *Jugans* has a double crossbar on the crura and about three crossbars on the thigh, whereas *ventrilineatus* has a single bar as does *parabates*. The ventral coloration of the three species is very distinct; the differences between *jugans* and *ventrilineatus* are well shown by Cochran (1941:34 and 35), the former having the belly heavily and irregularly pigmented, and *ventrilineatus* having the belly uniformly pigmented with a median ventral clear line. Thus, *parabates* has the least ventral pigmentation of the three.

Of the three species, *jugans* reaches the largest size (females to snout-vent length of 33.3), with *ventrilineatus* smaller (females to 30.6) and *parabates* smallest (females to 24.3). The single male of *ventrilineatus* (snout-vent length 24.9) is larger than the largest male *jugans* (22.5) or *parabates* (17.6). *Parabates* and *ventrilineatus* may be separated by the tympanum/tibia ratio; in the former, this ratio ranges (in females) between 15.6 and 17.3, in the latter (females) between 20.0 and 21.9; the single male *parabates* has a ratio of 13.7, the single male *ventrilineatus* 19.6. Tibia/snout-vent length ratio likewise is diagnostic between these two species, varying in *parabates* between 35.6 and 37.6 and in *ventrilineatus* between 38.3 and 43.0 (all females).

Observations and comments: The type series of *E. parabates* was collected under rocks and wood adjacent to a road through dense rain forest in the Sierra de Neiba (southern range). The forest in this area was composed of hardwoods and some *ebano verde* (*Magnolia dominguensis*) and in the vicinity were low areas which supported small marshes with cat-tails, a rather unusual feature for such a high elevation.

The members of the *dimidiatus* group, as presently understood are:

dimidiatus Cope (with its race *amelasma* Schwartz)

emiliae Dunn

intermedius Barbour and Shreve

albipes Barbour and Shreve
jugans Cochran
ventrilineatus Shreve
parabates Schwartz

Of these, four are Cuban and three are Hispaniolan; two of the Hispaniolan species occur on the south island, and the other just across the Cul de Sac-Valle de Neiba plain, in the Sierra de Neiba. *Ventrilineatus* and *parabates* are slightly aberrant in that they both possess short vomerine series. *Parabates* also has digital discs; as originally diagnosed (Dunn, 1926:210) this group was composed of members with very feebly developed discs. Aside from the color features which Dunn considered as diagnostic of the group, the structural features regarded as pertinent are: 1) discs present and small, or absent, 2) smooth belly, 3) long vomerine series (or short in two species), 4) no external vocal sac, 5) squatly habitus, and 6) inguinal glands absent. The last character may well not be valid; I have examined only *dimidiatus*, *jugans*, *ventrilineatus* and *parabates* for this feature.

Of the included species, *E. dimidiatus*, as Shreve and Williams (1963:338) pointed out, is somewhat different in that it lacks the stoeky build of the remaining forms. It too is the only known species which is not restricted to high elevations, although it does occur at high elevations in the Sierra de Trinidad and Sierra de Grand Piedra in Cuba. As far as known, *emiliae* occurs only in the Sierra de Trinidad, and *intermedius* and *albipes* in the Sierra Maestra.

There is a possibility that *E. unicolor* Stejneger is the single Puerto Rican representative of the *dimidiatus* group. Relying on Stejneger's (1904:597-598) description of the type, I feel that *unicolor* agrees with my concept of the group in all features except that the belly is granular rather than smooth. Additionally, it is a high mountain form, and thus agrees with most *dimidiatus* group species. No Jamaican species are obviously associated with the *dimidiatus* group.

I have had field experience only with *dimidiatus*. At least this species is vocal; the call is an insect-like twittering, males calling from the ground in mesic forested situations. No calls have been reported for any other species.

Specimens examined: Eleutherodactylus ventrilineatus: MCZ 19857-61, 19863 (type and paratypes), Mt. La Hotte (=Pic Macaya), Dépt. du Sud, Haiti; *Eleutherodactylus jugans*: MCZ

21594-95, MCZ 19852-56, plus four unnumbered specimens (type and paratypes), near La Visite, La Selle Range, Dépt. de l'Ouest, Haiti; USNM 95423-27 (paratypes), La Visite, Dépt. de l'Ouest, Haiti.

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B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS.

NOVEMBER 12, 1964

NUMBER 209

A NEW SKATE, *RAJA CERVIGONI*, FROM VENEZUELA AND THE GUIANAS

BY HENRY B. BIGELOW and WILLIAM C. SCHROEDER¹

RAJA CERVIGONI sp. nov.

Holotype: An immature male, 357 mm in total length, from 10 miles (16 km) northeast of Carúpano, in 20-30 fathoms (37-55 m), Museo Historia Natural La Salle, Venezuela, No. 873.

Paratypes: A male of 206 mm and a female of 229 mm from Punta Araya, Estado Sucre, in about 20 fathoms (37 m), from off the eastern part of Venezuela, and a male of 235 mm from off the Guianas, 07° 25' N, 54° 35' W, in 75-80 fathoms (137-145 m), "Oregon" station 2289.

Distinctive characters. Among rajids from the western Atlantic that have a pair of ocelli on the disc, *cervigoni* most closely resembles *Raja cyclophora* Regan 1903, but it differs in lacking dark mucous pores on the under surface, in having orbital and nuchal thorns, and 3 rows of thorns on the tail, whereas *cyclophora* has prominent blackish streaks below marking mucous pores, lacks orbital and nuchal thorns, and has a single row of thorns on the tail. In *cervigoni* the more sharply rounded outer corners of the disc, which is also relatively wider (averaging 73.2 per cent of the total length of the specimen on 4 individuals), distinguishes it from *texana* Chandler 1921 (average disc width 63.8 per cent on 23 specimens) and also from *ackleyi* Garman 1881 (average 59.4 per cent on 3 specimens): and its fewer thorns (16-26) in the midrow on the tail, between the axils of the pectorals and the first dorsal fin, together with the axis of greatest width further rearward (73-77 per cent, measured between the tip of the snout and axils of pectorals), set

¹ Contribution No. 1522 from the Woods Hole Oceanographic Institution.

it apart from *bahamensis* Bigelow and Schroeder² on which the thorns number 34-47 (4 specimens) and the greatest disc width is 64-69 per cent rearward.

Description of holotype. Proportional dimensions in per cent of total length.

Disc. — Extreme breadth 72.3; length 52.1.

Snout length. — In front of orbits 12.6; in front of mouth 14.6.

Orbits. — Horizontal diameter 4.4; distance between 4.2.

Spiracles. — Length 2.8; distance between 6.5.

Mouth. — Breadth 8.4.

Exposed nostrils. — Distance between inner ends 8.2.

Gill openings. — Length 1st 2.0; 3rd 2.0; 5th 1.5; distance between inner ends, 1st 15.6; 5th 8.0.

First dorsal fin. — Height 3.1; length of base 5.3.

Second dorsal fin. — Height 3.1; length of base 4.8.

Pelvics. — Anterior margin 13.2.

Distance. — From tip of snout to center of cloaca 47.6; from center of cloaca to 1st dorsal 33.0; to tip of tail 52.4; from rear end of 2nd dorsal to tip of tail 3.7.

Interspace. — 1st and 2nd dorsals 5.6.

Disc 1.4 times as broad as long; maximum angle is front of spiracles 102° ; snout pointed; anterior margins of disc nearly straight, outer corners sharply rounded; posterior and inner margins moderately convex. Axis of greatest breadth 73 per cent of distance back from tip of snout to axils of pectorals. Tail rather slender, the lateral folds low down, originating a little in advance of tips of pelvics, widening somewhat posteriorly as usual among rajids, reaching tip of tail; length of tail from center of cloaca to origin of first dorsal fin 0.70 times as great, and to its tip 1.10 times as great as distance from center of cloaca to tip of snout.

A row of 7 thorns along the anterior and inner margins of each orbit and a tiny thorn opposite inner margin of each spiracle and 2 over tip of rostrum. Three prominent thorns along the midline in the nuchal region, followed by a row of about 40 thorns which originates about midway between the rear margin of orbits and axils of pectorals, reaching to first dorsal fin, the first few thorns very small; 4 thorns in the interdorsal space. A row of about 30 thorns low down each side of the midrow on tail, beginning opposite axils of pelvics, reaching to opposite and second dorsal, very small rearward.

² In press (Bull. Mus. Comp. Zool.).

Most of the thorns on tail alternate in size. The upper surface of disc and tail otherwise smooth. A short row of 8 or 9 pale mucous pores each side and close to the first two nuchal thorns. Lower surface with small prickles on end of snout and in a narrow band along margin of disc from snout to about opposite mouth.

Snout in front of orbits 2.9 times as long as orbit; its length in front of mouth 1.8 times as great as distance between exposed nostrils. Distance between orbits about equal to length of orbit. Orbit 1.6 times as long as spiracle. Nasal curtain and expanded outer margin of nostrils fringed. Jaws moderately arched. Teeth $\frac{42}{40}$, arranged in quincunx, with ovate base and triangular cusp.

Distance between first gill openings 1.9 times as great as between exposed nostrils; between 5th openings about equal; first gill openings 0.45 times as long as longest diameter of orbit. Dorsals similar in shape, and nearly so in size, the interspace about equal to length of base of first dorsal. Second dorsal confluent with the caudal fin the base of which is shorter than that of the second dorsal. Pelvics deeply concave, scalloped along anterior side of excavation, weakly so rearward; anterior lobe slender, about $\frac{1}{5}$ as long as distance from its own origin to rear tip of pelvic; posterior lobe with sharply rounded tip, extending about $\frac{2}{5}$ the distance from axil of pectorals to first dorsal. The claspers of this immature specimen extend only to the tips of the pelvics. Rostral cartilage firm, narrow, extending nearly to tip of snout. Anterior pectoral rays reaching 58 per cent of the distance from axis through front margin of orbits to end of snout.

Color. Upper surface, including dorsals, plain medium brown. A prominent ocellus on each side of disc, situated a little posterior to the greatest axis of disc, its center from the midline of disc a distance about equal to that from tip of snout to anterior $\frac{1}{3}$ of orbit; distance between centers of ocelli 1.1 times distance to centers of orbits. The ocellus is formed by a narrow black-brown circle 14 mm in diameter, within which two dark spots are present on the left ocellus and one spot on the right. Below, plain whitish on disc and pelvics, with no dark mucous pores, the tail with pale brown blotches.

The three paratypes agree closely with the holotype in most proportional dimensions and otherwise, the chief variations being as follows: anterior angle of disc 104° - 109° ; orbital thorns 3, of which 2 are along anterior margin and 1 at inner rear

margin; 2 nuchal thorns; thorns in midline to first dorsal, beginning opposite axils of pectorals, 15-16; 2 thorns between dorsals; side row of thorns on tail, originating opposite axils of pelvics and ending opposite second dorsal, 16-21; these vary slightly in number from side to side; few of the tail thorns alternate in size; snout in front of orbits 2.6-2.8 times as long as orbit, its length in front of mouth 1.8-2.0 times as great as distance between nostrils; space between dorsals about $\frac{3}{5}$ - $\frac{4}{5}$ as long as base of first dorsal. Teeth $\frac{36}{33}$ — $\frac{40}{37}$, with low triangular cusp. On the lower surface, the narrow band of prickles along the anterior margin of disc is present, extending from near tip of snout to about opposite the axis midway between nostrils and mouth.

The color above is plain brown, the ocelli each with one small roundish dark brown spot centrally, on two specimens, the spot being irregular in shape on one specimen. Below, the disc and pelvics are pale, the tail with faint brownish blotches as on the holotype. The distance between centers of ocelli is about 0.9 times the distance to centers of orbits.

We thank Dr. Alwyne Wheeler of the British Museum (Natural History) for furnishing pertinent data on Regan's specimens of *cyclophora* and Drs. Paulo de Miranda Ribeiro and Azeu Lemos de Castro for checking certain characters on a number of *cyclophora* in the Museu Nacional collection, Rio de Janeiro; Harvey R. Bullis, Jr., of the U. S. Fish and Wildlife Service for the Guiana specimen of *cervigoni*; and Dr. Fernando Cervigón of the Estación de Investigaciones Marinas de Margarita for the opportunity to describe the Venezuela specimens and for whom we are pleased to name this species.

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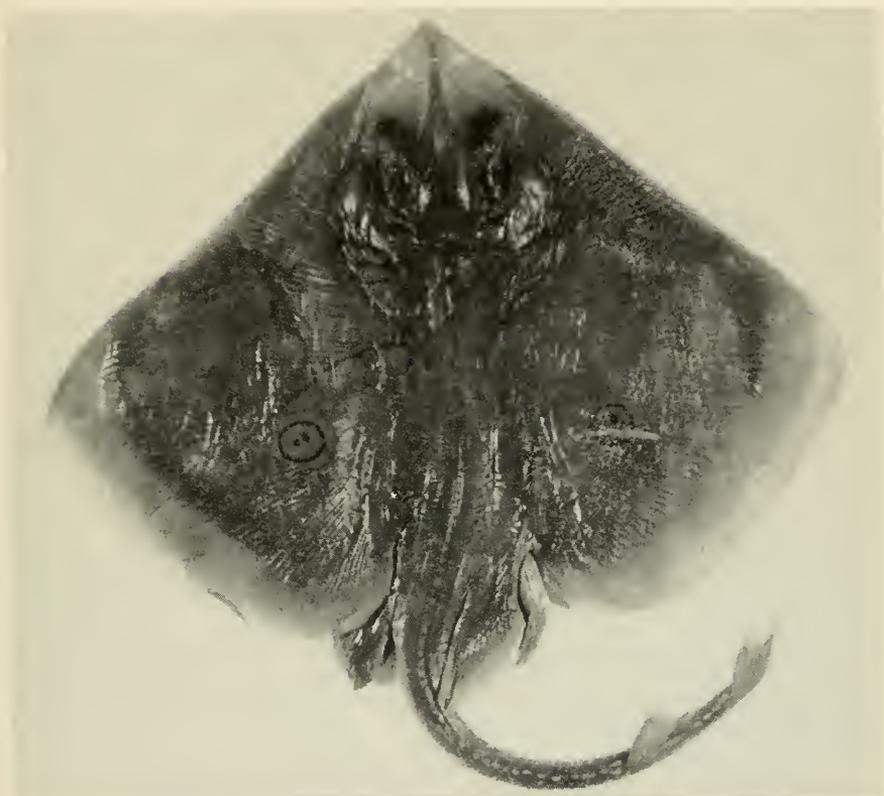
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Raja cervigoni sp. nov., holotype, immature male, 357 mm long.

B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS.

NOVEMBER 12, 1964

NUMBER 210

THE ANTS OF THE FLORIDA KEYS

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The Florida keys should be of more than usual interest to zoogeographers on several grounds. They are an extensive subtropical archipelago adjacent to the United States mainland, easily reached by a main highway that runs for almost their entire length. They are in the hurricane belt, providing an opportunity to study the effects of severe periodic storms on population dynamics and dispersal. Finally, they are separated by the Florida current of the Gulf Stream — a narrow but formidable faunistic barrier — from the topographically similar Bimini Islands, with which they can profitably be compared.

These advantages induced me to make a special collecting trip in June, 1958, to conduct an initial faunal survey. Time permitted only several islands to be investigated thoroughly. I selected Key Largo, Plantation Key, Big Pine Key, and Key West in order to insure the maximum geographic spread and diversity of habitats (see Davis, 1943, and Duellman and Schwarz, 1958). The ant fauna of the Bimini Islands had already been surveyed by M. R. Smith (1954), while other studies of Floridian ants were available in the publications of Wheeler (1932) and Van Pelt (1956, 1958).

The project was supported in part by a grant from the National Science Foundation. I am grateful to my wife Irene for her assistance in the collection of specimens and recording of ecological information.

ZOOGEOGRAPHIC ANALYSIS

In Table 1 the Keys fauna is classified according to nest site and probable origin. From a consideration of this partition plus

other data given in the Systematic List later, the following generalizations are permissible.

1. Elements introduced by human commerce are numerically more prominent in both species and individuals than on the Florida mainland. Eight of the 30 species recorded, or 26.7 per cent, are in this category. In the Welaka Reserve in central Florida, according to published data by Van Pelt (1958), 8 of 75 species, or only 10.7 per cent are in this category. The prevalence of introduced "tramp" species is shared with most other small islands in the tropics, including Bimini, hence is a distinctly "insular" trait. (Of 12 introduced species occurring jointly in the Keys and Welaka Reserve, only four are held in common: *Cardiocondyla emeryi*, *Tetramorium guineense*, *Monomorium floricola*, and *Paratrechina longicornis*.)

2. The Antillean elements are mostly arboricolous, whereas the Floridian elements are mostly terricolous.

3. Most of the arboricolous (hence Antillean) elements are very well adapted to life in the mangrove swamps, maintaining unusually dense populations there. The same species also occur, for the most part, in other habitats in the interiors of the Keys.

4. The arboricolous elements make up a disproportionate part of the Keys fauna. Twelve of the 30 species, or 40 per cent, are in this ecological category; on the other hand, only 12 of 75, or 16 per cent, are arboricolous in the Welaka Reserve of Central Florida. Judging from data by Smith (1954), the Bimini fauna resembles that of the Florida Keys in this respect; of 23 species for which there is ecological information, 8 or 34.8 per cent are arboricolous.

Generalizations (2), (3), and (4) are probably interrelated. The mangrove swamps provide an excellent portal into such small islands as the Florida Keys. They form an extensive, persistent habitat around most of the margins of the islands. During severe storms, such as the famous hurricanes of 1935 and 1960 (Craighead and Gilbert, 1962), the mangroves were badly damaged but not exterminated. In 1960 many tree branches were torn loose and undoubtedly transported long distances by sustained winds of 140 mph over a period of nearly 36 hours. Such debris, unless submerged in water or literally torn to shreds, should provide vehicles of transport for intact colonies

of the arboricolous ant species found in the Keys, although the point has not been confirmed. The rapid regrowth of the mangrove swamps would provide the means for the reproduction of these propagules.

The terricolous ant species, on the other hand, are not so well favored. Subterranean and log-dwelling colonies are not likely to be transported intact by the high winds. At the same time they are much more susceptible to mortality by drowning. In the hurricanes of 1935 and 1960, tides of 11 to 18 feet were reported. The effects on the ground ant fauna were not studied but must have been extensive.

In sum, it is reasonable to postulate a higher immigration rate and lower extinction rate for arboricolous species in comparison with terricolous species in the Florida Keys. Whether or not the fauna is in equilibrium (see MacArthur and Wilson, 1963), it follows that it should consist disproportionately of arboricolous species. Hence generalization (4) of the present study seems to have a reasonable explanation in one aspect of the physical environment. But further field studies before and after tropical storms are clearly needed to illuminate this interesting situation.

The faunas of the Florida Keys and Bimini Islands show some striking differences. There are, to begin with, the set of inferred ecological vicars listed in Table 2. In at least one case, *Solenopsis geminata* versus *Pheidole megacephala*, the two species are known to compete directly and replace each other on very small islands in the West Indies and Pacific. Whether this is also the case for the other pairs might be determined by experimental introductions. According to the hypothesis, such introductions of one vicar into the territory of the other should result in few successful colonizations.

Certain species appear to have no ecological equivalents. For the Bimini group this is true of the Antillean and endemic elements *Macromischa pastinifera*, *Smithistruma nigrescens*, and *Brachymyrmex obscurior*. For the Florida Keys it is evidently true of the species *Aphaenogaster miamiana* and *Xenomyrmex floridanus*. Again, experimental introductions, conducted for comparative purposes with exchanges of the hypothesized ecological equivalents listed above, might prove instructive. According to the hypothesis, this second class of introductions should prove relatively successful.

SYSTEMATIC LIST

PLATYTHYREA PUNCTATA (Fr. Smith)

Center of Key Largo, winged queen at light, June 14. Ranges from northern South America to southern Texas, also throughout the West Indies to the Bahamas and southern Florida.

ODONTOMACHUS RUGINODIS Wheeler

Key Largo, Big Pine Key.

According to W. L. Brown (*in litt.*) *ruginodis* is the correct name for the Floridian species, whereas *insularis* is correctly applied to the species referred to by Smith (1945) as *insularis* var. *pallens* Wheeler. *O. ruginodis* ranges from the United States through the West Indies to South America as far south as Paraguay. Within the United States it is found throughout Florida and reaches extreme southern Georgia and southeastern Alabama. An isolated population, probably introduced, occurs within the city limits of Mobile, Alabama.

This large ponerine, distinguished by its trap-like mandibles, was very abundant in undisturbed tropical hammocks in the center of Key Largo. Colonies were found nesting in cavities in the rather thick leaf litter. On Big Pine Key two colonies were found nesting beneath logs in open pine-palmetto woods.

PSEUDOMYRMEX ELONGATUS Mayr

Key Largo, Plantation Key, Big Pine Key, Key West (winged males in nest June 21).

Ranges from Brazil north through the West Indies to the Bahamas and southern Florida.

This typically tropical species was abundant on trees in open habitats, including mangrove swamps, lawns, and disturbed hammocks on Plantation Key. On Key Largo it did not penetrate the denser hammocks in the center of the island. Colonies were found nesting in hard dead twigs attached to living trees.

PSEUDOMYRMEX PALLIDUS Fr. Smith

Big Pine Key.

A species adapted primarily to savannas, *P. pallidus* ranges around the Caribbean from the West Indies through the coastal plain of the Gulf States into Mexico.

On Big Pine Key, *P. pallidus* occurred in both the mangrove swamps and on grass in the open pine-palmetto woods of the interior. Colonies were found nesting in dead hollow twigs attached to live mangrove trees.

CARDIOCONDYLA EMERYI Forel

Plantation Key, Key West.

A pantropical "tramp" species that originated in Africa and has been introduced in the New World, including the warmest parts of the Gulf States, by human commerce.

Workers were found foraging on hot, bare ground in open habitats during the day. The species is generally limited to the most disturbed habitats.

CREMATOGASTER ASHMEADI Mayr

Key Largo (a series in Museum of Comparative Zoology collected in 1904), Plantation Key, Big Pine Key, Key West.

Limited to the United States, from the Florida Keys north to North Carolina and southern Tennessee and west to Texas.

The workers occur in trees in mangrove swamps, lawns, and disturbed hardwood forest. None could be found in the deep hammocks of Key Largo. Nests were found in dead, dry branches of living trees and (in one instance) under loose bark on the trunk of a small tree.

PHEIDOLE FLORIDANA Emery

Big Pine Key (males in nest June 19-20).

The above specimens compare well with *floridana* syntypes and are closer to other Florida material placed with this species than to the closely related (and possibly conspecific) *flavens* Roger of Cuba and the Bahamas. Both *floridana* and *flavens* are highly variable but can be distinguished by apparently consistent sculptural characters in the soldier. *Floridana* is known only from Florida, and the Florida mainland is therefore the inferred source of the Keys population.

This small yellow species was abundant in open pine-palmetto woods, nesting in the soil beneath coral rock and rotting logs. Each colony appeared to contain between 100 and 200 workers.

APHAENOGASTER MIAMIANA Wheeler

Key Largo (North).

This native species, a typically Nearctic element, ranges over all or most of Florida, just reaching extreme southeastern Alabama.

A single colony, containing between 30 and 50 workers, was found nesting in a rotting log at the edge of a clearing in a dense tropical hammock.

TETRAMORIUM GUINEENSE (Fabricius)

Key Largo (Center).

This species originated in Africa and has been spread by human commerce throughout the tropics of both hemispheres. It is a characteristic element of disturbed habitats everywhere, even in the smallest, most remote oceanic islands.

Workers were found foraging at sunset on the trunk of a guava tree and fronds of a small royal palm in a lawn in the center of Key Largo.

TETRAMORIUM SIMILLIMUM (Fr. Smith)

Key West.

Like *T. guineense*, this little species evidently originated in Africa and has been spread by commerce throughout the tropics. Whereas *guineense* is predominantly arboreal, *simillimum* is mostly or entirely terrestrial.

PARACRYPTOCERUS (CYATHOMYRMEX) VARIANS (Fr. Smith)

Key Largo (North), Plantation Key (winged queens June 14), Big Pine Key, Key West.

According to W. W. Kempf (1958), *varians* occurs in southern Florida, south of Miami, in the Bahamas (Andros, New Providence, Bimini), and in Cuba and Jamaica. Previously published records of the species from Honduras, Trinidad, and northern South America were based on misdetermined specimens of *P. pallens* (Klug).

The species is abundant in the Florida Keys in a variety of major habitats. The workers are exclusively arboreal and nocturnal. Colonies were found nesting in hard, dead branches, one to two inches in diameter, attached to living trees of several species, including gumbo limbo, cocoplum, and mangrove. A

dealate queen, evidently in the act of nest-founding, was found in a dead branch on Plantation Key June 15. She was blocking the opening of a small cavity with her saucer-shaped head.

STRUMIGENYS GUNDLACHI (Roger)

Key Largo.

This characteristic Neotropical species also occurs in tropical Mexico, Central America, Trinidad, and the Greater Antilles. Brown (1959) records it from the Everglades National Park in Florida.

Two specimens, a worker and a dealate queen, were collected in leaf litter in a dense, relatively undisturbed hammock in northern Key Largo.

XENOMYRMEX FLORIDANUS Wheeler

Key Largo (North), Plantation Key (winged males June 14, winged males and queens June 16), Key West (males June 21).

According to the recent revision of the genus by Creighton (1957), *X. floridanus* occurs in southern and central Florida, the Bahamas, Cuba, and Mexico.

Colonies were found in abundance along the edge of forest and in mangrove swamps everywhere I collected. They nested exclusively in dead branches of trees. Workers were found foraging singly and in files during the day. They are apparently exclusively arboreal.

MONOMORIUM DESTRUCTOR (Jerdon)

Key Largo, Plantation Key.

This aggressive little species originated in the Old World tropics, possibly Asia, and has been spread by human commerce throughout the tropics.

Workers were abundant in lawns; a single colony was found nesting in the soil of a grassy roadstrip in North Key Largo.

MONOMORIUM FLORICOLA (Jerdon)

Key Largo (North), Plantation Key, Key West.

M. floricola is a pantropical tramp species that originated somewhere in the Old World tropics.

Several colonies were located in dead branches of standing trees at the edge of hammocks.

MONOMORIUM PHARAONIS (Linné)

Plantation Key.

This remarkable species is perhaps the ant most intimately associated with man. Originating in Africa, it has been spread by commerce throughout the world. In the tropics it nests out-of-doors in disturbed habitats, while in temperate zones it is abundant in greenhouses and dwellings. On Plantation Key it was discovered in both situations. Colonies were abundant in dead tree branches in disturbed native woods, and workers were foraging in the walls of a restaurant far from any native woods.

SOLENOPSIS (S.) GEMINATA (Fabricius)

Big Pine Key.

This species, commonly referred to as the native fire ant, is found throughout the New World tropics, ranging northward well into the Gulf States. A reddish color phase, to which the Big Pine Key series belongs, occurs through much of this range and in addition has been carried by human commerce to many parts of the Old World tropics. It is especially successful in open habitats.

On Big Pine Key workers were found foraging over the crushed coral surface of a parking lot.

SOLENOPSIS (EUOPHTHALMA) GLOBULARIA (Fr. Smith)

Plantation Key, Big Pine Key (winged queens in nest June 19-20).

S. globularia ranges from the extreme south of Alabama and Mississippi through Florida and the West Indies to Mexico, Central America, Brazil, and the Galapagoes (Creighton, 1930). Through much of this range it is limited to the coast. In coloration and propodeal sculpturing the Keys samples are closer to series from Florida (subsp. *littoralis* Creighton) than to series from Cuba, Haiti, and Puerto Rico. Hence the Keys population can be inferred to have originated from Florida.

Near the center of Big Pine Key a single colony was found nesting in soil under a piece of coralline rock in pine-palmetto woods.

SOLENOPSIS (DIPLORHOPTRUM) LONGICEPS M. R. Smith

Key Largo (North).

Workers collected at the above locality correspond well with

longiceps paratypes in body proportions, pilosity, and color but are somewhat smaller in size. *Longiceps* ranges from Florida to Texas north to Tennessee (Creighton, 1950).

A single colony was discovered nesting in a small cavity in firm leaf litter on the floor of an undisturbed tropical hammock.

SOLENOPSIS (DIPLORHOPTRUM) PICTA Emery

Plantation Key (winged queens and males in nest June 15, 1958); Lower Matecumbe Key (collection by W. M. Wheeler, 1930).

The species is known from extreme southern Alabama through Florida to the West Indies and Central America.

The Plantation Key colony was found nesting in a dead stem in disturbed native woods. *S. picta* is characteristically an arboreal species.

CYPHOMYRMEX MINUTUS Mayr

Key Largo (North) (winged queens and males in nest June 16); Plantation Key.

This common, primitive little fungus-grower ranges from extreme southern Alabama through Florida to the Bahamas, Greater Antilles, tropical Mexico, Trinidad, and South America as far south as Manaos.

On Key Largo a colony was discovered in a small, crumbling log in a relatively undisturbed tropical hammock. On Plantation Key one colony was nesting in the soil beneath a piece of coral-line rock. Another was in rotting wood in a tree hole about three feet from the ground. Both were in disturbed, open native woods.

TAPINOMA LITTORALE Wheeler

Key Largo (North), Plantation Key (males in nest June 15), Big Pine Key (males June 19-20), Windley Key (queens and males at light June 17).

The species is distributed from extreme southern Florida to the Bahamas, Cuba, and Puerto Rico.

This was one of the most abundant ant species in leaf litter on the floor of undisturbed tropical hammocks on Key Largo. Colonies were found nesting in small pieces of rotting wood buried in the litter. Colonies were also abundant in dead stems attached to living bushes and trees, especially in disturbed forest

on Plantation Key and the mangrove swamp around Big Pine Key. Each colony appeared to consist of 100 to 300 workers and, in at least one case, up to several nest queens.

CONOMYRMA PYRAMICA (Roger)

Big Pine Key, Key West.

This distinctive, terrestrial dolichoderine rauges from New Jersey to Florida west to Arizona and southward through the West Indies to Mexico, Central America, western South America and the Galapagos.

Colonies were found in open soil in elevated spots in the mangrove swamps.

PARATRECHINA (P.) LONGICORNIS (Latreille)

Key Largo, Plantation Key.

This species ranks with *Tetramorium guineense* as one of the most abundant and ubiquitous of all the pantropical "tramp" species of ants. It is characteristic of open, dry, highly disturbed habitats, from farmland to the centers of the largest cities. It originated somewhere in the Old World tropics.

On the Keys listed above, *P. longicornis* was common in completely open situations, especially around human dwellings. It was not found in the native woods. During a field trip to eastern Cuba in 1953, I noticed a similar distribution. *P. longicornis* workers abounded through sugar cane fields and along roads up to the very edge of the native forests that clung to limestone outcroppings; inside the forests, over a distance of only a few feet, they were replaced by native Cuban ant species.

PARATRECHINA (NYLANDERIA) BOURBONICA Forel

Key West.

This is another prominent pantropical "tramp" species of Old World origin. The Keys specimens have been compared with a syntype worker in the collection of the Museum of Comparative Zoology.

Workers were commonly seen foraging during the day at several locations on the streets of residential sections of Key West.

PARATRECHINA (NYLANDERIA) PARVULA (Mayr)

Key Largo (North).

The workers of species in the *parvula* complex are too similar

to make the present identification more than tentative. *P. parvula*, according to Creighton (1950), ranges from southern New York west to Iowa and Texas and south to Florida.

A single colony was found nesting in a small piece of rotting wood buried in leaf litter on the floor of a relatively undisturbed tropical hammock.

CAMPONOTUS ABDOMINALIS FLORIDANUS (Buckley)

Key Largo, Plantation Key, Big Pine Key.

C. floridanus is such a well-defined form with reference to the remainder of the *abdominalis* complex that it may well be a distinct biological species. I have used the trinomen in this case as an indication of the uncertainty of its biological status. *Floridanus* ranges from the east shore of Mobile Bay, Alabama, west through southern Georgia and south to the Florida Keys. The remainder of the *abdominalis* forms, which may or may not constitute a single species, range from southern Texas to Ecuador, the Amazon basin, and thence north again to the Lesser Antilles. The species is evidently absent from the Greater Antilles.

Floridanus is one of the most abundant and adaptable ant species in the Keys. It occurs in undisturbed and disturbed native hammocks and on the lawns around human dwellings but is evidently absent from mangrove swamps. Nests are formed in leaf litter, under rotting logs, and in dead branches of living trees. Workers forage during the day, mostly on vegetation.

CAMPONOTUS PLANATUS Roger

Plantation Key (winged queens and males in nest June 14-18), Key West.

The species is found in extreme southern Florida and Texas, Cuba, Mexico, and Central America.

C. planatus is a very abundant species in tropical hammocks but rare or absent elsewhere. On Big Pine Key one colony was found in a small, isolated hammock, but not a single specimen was collected in the extensive pine-palmetto woods that dominate the unsettled part of the island. Unlike *floridanus*, *planatus* is absent from the vicinity of human dwellings. Colonies were found nesting in dead tree branches, both attached to living trees and lying loose on the ground. The alert, swift-running workers forage during the day.

CAMPONOTUS TORTUGANUS Emery

Plantation Key (winged queen June 14), Big Pine Key.

As Creighton (1950) points out, the status of this form, originally described as a subspecies of the widespread tropical species *C. maculatus*, will remain unsettled until a careful revision can be made of the difficult species group to which it belongs. *Tortuganus* was originally described from the Dry Tortugas. As currently delimited it occurs on the Keys and in the Florida mainland as far north as Lake Worth.

A single colony was found beneath a rotting log in pine-palmetto woods on Big Pine Key.

CAMPONOTUS (COLOBOPSIS) sp.

Big Pine Key.

A single colony belonging to the subgenus *Colobopsis* was found nesting in a dead stem in a mangrove swamp on the south shore of Big Pine Key. It is similar to *C. impressus* (Roger) but differs sufficiently in the shape of the propodeum of the minor worker to warrant distinguishing it as a different, and possibly undescribed species. Additional materials considered in the context of a generic revision are needed to clarify the matter.

SUMMARY

Thirty ant species are listed from the Florida Keys. The disproportionate fraction of introduced species is cited as a typically insular feature of the fauna. Also, an exceptional prevalence of arboricolous (and Antillean) species is noted and is hypothesized to be the outcome of the periodic severe tropical storms that alter the Keys environment. Finally, comparisons are made with the nearby Bimini Islands fauna.

Table I

Ecology and Zoogeographic Origin of the Keys Species

Terrestrial

FLORIDIAN: *Aphaenogaster miamiana*, *Pheidole floridana*, *Solenopsis globularia*, *S. longiceps*, *Paratrechina parvula*.

ANTILLEAN: *Odontomachus ruginodis*, *Strumigenys gundlachi*, *Cyphomyrmex minutus*.

NATIVES OF UNCERTAIN ORIGIN: *Solenopsis geminata*, *Conomyrma pyramica*, *Camponotus tortuganus*.

INTRODUCED BY MAN: *Cardiocondyla emeryi*, *Tetramorium simillimum*, *Paratrechina longicornis*, *P. bourbonica*.

Arboreal

FLORIDIAN: *Crematogaster ashmeadi*.

ANTILLEAN: *Platythyrea punctata*, *Pseudomyrmex elongatus*, *Xenomyrmex floridanus*, *Solenopsis picta*, *Paracryptocerus varians*, *Tapinoma littorale*.

NATIVES OF UNCERTAIN ORIGIN: *Pseudomyrmex pallidus*, *Camponotus (Colobopsis) sp.*

INTRODUCED BY MAN: *Tetramorium guineense*, *Monomorium floricola*, *M. pharaonis*.

Both Terrestrial and Arboreal

FLORIDIAN: *Camponotus abdominalis floridanus*.

ANTILLEAN: *Camponotus planatus*.

INTRODUCED BY MAN: *Monomorium destructor*.

Table II

Ecological Equivalents (with Zoogeographic Origins)

Florida Keys	Bimini Islands	
<i>Odontomachus ruginodis</i>	<i>Odontomachus insularis</i>	
<i>Pheidole floridana</i> (Floridian)	<i>Pheidole flavens</i> (Antillean)	
<i>Solenopsis geminata</i> (Neotropical)	<i>Pheidole megacephala</i> (introduced)	
<i>Crematogaster ashmeadi</i> (Floridian)	<i>Crematogaster steinheili</i> (Antillean)	
<i>Cyphomyrmex minutus</i> (Antillean)	<i>Trachymyrmex jamaicensis</i> (Antillean)	
<i>Camponotus bermudezi</i> (Antillean)	} <i>Camponotus floridanus</i> (Antillean)	
<i>C. lucayanus</i> (endemic)		} <i>C. tortuganus</i> (Antillean?)
<i>C. ramulorum</i> (Antillean)		
<i>C. (Colobopsis) culmicola</i> (endemic?)		<i>C. (Colobopsis) sp.</i> (endemic?)

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B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS.

DECEMBER 21, 1964

NUMBER 211

A NEW SPECIES OF THE SNAKE *LEPTOTYPHLOPS* FROM COLOMBIA

BY BENJAMIN SHREVE

In a shipment of snakes sent to me for identification by Hermano Nicéforo Maria of the Instituto de La Salle of Bogotá, Colombia, one appears to represent an undescribed species. Another specimen, in the Museum of Comparative Zoology collection, is apparently of the same species.

Thanks are due the following individuals for lending comparative material from the collections in their charge: Mr. Charles M. Bogert of the American Museum of Natural History (AMNH), Dr. Doris M. Cochran of the United States National Museum (USNM), Miss Alice G. C. Grandison of the British Museum (Natural History) (BMNH), and Dr. William Duellman of the University of Kansas Museum of Natural History (UKMNH).

The new snake will be given a name suggested by the exceedingly low dorsal scale count.

LEPTOTYPHLOPS BREVISSIMA sp. nov.

Holotype. Museo del Instituto de La Salle No. 1311, from Florencia, Caquetá, Colombia, collected by Nicéforo Maria February 10, 1951.

Paratype. MCZ No. 38950 (taken from the stomach of *Micrurus mipartitus* (Duméril, Duméril and Bibron), MCZ No. 21988, from Sonsón, Antioquia, Colombia, collected by Nicéforo Maria in 1925. This specimen has about a third of the head missing on the right side.

Diagnosis. Apparently most closely related to *Leptotyphlops macrolepis* (Peters) and *L. anthracina* Bailey, from which it differs in a lower dorsal and subcaudal count (Table 1), and in

coloration (brown rather than black as in *anthracina* and without the prominent white borders of the ventral scales of *macrolepis*). Also related to *L. dugandi* Dunn to which it is nearest in longitudinal dorsal count (but without overlap, Table 1). *L. dugandi*, however, has still fewer subcaudals and a very different coloration: a whitish unmarked venter, a striped dorsal pattern, and a whitish fore part of the head.

Description. (Paratype variation in parentheses.) Snout rounded; supraocular present, small; rostral extending nearly to level of eyes; nasal completely divided into two; ocular bordering the lip; three labials, two in front of, and one behind the ocular; second labial not reaching the eye; six lower labials; 14 scales around body at midbody; dorsal scales from rostral to tail spine 152 (164); subcaudals 13 (14).

Coloration in alcohol. Above, dark brown; below, light brown; scales, both above and below, narrowly bordered with whitish. The coloration resembles quite closely that of *L. goudotii* (Duméril and Bibron).

MEASUREMENTS (in millimeters)

	head and body	tail
holotype	63	5
paratype	127	11

Remarks. The paratype was formerly identified as *L. macrolepis* by the late Karl P. Schmidt, who found it during his work on the coral snakes. It may be that other specimens of *brevissima* have been similarly misidentified; longitudinal counts have been made all too infrequently.

The dorsal coloration of the two species is quite similar.

The ventral coloration of *macrolepis* gives the impression of a whitish ground color covered with brown spots, as each ventral scale has a brown spot in its center with much of the ground color visible around it. In contrast, the ventral coloration of *brevissima* appears to be a uniform light brown, but on close examination it is seen that each scale has a very narrow light border.

The coloration of *anthracina* appears to be even more similar to that of the new form. The pattern of spotting on each scale seems identical, but the brown coloration of *brevissima* is represented by black in *anthracina* (or gray in some preserved animals).

In order to shed more light on the relationships, material referred to *macrolepis* was borrowed from various institutions. The following *macrolepis* were examined: *Venezuela*. Caracas: USNM 62206, 107891. Chama, 200 meters: BMNH 1905.5.31.63. El Valle, Federal District: AMNH 59406. Mérida, 1600 meters: BMNH 1903.4.28.12, 1904.6.30.2-5. Pauji, Acosta District: MCZ 48752-3, 48918. Puerto Cabello: BMNH 1913.9.10.2. No definite locality: BMNH R.R.1964.33. *Colombia*. In swampy country of the Choco: MCZ 39705. New Grenada, Amazonas: AMNH 17538 (in very poor condition). *Brazil*. Manés, Amazonas: AMNH 91642. *British Guiana*. Rupununi District, north of Aearahy Mts., west of New River: UKMNH 69821.

E. R. Dunn (1944, p. 52) lists specimens of *macrolepis* from the following localities of Colombia: *Norte de Santander*: Ocaña (1200 meters), two; *Santander*: Barichara (1336 meters), three; San Gil (1095 meters), four; *Tolima*: Mariquita (535 meters), one; Guamo (402 meters), one; Chaparral (800 meters), two.

It can be seen from this list and the material mentioned previously that there is no absolute evidence of sympatry between the new form and what is regarded as *macrolepis*. In addition, there is no positive evidence that all of Dunn's material was properly identified; he only reports the longitudinal dorsal scale count of one example and this is, of course, a critical point in separating the species. Unfortunately, all the Colombian material examined by Dunn was consumed by fire some years ago at the Museo del Instituto de La Salle.

The dorsal and subcaudal counts of the specimens of *macrolepis* examined, and those taken from the literature, are 202-246 and 16-26, respectively. Those taken from the literature are those of J. A. Roze (1952, p. 153), E. R. Dunn (1944, p. 52) and J. R. Bailey (1946, pp. 3, 4). It may be that with such a wide range of extremes in these counts, more than one form is involved. At all events, the dorsal scale counts are considerably higher than those of *brevissima* (152-164).

Among the specimens received on loan as *macrolepis* was AMNH 35953 from Balzapamba, Ecuador. This has 183 dorsal scales from rostral to tail spine, 16 subcaudals, the usual 14 scales around midbody, and a head and body measurement of 113 mm, tail 12 mm. In these characters and in coloration the specimen matches *anthracina*, the only member of this complex known from Ecuador; as *anthracina*, it represents the third known locality for this species.

L. anthracina with scale counts (J. R. Bailey, 1946, p. 3) of 182-189 dorsals and 15-19 subcaudals is closely related indeed to *brevissima*. It may be that *anthracina* and *brevissima* are only subspecifically distinct. If so, it may be that the very low dorsal counts of *brevissima* may represent "character displacement" in northern *anthracina* populations, sympatric with *macrolepis*.

However, the difference in coloration between *anthracina* and *brevissima* or *macrolepis* is not readily explainable on this hypothesis. It would be expected that *anthracina*, outside the range of *macrolepis*, would be as similar in coloration as it is in scales to *macrolepis*, instead of exhibiting a coloration which is more different from that of *macrolepis* than is that of *brevissima*.

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TABLE 1

	<i>brevissima</i>	<i>anthracina</i>	<i>macrolepis</i>	<i>dugandi</i>
dorsal longitudinal scale count:	152, 164	182-189	202-246	172-184
subcaudal scale count:	13, 14	15-19	16-26	9-12
dorsal color:	dark brown	black	brown	striped
ventral color:	light brown	black	spotted (scales with wide white borders)	whitish
head color:	dark brown	black	brown	whitish

B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS.

DECEMBER 30, 1964

NUMBER 212

A NEW SPECIES OF FRESHWATER GASTROPOD MOLLUSC OF THE GENUS *SAULCA* FROM THE MIOCENE OF KENYA

By THOMAS PAIN¹ AND DAWN BEATTY

The genus *Saulca* Gray 1867 (family Ampullariidae) has a thin, wholly corneous operculum, as found in the American genus *Pomacea*, and in this respect differs widely from the other African Ampullariidae, all of which have a calcareous operculum. The corneous opercula are unfortunately not known in a fossil state.

The only recent species of the genus *Saulca* is *S. vitrea* (Born)=*Helix vitrea* Born (1780, p. 383, pl. 15, figs. 15-16), originally described from an unknown locality, but now known to occur in the West African coastal regions of Liberia and Sierra Leone. The anatomy is at present unknown.

The possibility of the occurrence of *Saulca* in East Africa was first suggested by V. E. Fuchs (1936, p. 100) who considered a poorly preserved fossil from the Kaiso (Pleistocene) beds of Lake Albert as possibly referable to this genus. Adam (1957, p. 48), however, pointed out that this strongly carinated shell was more probably a *Viviparus*, perhaps a form of his own species *V. cori* from the same deposit, and he later (1959, p. 15), correctly in our opinion, listed it in the synonymy of that species.

In 1962, Dr. B. Verdecourt very kindly sent to the senior author for examination a fossil shell, in the form of an internal cast in limestone, from Miocene deposits at Kirimon, east of Lake Baringo, Kenya, which, in spite of its poor state of preservation, he had no hesitation in referring to the family Ampullariidae (Pain, *in* Verdecourt, 1963, p. 7, fig. 10). This species is dextral in form, with a short, conical spire and somewhat barrel-shaped body whorl, features typical of the genus *Saulca*.

It was not, however, sufficiently well preserved to make a description of it possible.

Recently we have, through the kindness of Prof. Bryan Patterson of the Museum of Comparative Zoology, Harvard University, received for study two further examples of this fossil collected at Kirimon by the Harvard University 1963 Kenya Expedition. These are both in a far better state of preservation than the original specimen, and have convinced us that all represent a so far unknown fossil species of *Saulca*, which is described and figured herein. It is to be hoped that future collecting at Kirimon will produce further and perhaps even better preserved specimens of this unique fossil, which has established beyond reasonable doubt the existence of this genus in East Africa in Miocene times, and its probably far wider distribution during the Tertiary period.

SAULEA Gray

Saulca Gray, 1867, p. 1000. Type species by monotypy: *Helix vitrea* Born.

SAULEA LITHOIDES n. sp.

Holotype. MCZ 28018, internal cast.

Paratype. MCZ 28017, internal cast.

Horizon and locality. Late(?) Miocene, at Kirimon, approximately 42 miles east of Lake Baringo and 38 miles SSE of Maralal, Kenya, East Africa.

Diagnosis and description. An internal cast in limestone; $5\frac{1}{2}$ whorls are preserved, the apex being decollate; the spire short, somewhat convex, the body-whorl oval or barrel-shaped in outline and a little inflated at the periphery, $\frac{3}{4}$ the total length; umbilicus very narrow, columella erect, curving slightly toward the base. Aperture of moderate width, vertical, oblong. The outer lip and base of the columella are missing in all the material examined.

Measurements (in millimetres; approx. only)

Length	Greatest width		
44	32	MCZ 28017	Paratype
39	27	MCZ 28018	Holotype
34	30	Coryndon Museum	Topotype

The authors' thanks are due to Prof. Bryan Patterson for the loan of material for study, to Mr. T. E. Crowley for much helpful advice and to Mr. R. F. Cumberland for photographing specimens for reproduction herein. The collection of the specimens was made possible under National Science Foundation Grant GP-1188.

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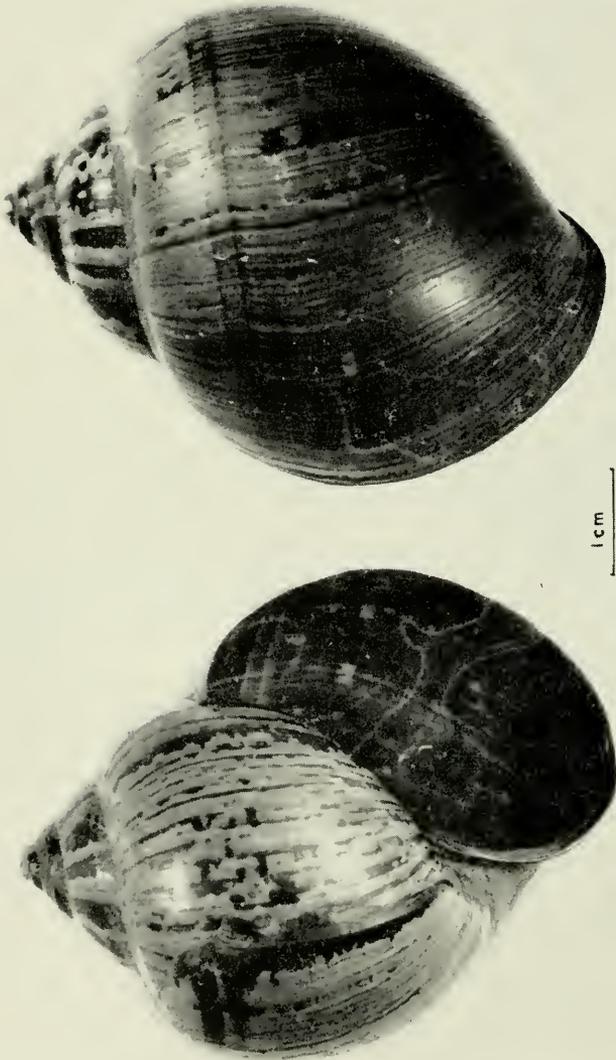


Plate 1. *Saulea villosa* (Born) Liberia (Pain Coll.).

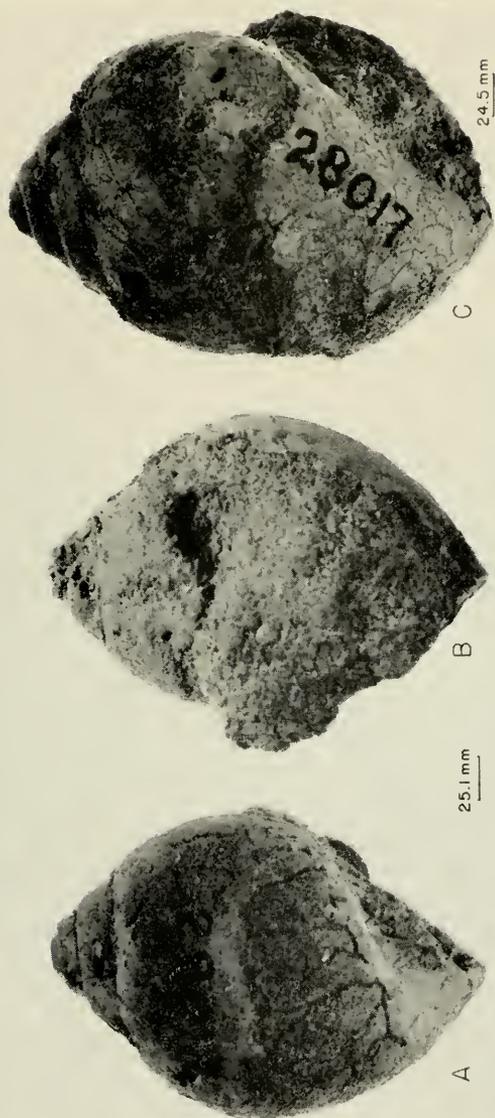


Plate 2. A, B, *Saulea lithoides* sp. nov. Kenya, Holotype (MCZ No. 28018). C, *Saulea lithoides* sp. nov. Paratype (MCZ No. 28017).

B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS.

JANUARY 11, 1965

NUMBER 213

A HITHERTO OVERLOOKED *ANODONTA* (MOLLUSCA: UNIONIDAE) FROM THE GULF DRAINAGE OF FLORIDA

By RICHARD I. JOHNSON

In their reports on the mollusks of the Gulf drainage of Florida, Vander Schalie and Clench and Turner have included under *Anodonta imbecilis* Say a number of records which belong to the species here described as distinct.

I take pleasure in naming this species for my wife Peggy, who along with our two small daughters and S. L. H. Fuller, accompanied me during an extensive survey of Florida for Unionidae during the summer of 1962.

ANODONTA PEGGYAE new species

Anodonta imbecilis [sic] Vander Schalie, H., 1940, *Lloydia*, 3:196, pl. 2, fig. 4; non Say 1829.

Anodonta imbecilis Say 1829, *partim*. Clench, W. J. and Turner, R. D., 1956, *Bull. Florida State Mus.*, 1:187, pl. 6, fig. 2. The figured specimen becomes a paratype of *Anodonta peggyae*, MCZ 251041.

Holotype: MCZ no. 251040, from the SE shore of Lake Talquin [formed by a dam on the Ochlockonee River], Leon County public fishing ground, Leon Co., Florida.

Paratypes: Figured paratypes, MCZ 251041; additional paratypes, MCZ 191840, all from the same locality as the holotype.

Measurements

Length	Height	Width	
mm	mm	mm	
71	43	24	Holotype
54	33	19	Paratype MCZ 251041
46	28	16	Paratype MCZ 251041

Description: Shell small to medium, reaching a little over 80 mm in length; length to height ratio approximately 2 to 1. Outline subrhomboidal, valves slightly inflated, thin, fragile and smooth. Anterior end regularly rounded, posterior end more broadly rounded and slightly biangulate just above the base. Ventral margin broadly curved and obliquely descending. Dorsal margin straight or slightly curved, usually forming a distinct wing-like angle where it meets the obliquely descending posterior margin. Posterior ridge broadly rounded, posterior slope sometimes slightly concave and located toward the anterior third of the shell. Umbos low and broad, not extending above the dorsal margin, their sculpture consisting of seven or eight low, delicate, slightly double-looped undulations. Periostracum smooth and shiny, except the posterior slope which may be slightly roughened, straw-yellow to yellowish green, sometimes very dark green, with numerous, generally fine, green rays over the entire surface. The rays are distinctly darker on the posterior slope.

No hinge plate or teeth; muscle scars inconspicuous and poorly defined. Naere bluish white and iridescent.

Habitat: Prefers sandy or muddy bottoms of ponds and sluggish streams.

Remarks: In the Gulf drainage, *Anodonta peggyac* can be confused with *A. imbecilis* Say, in whose company it is often found, and with *A. coupcrriana* Lea. These three species have umbos which do not extend above the dorsal margin, a character which distinguishes them from all other *Anodonta* of the Gulf drainage.

A. imbecilis has an elongate elliptical shell, with a posterior point which ends near the medial line, an almost straight ventral margin which is parallel to the dorsal one, and a periostracum which is rather uniformly green. *A. peggyac* differs from *imbecilis* in that, with the hinge line held horizontal, it has a subrhomboidal shell with a less acute point located near the base, a ventral margin which slopes obliquely from the dorsal one, and a periostracum which has numerous green rays that are especially fine on the disk.

A. coupcrriana differs from both *imbecilis* and *peggyac* in that *coupcrriana* has a shell which is much higher in proportion to its length than either of the others, with a posterior point which ends near the medial line as in *imbecilis*; and though the ventral margin is roughly parallel to the dorsal one, it is broadly

and uniformly curved. When *couperiana* has rays at all, they are usually even finer than those of *peggyac*.

From the Choctawhatchee River system to the Ochlockonee River system (the southern terminus of *imbecilis* Say) *A. imbecilis* and *A. peggyac* are often found together, while in peninsular Florida *A. peggyac* and *A. couperiana* are geographically separate.

As the figured holotype of *Anodonta couperiana* could not be located in the United States National Museum, the syntype, USNM 86673 is here selected as the lectotype and is figured on Plate 2, figure 4 of this report. The type of *Anodonta imbecilis* Say, which should be in the Academy of Natural Sciences of Philadelphia, is lost.

Distribution: Gulf drainage of Florida, from the Choctawhatchee River system to the Hillsborough River system.

SPECIMENS EXAMINED

CHOCTAWHATCHEE RIVER SYSTEM

Choctawhatchee River Drainage. — *Alabama*: Choctawhatchee River, 8 mi. SW Abbeville, Henry Co. Bushy Point Lake, Choctawhatchee River; Inlet Lakes, Choctawhatchee River; *both* Walton Co. Horseshore Lake, Choctawhatchee River, Washington Co.

Holmes Creek Drainage. — *Florida*: Holmes Creek, 1 mi. W Graceville, Jackson Co.

APALACHICOLA RIVER SYSTEM

Chipola River Drainage. — *Florida*: Spring Creek, Merritts Mill, 3 mi. E Marianna, Jackson Co. Chipola River, Scotts Ferry, Chipola River, Pole Bluff Landing; Dead Lake of Chipola River, Chipola Park; Dead Lake of Chipola River, Chipola Pines, Idlewood; *all* Calhoun Co.

Apalachicola River Drainage. — *Florida*: Mosquito Creek, Chattahoochee, Gadsden Co.

Flint River Drainage. — *Georgia*: Flint River, Bainbridge; Four Mile Creek, 3 mi. SW Bainbridge; Blue Spring, Flint River, 7½ mi. W Recovery; *all* Decatur Co. Spring Creek, 2½ mi. S Reynoldsville, Seminole Co.

OCHLOCKONEE RIVER SYSTEM

Ochlockonee River Drainage. — *Florida*: Little River, 7 mi. SW Havana, Gadsden Co. Ochlockonee River, 8 mi. W Tallahassee; SE shore, Lake Talquin; *both* Leon Co. Ochlockonee River, 7½ mi. E Hosford, Liberty Co.

WAKULLA RIVER SYSTEM

Florida: Wakulla River, 15 mi. S Tallahassee, Wakulla Co.

ST. MARKS RIVER SYSTEM

Florida: St. Marks River, Natural Bridge Sink, Leon Co.

SUWANNEE RIVER SYSTEM

Suwannee River Drainage. — *Florida*: Suwannee River, Oldtown, Dixie Co. Suwannee River, Fannin Springs, Gilchrist Co.

WITHLACOOCHIEE RIVER SYSTEM

Withlacoochee River Drainage. — *Florida*: Withlacoochee River, 1 mi. NW Lacoochee, Pasco Co. Little Withlacoochee River, Rerdell, Hernando Co. N shore, Lee's Lake, Panasoffkee; Lake, 6 mi. NNW Panasoffkee; *both* Sumter Co. SW shore, Lake Tsala Apopka, Floral City, Citrus Co. NW shore, Lake Tsala Apopka, Hernando Co.

HILLSBOROUGH RIVER SYSTEM

Florida: Blackwater Creek, 8 mi. N Plant City; Hillsborough River, 4 mi. NE Temple Terrace; *both* Hillsborough Co.

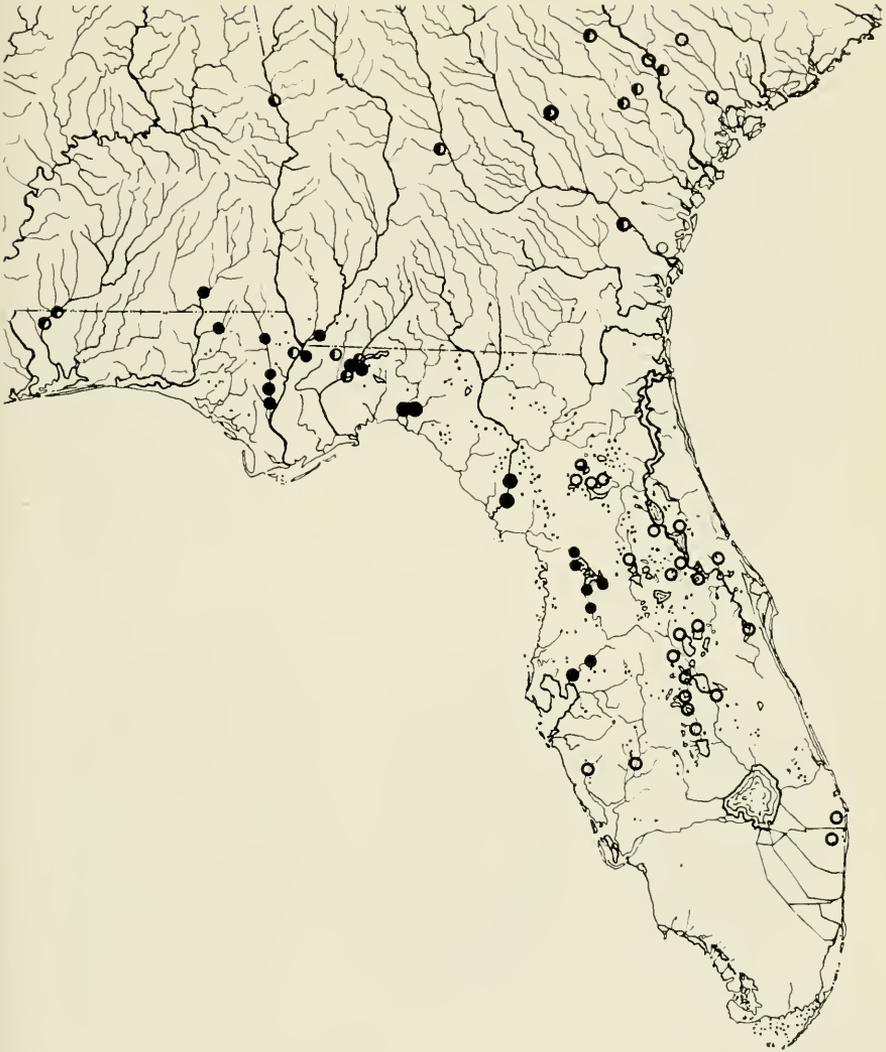


Plate 1

The known distribution of *Anodonta peggyae*, n. sp. in the Gulf drainage of Florida is represented by a closed circle.

The known distribution of *Anodonta imbecilis* Say in the southeastern United States is represented by a partially filled circle.

The known distribution of *Anodonta couperiana* Lea is represented by an open circle.

Plate 2

Fig. 1, *Anodonta peggyae*, n. sp. Lake Talquin, Leon Co., Florida. Holotype, MCZ 251040. Length 71, height 43, width 24 mm (slightly reduced).

Fig. 2, *Anodonta peggyae*, n. sp. Paratype, MCZ 251041. Length 54, height 33, width 19 mm (slightly reduced).

Fig. 3, *Anodonta peggyae*, n. sp. Paratype, MCZ 251041. Length 46, height 28, width 16 mm (slightly reduced).

Fig. 4, *Anodonta cooperiana* Lea. Hopeton, near Darien [McIntosh Co.], Georgia. Lectotype, here selected, USNM 86673. Length 67, height 38, width 29 mm (slightly reduced).

Fig. 5, *Anodonta imbecilis* Say. SE shore of Lake Talquin, Leon County public fishing ground, Leon Co., Florida. MCZ 251042. Length 71, height 38, width 25 mm (slightly reduced).

Fig. 6, *Anodonta imbecilis* Say. MCZ 251042. Length 71, height 36, width 22 mm (slightly reduced).



B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS.

FEBRUARY 15, 1965

NUMBER 214

A REVISED CLASSIFICATION OF THE DENDROCHIROTE HOLOTHURIANS

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Recent studies on some unusual dendrochirote holothurians and examination of available data on fossil holothurians have led us to conclude that the hitherto accepted classification of the dendrochirote holothurians conceals some important evolutionary trends. In this article a new classification is proposed in which tentacle numbers are abandoned as criteria for diagnosing major taxa; instead, importance is attached to the shape of the calcareous ring, the shape of the tentacles, and the calcareous deposits of the body wall. The reasons for such changes in classification are given in detail elsewhere (Fell and Pawson, in press).

NEW TAXA

Certain genera which were hitherto grouped in the order Dendrochirotida are known to lack the richly branched tentacles which are so characteristic of other genera within that order. These genera with essentially unbranched tentacles also share other important features, which suggest a natural grouping of three families. We therefore propose a new order to accommodate these families.

Order DACTYLOCHIROTIDA nov.

Diagnosis: Tentacles 8-30 in number, not branched but digitiform or digitate, the digits sometimes bifurcate. Body enclosed

in a test comprising imbricate plates. Calcareous ring simple, lacking complex posterior processes.

Included families: Ypsilothuriidae Heding, 1942; Rhopalodiniidae Perrier, 1902; and a third family, diagnosed here as new:

Family VANEYELLIDAE nov.

Diagnosis: Anus and mouth at opposite ends of the body, which is U-shaped or fusiform. Plates in the body wall with or without small spires. Tentacles 10-20 in number.

Included extant genera: *Vaneyella* Heding and Panning, 1954 (type genus by tautonymy); *Mitsukuriella* Heding and Panning, 1954.

The order Dendrochirotida as now restricted may be diagnosed as follows:

Order DENDROCHIROTIDA Grube, 1840
(restricted herein)

Diagnosis: Tentacles 10-30 in number, richly branched. Calcareous ring simple or with complex posterior processes. Test sometimes well developed, or reduced to non-contiguous calcareous spicules.

Morphological and paleontological evidence (Fell and Pawson, in press) suggests that this order includes some very primitive extant holothurian genera. These genera seem best assigned to new families; one new genus and two new families are diagnosed here:

Family PLACOTHURIIDAE nov.

Diagnosis: Body completely enclosed in a test of imbricate plates without spires. Sole lacking. Calcareous ring long, slender, with long posterior processes.

Included extant genus: *Placothuria* n.g.

PLACOTHURIA n.g.

Diagnosis: Tentacles 10, richly branched. Body U-shaped. Calcareous ring long, with posterior processes composed of a mosaic of small pieces.

Type-species: *Stolus huttoni* (Dendy) (illustrated in Pawson, 1963, pl. 7).

Etymology: The generic name is derived from the Greek *plax* (a plate) and *Holothuria*, and refers to the test formed by overlapping plates. Gender, feminine.

A second new family within the order Dendrochirotida is proposed:

Family PARACUCUMIDAE nov.

Diagnosis: Body completely invested in a test of imbricate scales with spires. Sole lacking. Calcareous ring simple, lacking posterior processes.

Included extant genus: *Paracucumis* Mortensen, 1925.

A REVISED CLASSIFICATION

The relationships of the orders Dendrochirotida and Dactylochirotida are discussed elsewhere, in the broad context of the inferred evolution of the Holothuroidea (Fell and Pawson, in press). From the new data the following revised classification of holothurians emerges:

Subclass DENDROCHIROTACEA Grube, 1840

(Nomen translatum herein, ex Dendrochirotae Grube, 1840)

Introvert (with retractor muscles) always present. Tubefeet and respiratory trees usually present. Madreporite free in the body cavity. Mesentery of the posterior loop of the intestine in the right or left ventral interradius. Free tentacle ampullae lacking. Gonad in two tufts, one tuft to each side of the dorsal mesentery.

Order DENDROCHIROTIDA Grube, 1840

(restricted herein)

Tentacles richly branched, 10-30 in number.

Key to Included Families

- 1 (6) Body partly or completely invested by plates.
- 2 (5) Body enclosed by a test comprising conspicuous imbricate plates; sole lacking.
- 3 (4) Calcareous ring complex, with long paired posterior processes.
 Placothuriidae nov. (Included extant genus: *Placothuria* nov.)

- 4 (3) Calcareous ring simple, lacking posterior processes Paracucumidae nov. (Included extant genus: *Paracucumis* Mortensen, 1925)
- 5 (2) Body invested dorsally by conspicuous plates; sole present. Psolidae Perrier, 1902 (Included extant genera: *Psolus* Oken, 1815; *Stolinus* Selenka, 1868; *Psolidium* Ludwig, 1886; *Lepidopsolus* Bronn, 1860; *Thyonepsolus* Clark, 1901)
- 6 (1) Body more or less naked, not enclosed by a test; calcareous deposits small, inconspicuous.
- 7 (10) Calcareous ring complex, with paired or unpaired posterior processes.
- 8 (9) Processes composed of a mosaic of small pieces Phyllophoridae Ostergren, 1907 (emend. herein). (Included subfamilies: Phyllophorinae Ostergren, 1907; Sempieriellinae Heding and Panning, 1954; Thyoninae Panning, 1949).
- 9 (8) Processes entire Sclerodactylidae Panning, 1949 (Nomen translatum herein, ex Sclerodactylinae Panning, 1949). (Included subfamilies: Sclerodactylinae Panning, 1949; Cladolabinae Heding and Panning, 1954).
- 10 (7) Calcareous ring simple, lacking posterior processes Cucumariidae Ludwig, 1894 (emend. herein). (Included subfamilies: Cucumariinae Ludwig, 1894; Colochirinae Panning, 1949 [partim?]; Thyonidiinae Heding and Panning, 1954).

Order DACTYLOCHIROTIDA nov.

Tentacles digitiform or digitate, the digits sometimes bifurcate, 8-30 in number. Body enclosed by a test comprising imbricate plates. Calcareous ring simple, lacking complex posterior processes.

Key to Included Families

- 1 (4) Anus and mouth at opposite ends of the body, which is fusiform or U-shaped.
- 2 (3) Plates with a prominent spine. Tentacles 8-10 in number. Ypsilothuriidae Heding, 1942 (Included extant genera: *Ypsilothuria* Perrier, 1886; *Echinocucumis* Sars, 1895; *Ypsilocucumis* Panning, 1949)
- 3 (2) Plates with small spines, or none. Tentacles 10-20 in number. Vancyellidae nov. (Included extant genera: *Vancyella* Heding and Panning, 1954; *Mitsukuriella* Heding and Panning, 1954)
- 4 (1) Anus and mouth opening close together, body flask-shaped. Rhopalodinidae Perrier, 1902 (Included

extant genera: *Rhopalodina* Gray, 1853; *Rhopalodinopsis* Heding, 1937).

The above arrangement of taxa is believed to reflect phylogenetic relationships more satisfactorily than that currently employed.

Of the fossil holothurian families defined by Frizzell and Exline (1955), the Calclamnidae (including genus *Thuroholia*) and some members of the Stichopitidae and Priscopedatidae should be included within this subclass.

OTHER HOLOTHURIAN GROUPS

In view of the above proposed revision of the Dendrochirotida, it is desirable to consider briefly the arrangement of the remaining holothurian orders, the Aspidochirotida, Elasipodida, Apodida and Molpadida.

ASPIDOCHIROTIDA AND ELASIPODIDA

Both the aspidochirotes and elasipods have tentacles which terminate in an approximately circular disc. The body is usually bilaterally symmetrical in both groups, with the dorsal tubefeet modified into papillae or warts (Aspidochirotida) or into elongate sensory processes (Elasipodida). The two groups are distinguishable on the basis of some anatomical features, but both may be conveniently placed into a single subclass, as follows:

Subclass ASPIDOCHIROTACEA Grube, 1840

(Nomen translatum herein, ex Aspidochirotae Grube, 1840)

Diagnosis: Tubefeet present, tentacles shield-shaped, 10-30 in number. No introvert, hence retractor muscles lacking. Body with conspicuous bilateral symmetry.

Key to Included Orders

- | | | |
|---|---------------------------------------------------------------------------------------------------------------------|-----------------------------|
| 1 | (2) Respiratory trees present. Mesentery of posterior loop of intestine attached to right ventral interradius | Aspidochirotida Grube, 1840 |
| 2 | (1) Respiratory trees lacking. Mesentery of posterior loop of intestine attached to right dorsal interradius | Elasipodida Theel, 1882 |

Theel (1882) has discussed the possible antiquity of the elaspod holothurians and concluded that they are certainly not representative of an ancestral holothurian stock; rather they are secondarily adapted to deep-sea life. In elaspods, and in some aspidochirotcs, the madreporite opens to the exterior, and does not hang free in the body cavity. This can be regarded, not as a primitive feature, but as a logical compensatory consequence of the absence of respiratory trees. The extremely fragile calcareous ring in elaspods is apparently secondarily reduced.

Within this subclass should be placed some representatives of the fossil families Priscopedatidae and Theelidae as defined by Frizzell and Exline (1955).

APODIDA AND MOLPADIDA

The important character shared by apodids and molpadids is the almost complete absence of tubefeet. Also both groups have simple digitate or pinnate tentacles. It is possible that the apodids and molpadids bear no close relation to each other, and the characters they have in common may have arisen through parallel evolution and convergence.

Subclass APODACEA Brandt, 1835

(Nomen translatum herein, ex Apodes Brandt, 1835)

Diagnosis: Tentacles simple, digitate or pinnate. Tubefeet markedly reduced, or, more usually, lacking altogether. No introvert, hence retractor muscles lacking. Deposits may include anchors and anchor plates.

Key to Included Orders

- 1 (2) Body cylindrical. Respiratory trees and anal papillae lacking. Deposits often include wheels Apodida Brandt, 1835
- 2 (1) Body fusiform, often with tapering caudal portion. Respiratory trees and anal papillae present. Wheels lacking Molpadida Haeckel, 1896

It is remarkable that some members of both Apodida and Molpadida have anchors and anchor plates in the body wall. The anchors and their plates differ morphologically in the two orders, but presumably have the same functional significance as accessory locomotor organs, since the anchors project through the body wall.

The fossil family Achistridae and some members of the fossil families Stichopitidae, Theelidae, Synaptitidae and Calcanoridae as defined by Frizzell and Exline (1955) may be included in this subclass.

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B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS.

FEBRUARY 15, 1965

NUMBER 215

TWO NEW SUBSPECIES OF *AMPHISBAENA* (AMPHISBAENIA, REPTILIA) FROM THE BARAHONA PENINSULA OF HISPANIOLA

By RICHARD THOMAS¹

As a result of collecting sponsored and led by Dr. Albert Schwartz during the summers of 1963 and 1964 in which I was fortunate to be able to participate, 33 specimens of *Amphisbaena* were collected in the low areas on and near the Barahona Peninsula of the Dominican Republic. The general affinities of these specimens are with *Amphisbaena innocens* Weinland. Comparison of the Barahona Peninsula specimens with representatives of the forms assigned to the species *innocens* shows them to be distinct in themselves, but to resemble most closely *A. i. gonavensis* Gans and Alexander. These authors, in their recent study of West Indian amphisbaenids (1962), examined the available Hispaniolan specimens and reviewed the forms. The combination *Amphisbaena innocens caudalis* Cochran was first used by them, and the new name *Amphisbaena innocens gonavensis* was proposed for the population on Gonave Island. Fourteen additional specimens of *gonavensis*, recently acquired by Dr. Ernest Williams, allow a better comparison of the Gonave and Barahona populations than was possible previously. Although the differences between the two populations are perhaps on a level of specific separation, their relationship with one another is obvious. I feel that relationships are best expressed by regarding these two as conspecific and distinct from *A. innocens*. These related amphisbaenids of Gonave Island and the Barahona Peninsula should therefore be known as *Amphisbaena gonavensis* Gans and Alexander.

In lacking major fusion of the head scales, *Amphisbaena gonavensis* is separable from all other West Indian *Amphisbaena* except *innocens* Weinland, *caeca* Cuvier, *bakeri* Stejneger

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and *fenestrata* Cope. From *fenestrata* and *bakeri* it is immediately separable on the basis of lower number of body annuli, 199-225 for *gonavensis* versus 236-249 for *fenestrata* and 239-254 for *bakeri*; from *fenestrata* it is additionally different in lacking the backward penetration of the rostral between the

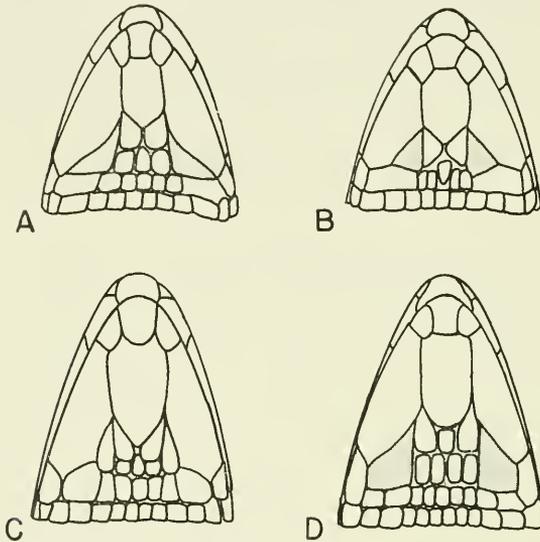


FIG. 1. Ventral views of the heads of four forms of *Amphisbaena*. The malar scales are stippled for points of reference. A, *A. g. gonavensis* (MCZ 80296), note three rows of postgenials and anterior penetration of first postgenials between genial and second infralabial; B, *A. g. leberi* (ASFS V2596), note two rows of postgenials and lack of anterior penetration of first postgenials (position of first two postgenials in *hyporissor* is intermediate between A and B); C, *A. innocens* (ASFS X3114); D, *A. caeca* (ASFS X7382).

nasals. From *A. caeca*, *A. gonavensis* may be distinguished in the possession of two scales in the first and second rows of postgenials (versus three for *caeca*). *Gonavensis* also differs from *caeca* in having enlarged precloacal scales forming a distinct convex flap as opposed to the relatively undifferentiated precloacals of *caeca*, and in hemipenial structure (see discussion).

Employing the concept of accessory dorsal half-annuli in the nuchal region, as expressed by Gans and Alexander (1962: 79-80), the first two body annuli in *innocens*, *gonavensis* and *cacca* typically correspond to three dorsal half-annuli (Fig. 2). *Gonavensis* (and *innocens*, typically) has the first complete annulus including (continuous with) the anteriormost of the first three dorsal half-annuli (temporals, postoculars, frontals) (Fig. 2, B-D). Exceptionally, the condition depicted in Figure 2 A occurs in *innocens*. Examination of 49 specimens of *A. cacca* shows the anteriormost half-annulus to appear split off from, instead of continuous with, the first complete body annulus (i.e. first ventral half-annulus) (Fig. 2, E-F).

A. gonavensis differs from its neighbor species *A. innocens* in the possession of a malar scale¹ (related to this are differences in shape and arrangement of the ventral head scales, Fig. 1), and in the condition of the first pair of parietal scales which normally are in contact apically (thus only narrowly) with one another at the midline or may even be slightly separated from contact by the second pair of parietals (Fig. 2, C-D). In *innocens* by contrast there are typically two or four large squarish parietals (there may be other small supernumerary scales present, but these do not alter the basic appearance) formed by the median scales of the second and third dorsal half-annuli (Fig. 2, A, B). *Gonavensis* is additionally distinguished from *innocens* in the shape of the tail which is rounded rather than tapered (Fig. 3, A, B), in the precloacal scales which form a more prominently convex flap, and in hemipenial structure (see below).

A. gonavensis is broader and shorter headed, has a less sharply pointed snout, and is distinctly smaller than *innocens*. The largest of 55 specimens of *gonavensis* measures 242 mm; of 73 *innocens* 17 measure more than 242 mm, the

¹The malar scale as defined by Gans and Alexander is a major and obvious difference between those *Amphisbaena* which possess it and those which do not. With respect to the species discussed here, the malar, possessed by *A. gonavensis*, seems at least in part homologous to the two end scales of the second row of postgenials of *A. innocens*. The advisability of denoting this scale with a separate name seems somewhat dubious inasmuch as it implies an all-or-nothing difference where there is really one of degree. Further, the designation of the row of scales behind the malar (the row just in front of the first body annulus) as postmalars in contrast to this row being merely the third row of postgenials in forms having no malar seems also inadvisable and misleading. The term "malar," however, is a very convenient one in description, and its usage is retained with the above comments duly noted. The postgenials are here used to apply to all rows of small scales between the genial and the first body annulus, including the "postmalar row" used by Gans and Alexander.

largest being 279 mm. Gans and Alexander noted that a single specimen from Petite Gonave (MCZ 25549) was at that end of the range of values (Gonave population) of several characters which was closest to the Cul-de-Sac sample of *innocens*. On the basis of the new material, this specimen falls within the range of the Gonave population in those characters for which the trend was most noticeable (body annuli, dorsal segments, postloacals). Numerical data used in above comparisons and in "Comparisons

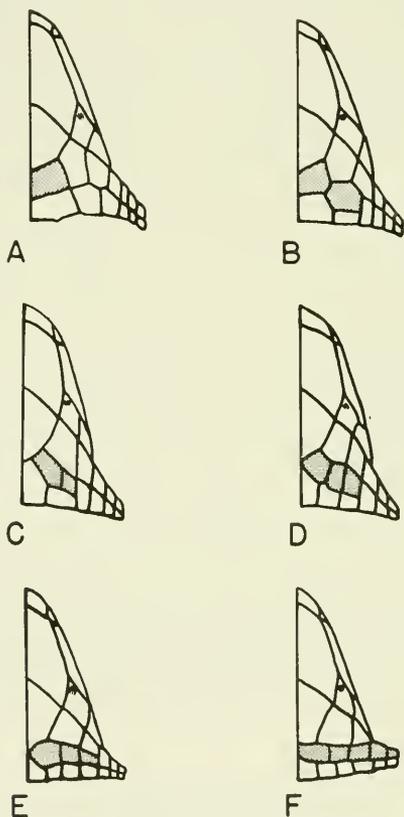


FIG. 2. Diagrammatic illustrations of *Amphisbaena* heads (dorsal view, half-heads) showing scalation differences. First two body annuli are shown "peeled out" from heads. *A*, atypical *A. innocens* (Camp Perrin); *B*, typical *A. innocens* (Camp Perrin); *C* and *D*, alternative common conditions of *A. gonavensis*; *E* and *F*, *A. cacca*. Stippled scales are second dorsal half-annuli (complete annulus in *F*). In *A-D* the second half-annuli are "accessory"; in *E* and *F* the first are "accessory."

and Discussion" below are in part obtained from Gans and Alexander's paper and in part from personal observation (see "Specimens Examined").

AMPHISBAENA GONAVENSIS HYPORISSOR new subspecies

Holotype: MCZ 77149, an adult male, collected 13.1 mi. (20.9 km) SW of Enriquillo, Pedernales Province, República Dominicana, 30 July 1963, by David C. Leber and Richard Thomas.

Paratypes: KU 79824-25, same locality as type, 22 July 1963, Richard Thomas; ASFS X9974-76, AMNH 92792-95, RT 754-55, UIMNH 55600-02, same data as type; MCZ 77150, República Dominicana, Pedernales Province, 5 mi. (8 km) NE Oviedo, 30 July 1963, Richard Thomas.

Diagnosis: A subspecies of *Amphisbaena gonavensis* characterized by lack of fusions of head scales, a high number of caudal annuli, more than six preloacals; an occasional caudal autotomy; and a mottled but faded coloration.

Range: Presently known from the southeastern portion of the Barahona Peninsula of Hispaniola.

Description of type (Fig. 4): (Methods of counting and terminology follow Gans and Alexander, except for differences in terminology already noted). Head scales not fused; prefrontals as broad or slightly broader anteriorly than posteriorly. First two body annuli correspond to three dorsal half-annuli. First pair of parietals border anteromedially on frontals and are occluded from apical contact by an anterior extension of the left second parietal. Genial .81 times as broad as long. Three rows of postgenials present; first row with two enlarged scales (an abnormal, minute middle scale is present), apex of each scale projecting slightly beyond malar-second infralabial suture between genial and second infralabial; second row with three scales not including the two large triangular malars at each end; third row with four scales not including the two enlarged, terminal "postmalars." Body annuli 213, four laterals on each side, and 20 caudal annuli. Sixteen dorsal segments and 24 ventral segments to an annulus counted at midbody. Four cloacal pores; 8 preloacal scales and 13 postloacals, including 2 median, rectangular postloacals. Snout-vent length 200 mm; tail 20 mm. Overall coloration tan, becoming darker and slightly mottled dorsally due to increasing amount of central dark pigmentation on more dorsal segments; four ventralmost segment rows without dark pigment spots.

Variation: The paratypes are similar to the type in the configuration of the first pair of parietals. Two have the first parietals in broad contact and squarish; in six they do not meet at the midline, the second pair of parietals contacting the frontals (Fig. 2C); in the balance of the paratypes the first pair of parietals are in apical or only narrow contact. Considerable asymmetry occurs in the degree of contact of the first pair of parietals with the midline. In all specimens of *hyporissor* the two scales of the first row of postgenials project not at all or only slightly beyond the malar-second infralabial suture and thus between the genial and second infralabial (Fig. 1). All paratypes have three rows of postgenials, the modal count being 2 + 3 + 4 but with variants of four and five in the second row and five in the third row. Body annuli vary from 199 to 221; laterals two to five (mode four), most permutations of these counts occurring except 2/2, 5/5, 4/5, and 5/2; caudal

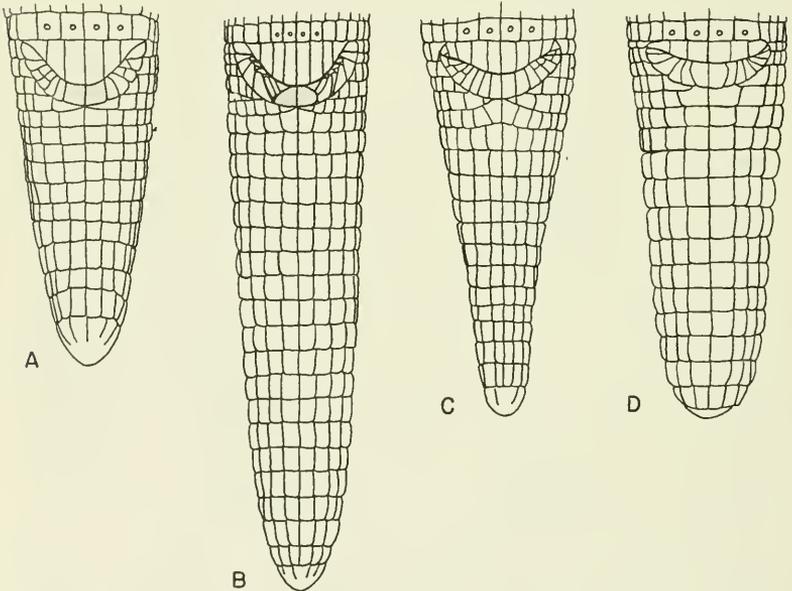


FIG. 3. Ventral views of the caudal and cloacal region of four forms. *A*, *A. g. gonavensis* (MCZ 80291); *B*, *A. g. leberi* (ASFS V2596, except for median postcloacals, is also typical of *hyporissor*); *C*, *A. innocens* (ASFS X3111); *D*, *A. caeca* (ASFS X940). Median postcloacals of *A* and *B* are stippled; those of *A* are typical of *gonavensis* and *hyporissor*; those of *B* are diagnostic of *leberi*.

annuli vary from 19 to 21 (mode 19). Dorsal segments of a midbody annulus are 16 (mode), 17 or 18; ventral segments are 22 (mode), 23 or 24; totalled midbody segments 38-42. Pre-cloacal scales range from eight to eleven; postcloacals from 12 to 14; totalled cloacals 20-24. There are two enlarged, median postcloacals; these are typically straight-sided (Fig. 3A). Cloacal pores are four in every specimen. The smallest specimen measures 106 mm total length (tail 10 mm), the largest 231 mm (tail 20 mm). Apparent caudal autotomy constrictions are evident between the fifth and sixth annuli of the tails of some of the juvenile specimens; adults do not possess obvious autotomy constrictions. One medium size specimen possesses a broken tail, presumably autotomized, missing beyond the fifth annulus. The coloration is pale tan, darker dorsally and with some scattered dark mottling; some specimens were noted as being purplish dorsally in life.

Specimens collected in the vicinity of the town of Pedernales in the northwestern section of the Barahona Peninsula represent a subspecies distinct from the other two known populations of this species. This form is named in honor of Mr. David C. Leber, for his enthusiastic participation in collecting in the Dominican Republic.

AMPHISBAENA GONAVENSIS LEBERI new subspecies

Holotype: MCZ 77218, an adult male, collected 5 km N of Pedernales, Pedernales Province, República Dominicana, 25 June 1964 by Richard Thomas.

Paratypes: MCZ 77219, same data as type; ASFS V2595-96, 8 km N of Pedernales, 26 June 1964, Richard Thomas; KU 79855-56, UIMNH 55627-28, ASFS V2676-78, AMNH 92827-28, Pedernales, 29 June 1964, Richard Thomas; RT 985, same locality as previous series, 3 July 1964, Richard Thomas. All specimens from Pedernales Province, República Dominicana.

Diagnosis: A subspecies of *Amphisbaena gonavensis* most closely related to *A. g. hyporissor* in the possession of a high number of caudal annuli, but differing from that form in contact of first pair of parietals with one another, in having typically two rows of postgenials, and in the configuration of the median postcloacals.

Distribution: Known presently from the low elevations of the northwestern portion of the Barahona peninsular region of Hispaniola.

Description of type: Head scalation much like that described for the type of *hyporissor*. First pair of parietals in broad contact across the midline giving a squarish appearance to the parietals. Two rows of postgenials present, two scales in the first row and five in the second. Anterior penetration of first two postgenials between the genial and second supralabial very slight. Body annuli 212; four laterals on each side; 16 caudal annuli. Sixteen dorsal segments and 22 ventral segments to an annulus counted at midbody. Four cloacal pores, nine precloacal scales and 14 postcloacal scales. Enlarged median postcloacal scales four. On each side of the midline, two median postcloacals separated by a transverse suture which curves posteriorly and laterally giving a rounded outline to the posterior two of these four scales (Fig. 3B). Total length 223 mm, tail 19 mm. Coloration generally like that of the type of *hyporissor*, but the tan is more uniform with less dark mottling.

Variation: Head scalation of the paratypes is much like that of the type. The first pair of parietals are in broad contact medially in all but one specimen in which the contact is slightly more than apical. First two postgenials typically have none or only slight anterior penetration between the genial and the second infralabial; the characteristic condition is that illustrated in Figure 1 B. Body annuli vary from 207 to 220; laterals two to five with the same variation noted for *hyporissor*; caudal annuli range from 16 to 19 (mode 19). Many specimens have the tips of their tails scarred; were this not so, higher caudal counts would probably be obtained. Dorsal segments of a midbody annulus are 15 (two specimens) or 16; ventral segments 22-25 (mode 24); totalled midbody segments 38-41. Precloacal scales range from 9 to 11; postcloacals 11-14; total cloacals 20-24. Median postcloacals are essentially the same as described for the type in all except one specimen in which they are very abnormal and fragmented and another in which the posterior scales reach the cloacal border between the two anterior scales which are reduced. Apparent caudal autotomy is found in one of the paratypes of *leberi* (UIMNH 55628) and in another specimen from Pedernales which is currently being kept alive. In both the tail is missing beyond the fifth annulus. Coloration is generally darker and more uniform than that of *hyporissor*. Hemipenes are everted or partially everted in four specimens; the organs are attenuated and naked; apparently they are only slightly bilobed (the most completely everted organs are not

bilobed, but terminal bifurcation of the dissected retractor penis indicates that they may be slightly bilobed when completely everted).

Comparisons and discussion: To facilitate comparisons of the three races of *A. gonavensis* the following table showing scale count data is presented.

TABLE 1. Scale count ranges for the three races of
A. gonavensis

	Body annuli	Caudal annuli	Total midbody segments	Pre-cloacals	Post-cloacals	Total cloacals
<i>gonavensis</i>	207-225	10-12	36-41	6-7	11-14	16-20
<i>hyporissor</i>	199-221	19-21	38-42	8-11	12-14	22-24
<i>leberi</i>	207-220	16-19	38-41	9-11	11-14	20-24

As shown by the table, *gonavensis* differs strikingly from the Barahona populations in the low number of caudal annuli. It further differs in scalation in the low number of preloacals (the condition of seven preloacals occurs in only one specimen), and in total cloacals. The specimens of *gonavensis* examined by me (18) and the type (not seen by me but illustrated by Gans and Alexander) are rather uniformly characterized by the first pair of parietals meeting in apical contact at the midline; in but three specimens was there a short suture between the parietals. As described above, *hyporissor* is generally, but much more variably, characterized by narrow contact of the first pair of parietals, while in *leberi* the parietals with one exception are in comparatively broad contact with one another. *Gonavensis* and *hyporissor* uniformly have three rows of postgenials, while *leberi* is typically missing a segment in the gular region and consequently has only two rows. Of the three exceptions noted, one is abnormal in having the "missing" segment partly intercalated between the second postgenial row and the first body annulus, a postgenial count of 2 + 4 + 2 being the result. The two scales of the first row of postgenials penetrate very far forward between the genial and the second infralabial in *gonavensis* (with 35 to 69 per cent of the length of the scale lying anterior to the malar-second infralabial suture); in *hyporissor* the penetration is less (10-30 per cent, four scales have no penetration); and in *leberi* even less (6-18 per cent, 11 scales have no penetration). The corresponding differences in the configuration of these scales can be seen in Figure 1 A, B. In the condition of the median postloacals, *gonavensis* and *hyporissor*

agree in having but two roughly rectangular, undivided scales (small marginal scales which are normally folded inside the cloaca are not considered). The condition which characterizes *leberi* and the one exception have already been noted. One specimen (ASF'S V2507) from approximately 10 km NW of Oviedo

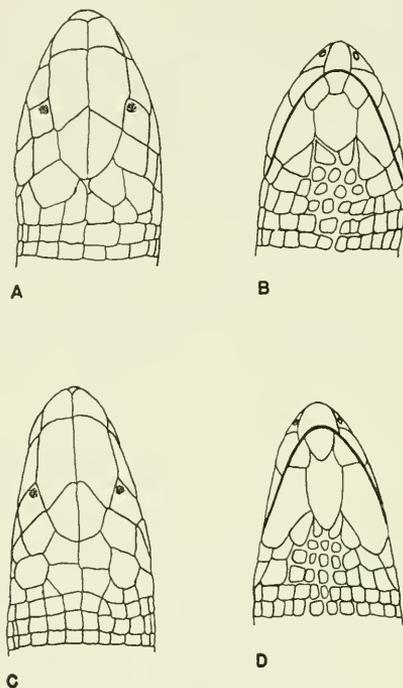


FIG. 4. A and B, dorsal and ventral views of the head of the type of *A. g. hyporissor* (MCZ 77149); C and D, dorsal and ventral views of a specimen of *A. innocens* from Camp Perrin (ASF'S X3123).

on the road to Pedernales has the *leberi* configuration of the median postcloacals; it also agrees more with *leberi* in the condition of the parietals, while in having three rows of postgenials it agrees more with *hyporissor*. More specimens are necessary from intermediate regions before the status of this specimen can be determined.

The presumed caudal autotomy noted for some specimens of *hyporissor* and *leberi* has not been observed in *gonavensis*, nor does it occur in *A. innocens* (both have relatively short tails).

Gans and Alexander noted that caudal autotomy is variable in some forms, e. g. *A. caeca*.

If the hemipenial structure noted for *leberi* holds true for the species as a whole, this will serve as an additional distinction from *A. innocens* and *A. caeca*. In contrast to the simple, naked structure of *leberi*, the hemipenis of *innocens* is strongly bilobed, very heavy and fleshy; the sulcus spermaticus bifurcates at the fork of the organ and each branch proceeds to the non-sulcate side and thence to the apices of the lobes which are flattened and disk-like. Proceeding from each branch of the sulcus spermaticus over each lobe and onto the distal sulcate surface of the organ are very fine but regular flounces. The non-sulcate surface is naked (from ASFS X3112). The hemipenes of *caeca* are of the same general appearance as those of *innocens*, but the sulcus spermaticus is much more prominent (thick edged) and forks slightly before the bifurcation of the organ itself; the apices are rounded not flattened, and there is no evidence of flouncing (from ASFS X937, X4111).

The distribution of the races of *Amphisbaena gonavensis* appears zoogeographically a bit strange at first glance (see Fig. 5). The possibility exists that it is in reality not so strange. The Cul-de-Sac plain, a channel (in places below sea level) between the north and south "islands" of Hispaniola (Williams, 1961) bordered on both sides by mountainous regions, debouches to the west at the angle between the Tiburon Peninsula and the main part of the island and to the east at the northeastern corner of the Barahona Peninsula just east of the Sierra de Baoruco. *A. gonavensis* may occur (or have occurred in the recent geologic past) up the eastern coastal fringe of the Barahona (presently almost nonexistent in places) and into the Cul-de-Sac plain. This being so, the island of Gonave would not be an unlogical extension of its range. The close affinities of *hyporissor* with *gonavensis* seem to support such a distribution. It is interesting to note that at least two other Hispaniolan lizards have a similar distribution. *Anolis brevirostris* Bocourt occurs along the eastern Barahona into the Cul-de-Sac, east to the Golfe de Gonave and on Gonave. *Diploglossus curtissi* Grant, though of wider distribution to the east and north (Schwartz, in press), also occurs along the eastern Barahona coast and is channelled to the west through the Cul-de-Sac (locality records not continuous) and occurs on Gonave.

It is interesting to note that despite the geographic continuity of the Sierra de Baoruco with the mountain mass of the Tiburon Peninsula, *Amphisbaena innocens* is not known from the Baoruco. On the contrary it is *A. manni*¹ which has been collected there. Gans and Alexander record four specimens of *manni* from near Paraiso at 1800 feet (about 600 m) (Fig. 5). In the summers of 1963 and 1964 we obtained four additional specimens (ASFS X9907-09, V2911) from the eastern end of the Sierra de Baoruco (see Fig. 5) at an elevation of 2600 feet. (790m). Although further collecting may prove otherwise, it appears that *manni* is geographically the nearest *Amphisbaena* to *hyporissor*, possibly even interposed between it and *innocens*. Comparable geographic relationships are seen in the species mentioned above as having distributions similar to the one predicated for *A. gonavensis*. *Diploglossus curtissi* and *Anolis brevirostris* are "replaced" in the highlands of the Sierra de Baoruco by other related species (*Diploglossus costatus* Cope and *Anolis distichus* Cope).

The type and most of the paratypes of *A. g. hyporissor* were collected in one of those occasional but not altogether rare situations where fossorial creatures such as *Amphisbaena* and *Typhlops* are found concentrated near the surface. Such localities are generally but not invariably characterized by a rather friable soil, a scattering of moderate to large sized trees, a covering of plant litter, and an abundance of rocks. This particular locality is a region of xeric woods inland from the western mangrove margin of the Laguna de Oviedo. The locality generally satisfied the above conditions; an abundance of limestone rocks was present. Aside from the amphisbaenids, two species of *Typhlops* were found in this region, *Typhlops* cf. *sulcatus* and another species (Thomas, MS). The localities to the north of Pedernales where *A. g. lcberti* was collected were similar to the locality just described, at least in degree of aridity. The locality at Pedernales, however, was somewhat more xeric; the tree cover was primarily *Acacia* with an undergrowth of scattered clumps of *Opuntia* growing among outcroppings of limestone rock; the soil was sandy. *Typhlops haitiensis*, *Typhlops*

¹ A further note of comparison between *gonavensis* and *manni* may be in order. *A. manni*, though distinct from *gonavensis* in having the nasals fused with the rostral, differs further in having the condition of the half-annuli in the nuchal region as described for *cacca* (vide supra), 6-9 (versus 4) cloacal pores, a comparatively stout tail with a very prominent autotomy constriction, and a deeply bilobed hemipenis. In meristic characters there are no striking differences.

sp. and *Leptotyphlops* sp. (Thomas, MS) were found in the same macrohabitat with *A. g. leberi* in the Pedernales region. In both of the localities where the two largest series were obtained, numbers of shed skins of these amphisbaenids were seen while collecting. Little can be said about the habits of these lizards from our encounter with them. They were mostly collected under rocks; their passageways were frequently evident. One grasped and held onto a rootlet with its mouth in a possible attempt to resist capture. None were found above ground in the open, and their abundance did not seem to be correlated with any weather phenomena.

SPECIMENS EXAMINED

Amphisbaena gonavensis hyporissor: As listed for type and paratypes.

Amphisbaena gonavensis leberi: As listed for type and paratypes.

Amphisbaena gonavensis hyporissor x *leberi*: República Dominicana; Pedernales Province, ca. 10 km NW Oviedo, ASFS V2507.

Amphisbaena gonavensis gonavensis: Haiti: Gonave Island: Pointe-à-Raquette, PM 3385 (allotype), PM 3386, 3388 (paratypes), MCZ 80289; Ti Palmiste, 6 km from Pointe-à-Raquette, MCZ 80290-302.

Amphisbaena innocens innocens: Haiti: Département de l'Ouest, Manneville, MCZ 62511, MCZ 8748; Thomazeau, MCZ 37595-97; Furey, MCZ 51417, ASFS X3862; Département du Sud, Camp Perrin, ASFS X3109-34, X3240-41, DRP 2403.

Amphisbaena innocens caudalis: Haiti, Grande Cayemite Island, MCZ 25550 (type), MCZ 25551 (paratype).

Amphisbaena caeca: Puerto Rico: Isla Verde, ASFS X937-43, X4104-25, X7381-98; 2.2 mi. SW Sabana, ASFS X7433-34.

ACKNOWLEDGMENTS

I wish to express my appreciation to Dr. Albert Schwartz, who allowed me to study this material gained as a result of his West Indian collecting; to Dr. Ernest E. Williams, Museum of Comparative Zoology at Harvard; Dr. Charles A. Reed, Yale Peabody Museum (PM); and Mr. Dennis R. Paulson (private collection, DRP) for loan of specimens in their care. I also wish to thank Mr. Ronald E. Klinikowski for executing some of the illustrations for this paper.

Types and paratypes designated herein now reside in the following collections: Museum of Comparative Zoology at Harvard (MCZ), American Museum of Natural History (AMNH),

University of Kansas Museum of Natural History (KU), University of Illinois Museum of Natural History (UIMNH), Albert Schwartz Field Series (ASFS), Richard Thomas private collection (RT).

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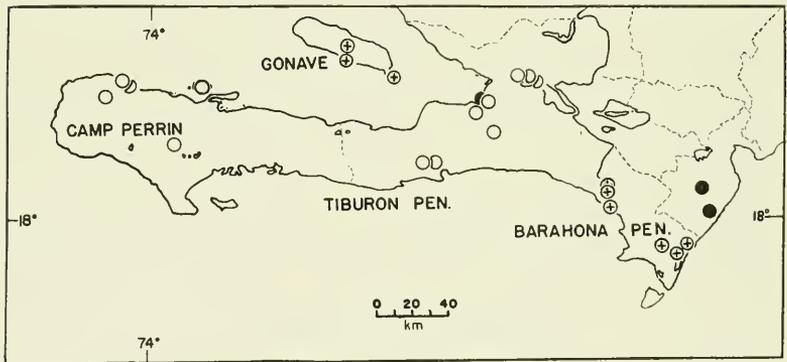


FIG. 5. Map of southwestern Hispaniola showing Gonave Island, the Tiburon Peninsula and the Barahona Peninsula with localities for the species of *Amphisbaena* (some localities are from Gans and Alexander, 1962). Hollow circles, *A. innocens*; circles with crosses, *A. gonavensis*; solid circles, *A. manni*.

B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS.

FEBRUARY 15, 1965

NUMBER 216

THE GEOGRAPHICAL VARIATION OF THE FROG *HYPEROLIUS MARMORATUS* (FAMILY HYPEROLIIDAE) IN RHODESIA, NYASALAND AND TANGANYIKA

By R. F. LAURENT

Mr. Vesey-Fitzgerald has generously provided the Museum of Comparative Zoology with several very interesting series of tree frogs collected in various localities of Rhodesia, Nyasaland and Tanganyika. Some of them belong to the marbled tree frog *Hyperolius marmoratus* Rapp, the geographical variation of which is so striking and has already required the recognition of many subspecies. This new material permits a summary of our knowledge of this species in eastern Africa plus some significant additions, including one very distinct new subspecies.

Thus far, the *marmoratus* subspecies recognized in the present area are as follows:

argentovittis Ahl: Shores of Lake Tanganyika.

rhodoscelis (Boulenger): Luapula River drainage and Lake Rukwa, Tanganyika. This is apparently a disjunct range and suggests that Lake Rukwa might have been part of the drainage of the Chambeshi River, which is itself loosely connected with the Luapula drainage through a swampy area south of Lake Bangweolo.

lestagci Laurent (a doubtful form): Lake Bangweolo.

melanoleucus Laurent: Primarily the Lufira basin in the Congo, but samples from Sakania (near the Rhodesian border) show conclusively that its range exceeds the limits of this drainage in a southward direction.

alborufus Laurent: Recently described (Laurent, 1964) from the Moxico Province, Angola, but also present in the Luabala District (southwestern Katanga). This race is likely to be found in the extreme northwestern part of Rhodesia.

aposematicus Laurent: Only known to me from Lealui. Probably restricted to Barotseland. Possibly intergrading with *alborufus* to the north.

rhodesianus Laurent: Described from Matetsi, Southern Rhodesia and presumably ranging into the Wankie region.

swynnertoni FitzSimons: Described from Chirinda, eastern Southern Rhodesia.

taeniatus Peters: Lowlands in Mozambique southward to northern Natal and eastern Transvaal.

albofasciatus Hoffman: Southern Nyasaland.

nyassae Ahl: Described from Langenburg. The precise location of this locality appears controversial. Loveridge has stated (1957, p. 329) that it is Manda, Lake Nyasa. Manda is on the eastern shore at 10°28' S. In the Gazetteer No. 1 (British East Africa) published by the United States Board on Geographic Names, no Langenburg is found, but there is a New Langenburg, which is Tukuyu. Tukuyu is near Rungwe where many other specimens of *nyassae* and *fülleborni* (which is a synonym) have been collected. This, therefore, sounds more probable as a type locality than Manda which is rather far from the Rungwe Mountains. Lastly, according to Stieler's Atlas (1905), Langenburg is on the eastern shore of Lake Nyasa, but almost at its northern tip. It would require fresh material from the Rungwe region and the northern part of Lake Nyasa to resolve the point.

Vesey-Fitzgerald's material includes good series from Lusaka, Seremje, Mazabuka and Lake Chilwa, in addition to series from Lake Tanganyika and Lake Rukwa, which merely confirm that *argentovittis* Ahl and *rhodoscelis* (Boulenger) are respectively present there.

HYPEROLIUS MARMORATUS MELANOLEUCUS LAURENT

Hyperolius melanoleucus Laurent, 1941, Rev. Zool. Bot. Afr., 34: 157, pl. VIII, figs. D, E, F. — Lukafu, Upper Katanga, Congo.

New material. 3 ♂♂, 1 ♀ (MCZ 37362-65), Lusaka, North Rhodesia, 7-9-III-1962; 1 ♀ (MCZ 38824), River Mwambeshi, north of Lusaka, North Rhodesia, 14-III-1963; 2 ♀♀ (MCZ 38807-08), Mkushi District, North Rhodesia, 3-IV-1963.

Color pattern. Two males (31-34 mm) have still the juvenile dull color pattern. The third male which is small (26 mm) and the female (34 mm) have the vivid "*melanoleucus*" markings: black with white bands and a few white spots. The pattern comprises essentially one mediodorsal and two laterodorsal main elements with some irregularities (branches, lumbar inflexions and isolated spots); in the female, the center or the axis of these white spots and bands shows red spots or lines. In the male with the adult pattern, these red markings exist only on the sides. The belly also shows red spots. In live specimens (I saw them very often when I was in Katanga) these red ventral markings stand out on the paler pink general coloration.

The female from Mwambeshi River (30 mm) has a somewhat disrupted pattern with red only on the sides, the belly and the throat. The two females from the Mkushi District have the usual pattern, with the remarkable feature that the red dorsal lines are very broad.

Range. The older record of this subspecies at Sakanian was already a proof that its range was not limited to the upper Lufira drainage. The specimens from North Rhodesia suggest that this range actually overlaps the Zambesi basin, at least in the Kafue drainage. It must be remembered, however, that two specimens with an adult pattern are far from an adequate sample and that a situation similar to that which I shall describe for the Serenje population is surely not excluded.

HYPEROLIUS MARMORATUS NYASSAE Ahl

Hyperolius nyassae Ahl, 1931, Das Tierreich, 55: 339, fig. 213. "Langenburg," northeastern shore of Lake Nyasa, Tanganyika.

Hyperolius fülleborni Ahl, 1931, Das Tierreich, 55: 349, fig. 224. "Langenburg," northeastern shore of Lake Nyasa, Tanganyika.

New material. 13 ♂♂, 2 ♀♀ (MCZ 38809-38823), Serenje, Chikoli River, North Rhodesia, 10-III-1963.

Color pattern. Three males have the juvenile pattern. One has a "*melanoleucus*" adult pattern. The nine others have irregular black spots, a few large ones or many small ones, with a general predominance of the light ground color. Red lines in the middle of the light network are generally distinct, but they are less conspicuous when the black spots are small and numerous. Three of the males have still a white mediodorsal band free of black spots (this is a remnant of a "*melanoleucus*")

pattern) as well as the red markings. One of the males has red spots on the throat. One of the females has a moderately disrupted "*melanoleucus*" pattern, with heavy red markings; in the other, the pattern is strongly disrupted and, like most males, still with clear red lines.

Size. Males with juvenile pattern: 31, 32, 35 mm. Males with adult pattern: 31 (2 specimens), 32 (1), 33 (4), 34 (1), 36 (2) mm. Females: 35, 36 mm.

Discussion and range. The pattern displayed by the majority of the specimens is quite different from the "*melanoleucus*" pattern. On the other hand, it appears identical with that of *fülleborni* Ahl over which the name *nyassae* Ahl, based on specimens with a juvenile pattern, has page priority. This judgment is confirmed by the comparison with two *fülleborni* paratypes. I still have misgivings about the identification of the new material from the Chikoli River because *nyassae* and *fülleborni* are based on populations coming from the northern part of the Lake Nyasa basin, while the Chikoli River seems to belong to the Luangwa drainage. However, there are already several examples in *Hyperolius marmoratus* of ranges which overlap two adjacent drainages while, on the other hand, ranges can also be separated by dividing crests or highlands as well as by escarpments and falls. Therefore, we must now admit that the range of the *nyassae* subspecies should be extended to include the Luangwa basin.

HYPEROLIUS MARMORATUS ALBOFASCIATUS Hoffman

Hyperolius albofasciatus Hoffman, 1944, Soolog. Navors. Nas. Mus. Bloemfontein: 178, fig. 8. Limbe, Nyasaland.

Hyperolius marmoratus albofasciatus, Loveridge, 1953, Bull. Mus. Comp. Zool., 110: 350. Limbe, Mtimbuka, Ruo River, Nyasaland.

New material. 3 ♂♂, 1 ♀, 6 juv. (MCZ 46186-95). Lake Chilwa (= Lake Shirwa), Nyasa, 3-X-1943.

Size. Males: 20.9, 22.7, and 23.9 mm. Female: 22.4 mm.

Color pattern. The four adults have the typical *albofasciatus* pattern; in the smallest male, however, the dark coloration is brown rather than black, reminiscent of the juvenile color. The juveniles show a strong tendency towards a longitudinal pattern similar to the "*bayoni*" pattern; this is not surprising, since this pattern is established in *taeniatus*, a Mozambican subspecies, which occurs not far from southern Nyasa. The shift to a longitudinal pattern occurs by the elongation in a backward direction

of the hour-glass spots which are located between the eyes and in the scapular region in the juvenile "undulatus" pattern. Similarly, the lumbar undulations of the *undulatus* pattern are also elongated, but in a forward direction.

Discussion. Loveridge (1953) rightly objected to my synonymizing *melanoleucus* with *albofasciatus* (Laurent, 1947b). Indeed, the red elements characteristic of the "melanoleucus" pattern are not apparent in *albofasciatus*. Another difference is that the sides are predominantly white in *albofasciatus*. This is similar to the situation in the southern subspecies (*marmoratus* and *verrucosus*) where the dark dorsal pattern is generally restricted to the back, showing no encroachment on the flanks. In *melanoleucus*, there is still a large black elongated spot on the sides or several smaller black markings. In addition, the juvenile pattern does not show any kind of elongation in *melanoleucus*.

The size of the specimens from Lake Chilwa is unusually small for the species. This striking peculiarity is not shared by the series collected at Limbe (type locality of *albofasciatus*), Mtimbuka and the Ruo River (Loveridge, 1953). Apparently the populations from Lake Chilwa, which seems completely isolated (i.e. without any efferent river), are dwarfed. An additional problem derives from the fact that the type of *albofasciatus* is an adult female of only 24 mm, which does not match the size of the frogs collected at Limbe by Loveridge, but corresponds to our Lake Chilwa series. Consequently, I wonder if the type was not actually collected on the shores of Lake Chilwa.

HYPEROLIUS MARMORATUS PYRRHODICTYON¹ subsp. n.

Holotype. 1 ♀ (MCZ 46182), Mazabuka, in the water-grass fringe of the Kafue River, 31-I-1963, North Rhodesia, Vesey-Fitzgerald coll.

Paratypes. 2 ♀ ♀, 1 juvenile, same data (MCZ 46183-85).

Diagnosis. A race of *Hyperolius marmoratus*, characterized by the absence of any spots or marbling on the back, and the presence of a dark red network on the belly and throat.

Color pattern. The absence of any definite dorsal pattern is not quite unique in the *marmoratus* group: it is characteristic of some well differentiated subspecies such as *rhodoscelis* (Boulenger) of the Luapula drainage (Congo and North Rhodesia)

¹ From the Greek for "red network."

and *karissimbiensis* Ahl of the region of the Karisimbi volcano. These two races differ in their juvenile patterns and their coloration in life: belly vermilion red with bluish flanks and a white laterodorsal streak in *rhodoscelis*, belly purple red with back almost entirely dark blue in *karissimbiensis*. I don't know the colors in life of *pyrrhodietyon*, but a red network on an otherwise white belly is a quite unknown feature in any other member of the genus *Hyperolius*.

On close examination under the binocular, it appears that some black spots may be present on the flanks, around the vent, and on the limbs along the boundary between the dorsal gray or brown (in alcohol) and the ventral red which becomes a solid color (not reduced to a network) on all the parts of the limbs that are hidden in the normal resting position of the tree frog. Therefore, as generally in the genus, the thigh is almost entirely vividly colored (red in this case) except for a dorsal stripe which is gray or brown. In the smallest of the two female paratypes, the black spots are also distinct on the throat between the meshes of the red network.

The juvenile is almost uniformly greyish.

Discussion. Since the juvenile, as sometimes happens in the *marmoratus* group, has no distinct pattern, specific identification may seem questionable. However, the morphology appears to be that of *H. marmoratus* which is different enough from that of other species to be relied upon at least tentatively.

Size. The holotype measures 32 mm, the two adult paratypes 30 and 26 mm respectively.

Range. Since there are only the four specimens from Mazabuka, we do not know the range of this form. Mazabuka is not far from the right bank of the Kafue River. We already know that the left part of the Kafue drainage is inhabited by *melanoleucus*, that *aposematicus* lives in the Upper Zambezi region (Barotseland), and *rhodesianus* exists to the south of the Zambezi in western Southern Rhodesia. Poynton (*in litt.*) believes that *aposematicus* cannot belong to the same species as *rhodesianus* since they do not form hybrid populations where they meet; if he is correct, we can expect similar discoveries in the future and the species *Hyperolius marmoratus* would then have to be split into several species. However, if the dividing line is the Zambezi itself or the Victoria Falls, the lack of a hybrid belt has no meaning at all, reflecting as it does mere physical inability to meet.

The real relations of *pyrrhodictyon* with the surrounding populations attributed to *H. marmoratus* will thus remain uncertain until more material is collected.

Acknowledgment. This work has been supported by National Science Foundation Grant NSF G-1342.

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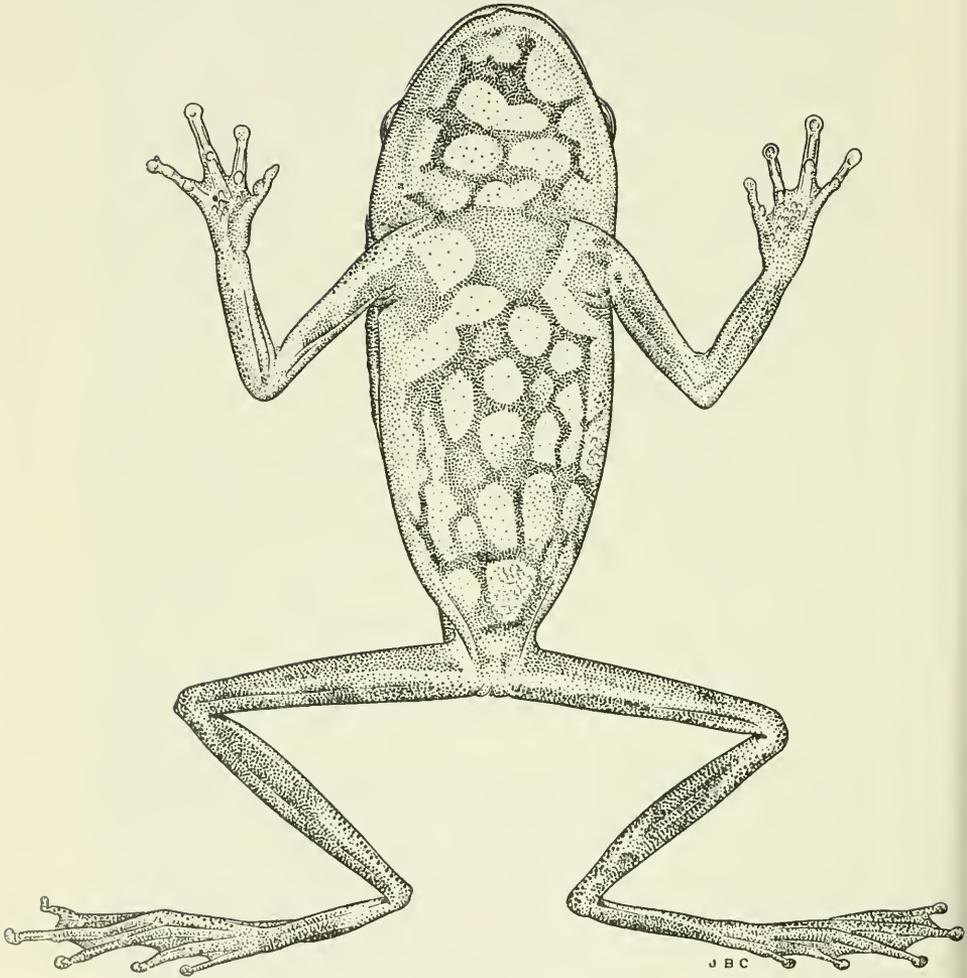


FIG. 1. Ventral aspect of *Hyperolius marmoratus pyrrhodictyon* n.sp. Type, MCZ 46182.

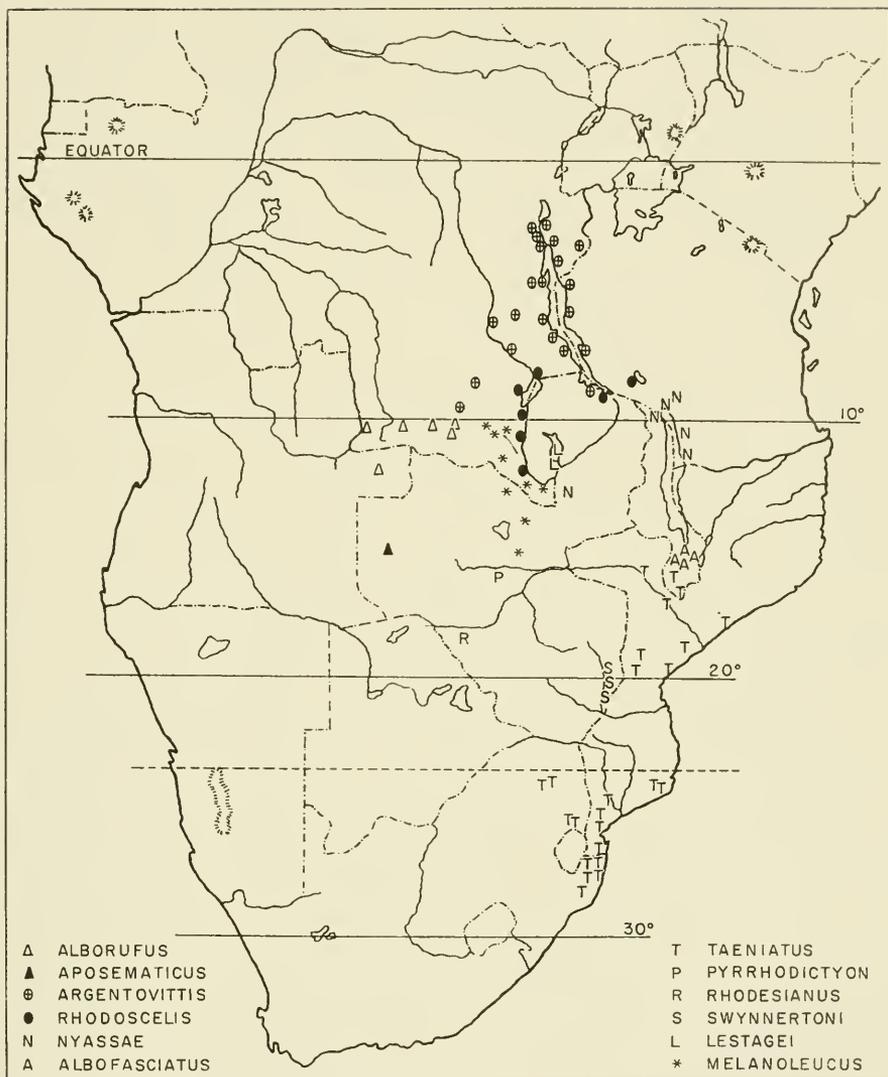


FIG. 2. Map of the localities for the subspecies of *Hyperolius marmoratus* in East Africa.

B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS.

MARCH 1, 1965

NUMBER 217

THE AUDITORY REGION OF THE BORHYAENID MARSUPIAL *CLADOSICTIS*

By

BRYAN PATTERSON

Since the appearance of Sinclair's memoir on the marsupials of the Santa Cruz formation of Patagonia (1906), it has been known that certain members of the Borhyaenidae, such as *Borhyaena* and *Prothylacynus*, were peculiar among marsupials in lacking a tympanic process, or bulla, of the alisphenoid. So far, indeed, had reduction of this bone been carried in *Borhyaena* that all trace of the foramen ovale had disappeared, the mandibular nerve evidently having passed out between alisphenoid and tympanic without so much as a notch to mark its passage. Sinclair was, however, able to show that lack of a tympanic process of the alisphenoid was not characteristic of the family as a whole, this structure being present in at least two genera, *Cladosictis* and "*Amphiproviverra*" (= *Thylacodictis*). His observations have been confirmed by others (e.g. Wood, 1924). Recently, the surprising statement has been made by McDowell (1958, p. 173) that "the borhyaenines show no clear relationship to other marsupials (they have no alisphenoid bulla, otherwise characteristic of marsupials, for example)." Even if this claim were correct, these animals would not be unique in this respect within their order. As has long been known (e.g. van Kampen, 1905, pp. 406-407), *Phascolomis* lacks an alisphenoid bulla, although it is remarkable in possessing a process from the squamosal that fulfills the same function.

In the course of a recent visit to Princeton University, I was able once more to examine the borhyaenid material described by Sinclair and reassure myself that his descriptions were correct. In the course of this examination I came across an undescribed

specimen that adds to knowledge of the borhyaenid auditory region. This is Princeton University no. 15705, consisting of various fragments, among which is an incomplete cranium. It had been identified, presumably by Sinclair himself, as *Cladosictis lustratus* Ameghino, a determination which there is no reason to doubt. From the fact that Sinclair made no mention of the specimen in his memoir, I suspect that it was not prepared prior to publication. Professor Glenn L. Jepsen very kindly loaned me the cranium for description. The accompanying figures are the work of Mrs. Dorothy Marsh.

DESCRIPTION

The cranium is broken off anteriorly in the vicinity of the postorbital constriction and has been considerably damaged by weathering, which has removed the condyles, the bases of the zygomatic arches together with the glenoid cavities, and much of the bone of the right side. Compensating for these losses is the almost complete lack of crushing, something that cannot be said for the specimens of this species that Sinclair described and figured.

As in other borhyaenines, and unlike the crushed specimen figured by Sinclair (pl. 55, fig. 1), the basisphenoid and basioccipital progressively increase in width posteriorly. As he noted, neither bone has a distinct median keel and both are relatively flat transversely; at the suture they form a fairly prominent transverse ridge. No carotid foramen is to be seen in the basisphenoid; in fact the only foramen visible in this bone is a minute one immediately antero-internal to the foramen ovale. Between basioccipital and petiotic there is a conspicuous foramen antero-internal to and almost as large as the foramen lacerum posterius. This is the posterior carotid foramen of Gregory (1910, p. 233); a wide, deep groove in the postero-lateral portion of the basioccipital leads forward to it. The significance of this foramen is discussed below. The pars petrosa of the petiotic, as is clearly seen on the left side, is rather sharply pointed anteriorly and extends far forward. Except for the opening of the foramen just described, the medial border of the pars petrosa abuts very closely against the basioccipital and basisphenoid.

There is a long and low, slightly curved and narrow auditory bulla that does not project ventrally below the basiscranium. The

anterior two-thirds of this structure is formed by the alisphenoid. Antero-externally, this portion is suturally united with the squamosal (part of this area is broken away in the specimen). Medially, there is a long, fairly wide and deep depression between the basieranium and the alisphenoid, which is roofed by the pars petrosa. The Eustachian tube opened into the posterior portion of this depression and passed forward within it. On the

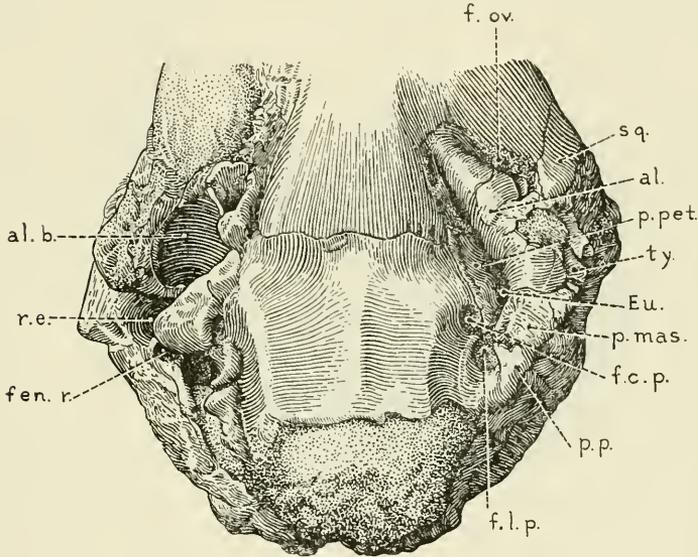


Fig. 1. *Cladosictis lustratus* Ameghino. Ventral view of incomplete cranium. Princeton University no. 15705, X2. Abbreviations: *al.*, alisphenoid; *al. b.*, alisphenoid bulla; *Eu.*, opening for Eustachian tube; *f. c. p.*, posterior carotid foramen; *f. l. p.*, foramen lacerum posterius; *f. ov.*, foramen ovale; *fen. r.*, fenestra rotunda; *p. mas.*, pars mastoidea of periotic; *p. p.*, paroccipital process; *p. pet.*, pars petrosa of periotic; *r. e.*, epitympanic recess; *sq.*, squamosal; *ty.*, tympanic.

broken right side of the specimen a natural section of the alisphenoid portion of the bulla is preserved. This is revealed as a deep, oval chamber situated almost entirely within the lateral wall of the cranium. It is separated from the rather large, circular epitympanic recess by a low ridge formed by the alisphenoid anteriorly and the squamosal posteriorly. The remaining third of the bulla is formed by the periotic, which meets the

alisphenoid in a suture anteriorly and is clasped posteriorly by the heavy, squat and blunt paroccipital process. The portion of the periotic involved is not the pars petrosa, which, as in other borhyaenines, exhibits no trace whatever of a tympanic process, but the pars mastoidea, which, in this form at least, had enlarged downward and forward from the ventro-lateral corner of the occipital surface.

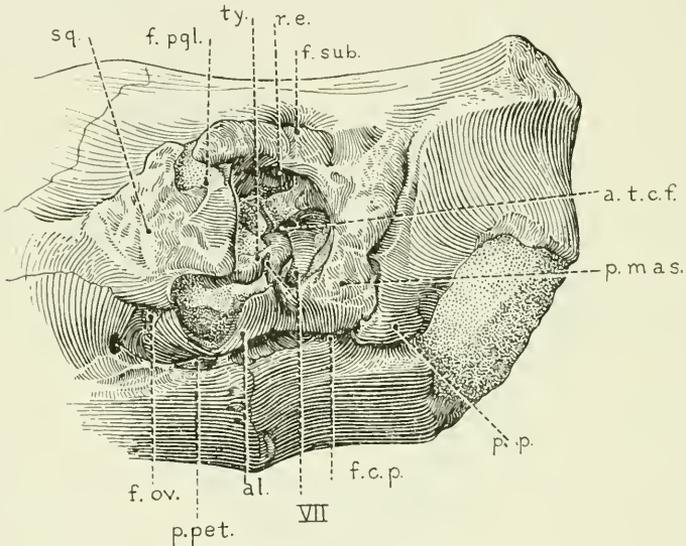


Fig. 2. *Cladosictis lustratus* Ameghino. Lateral and slightly ventral view of incomplete cranium. Princeton University no. 15705, X2. *a. t. c. f.*, apertura tympanici canalis facialis; *f. pgl.*, postglenoid foramen; *f. sub.*, subsquamosal foramen; *VII*, grooves for facial nerve; other abbreviations as in Figure 1.

The meatus — a meatus spurious — is large, very short, and deeper than long; it is bounded anteriorly and dorsally by the squamosal, posteriorly by the squamosal above and the pars mastoidea below (the suture between these bones is unfortunately not distinct), and ventrally by the alisphenoid in front and the pars mastoidea behind. The tympanic is present on the left side. It is free of the bulla and gives the appearance of having been situated wholly or almost wholly within it, although evidently lying close to the bony meatus. The bone has the primitive

horseshoe shape so frequently encountered in the order; it is, so far as can be seen, slightly enlarged ventrally, and has a short, dorsally tapering posterior crus. Due to slight forward displacement, the anterior crus is concealed by the squamosal; this displacement is evidence that, as is usual in marsupials, the tympanic was not fused to the skull. The internal surface of the pars mastoidea is grooved anteriorly for the passage of the facial nerve, and there is a corresponding slit in the ventral face of the tympanic.

DISCUSSION

This is the first specimen of a borhyaenine in which a fully formed auditory bulla has been preserved, but it is not unique in the family. A complete bulla, superficially similar to that of the machairodontines, is known in *Thylacosmilus*. In a brief description that I gave of this structure (*in* Riggs, 1934, p. 13), the alisphenoid was identified as a component, although the extent of its participation could not be determined, and the pars mastoidea and paroccipital were recorded as "overlapping" the bulla; uncertainty was expressed as to whether or not the tympanic and a tympanic wing of the pars petrosa also participated. With Princeton University no. 15705 in hand I have recently gone over the *Thylacosmilus* material in the Chicago Natural History Museum, hoping for a clearer interpretation in the light of this new evidence. It now seems virtually certain that the tympanic was situated within the bulla, as in *Cladosictis*, but, for the rest, cracks, absence of recognizable sutures and slight distortion prevent any assurance regarding the elements contributing to the posterior portion of the bulla. I am now very dubious as to the existence of a tympanic wing of the pars petrosa and suspect that only the pars mastoidea was involved in the bulla, but certainty on these points can only come with additional evidence.

As has long been known, the borhyaenids show very definite resemblances to two marsupial groups, the Didelphoidea and the Dasyuroidea, and there has been controversy as to whether they were definitely dasyuroid, even thylacinine, or an offshoot from the didelphoid stock. The evidence has been summed up by Simpson (1941), who, in general agreement with such earlier authors as Winge, Ameghino, and Matthew, concluded that while all three groups are clearly related, and very probably had a common ancestry, the Borhyaenidae were descended from the

Didelphoidea, the resemblances between them and the larger members of the Dasyuridae being due to parallelism. With this view I am in complete accord, and the structure of the auditory region contributes a few additional points to its support. In the Dasyuridae there is a large depression or recess in the squamosal, postero-lateral to the small recessus epitympanicus, which is covered by the pars flaccida of the tympanic membrane; no such depression is present in the Didelphidae and Borhyaenidae. The facial nerve in dasyurids, after leaving the middle ear cavity, runs through a bony canal formed mainly by the pars mastoidea with the squamosal contributing antero-ventrally (*Thylacinus*, in which there is only a groove in the pars mastoidea, is an exception); no such canal occurs in didelphids and borhyaenids. Borhyaenids, so far as known, lack a tympanic process of the pars petrosa. In the Didelphidae this process is less developed than in the Dasyuridae, in which it usually contributes largely toward the formation of the bulla (*Thylacinus*, which lacks the process, is again an exception). Two borhyaenine genera are known to lack an alisphenoid bulla. This structure is smaller in a number of didelphids than is the rule among dasyurids. *Cladosictis* is peculiar among marsupials in the participation of the pars mastoidea in the bulla, but it is not unique in this respect. The remarkable little *Dromiciops*, which, with Reig (1955), I believe to be a surviving microbiotheriine didelphid, has a large, complete bulla in which, in addition to a tympanic wing of the pars petrosa, the pars mastoidea is involved posteriorly. Sinclair (p. 410, pl. 62, fig. 7) has figured a specimen of *Microbiotherium* with a fully formed bulla, to which this element may well have contributed, and, as noted above, the same may well have been true of *Thylacosmilus*.

THE INTERNAL CAROTID ARTERY IN THE THERIA

Shortly after preparing this description I had the opportunity to make a field dissection of the head of an opossum (*Didelphis marsupialis*). In the course of this, I noted a small branch leaving the internal carotid artery at the level of the foramen lacerum posterius, passing into the cranial cavity through the posterior carotid foramen and there joining the circle of Willis. The observation was subsequently confirmed in injected specimens by Miss Suzanne Kreinbrook in the Biological Laboratories, Harvard University. This condition is widespread in the Marsupialia, to judge from the nearly universal occurrence of the

posterior carotid foramen. Among the Recent genera I have been able to examine, the foramen appears to be lacking only in the microbiotheriines, and in *Acrobates* — and possibly *Phascolarctos* — among the Phalangeridae. Even in these cases it is impossible to be certain short of dissection, for the foramen may be little more than a slit between the basioccipital and the periotic, as in caenolestids, or, apparently, confluent with the foramen lacerum posterius, as in some macropodids.

The internal carotid artery passes through the basisphenoid in pelycosaurs and therapsids (e.g. Romer and Price, 1940; Olson 1944), and also in non-therian mammals so far as known — Monotremata, Triconodonta (Kermack, 1963) and Multituberculata (Simpson, 1937). The marsupials have retained this primitive condition, but have an alternate route in the small branch of the artery that passes through the posterior carotid foramen. *Cladosictis*, so far as I am aware, is the only member of the order in which this alternate route was fully followed, and in which the anterior portion of the artery and the foramen in the basisphenoid was lost. *Cladosictis* had, in fact, essentially and independently achieved the placental condition.

Retention of the primitive condition in marsupials suggests that the placental arrangements were not attained until after the eutherian-metatherian dichotomy, presumably at some time or times during the Cretaceous. Just how these arrangements came about is, of course, unknown. The posterior carotid foramen alternate route may have been followed by all or by some placental groups, but the possibility would appear to exist that a small, more anterior branch may have reached the cranial cavity via an opening antero-internal to the tympanic region (a forerunner of the foramen lacerum medium), and that this eventually became the anterior portion of the internal carotid. In either case the artery would have run forward along the medial edge of the periotic and could thus have readily become enclosed in a groove or canal between basicranial and auditory elements. The stapedia artery presumably came into existence quite early in placental history. Matthew (1909), who recorded its presence in arctocyonids, creodonts and miacids, suggested, rightly I suspect, that the internal carotid early became divided into medial and lateral (stapedial) divisions. With the establishment of these main branches, and given the relative ease with which blood vessel patterns may change, a variety of combinations became possible. Independent acquisitions of similar patterns could have

occurred and almost surely did occur. Since the supply of blood rather than the route taken by it is the important thing, it is doubtful if there is any selective advantage in one vessel pattern over another. How varied these patterns may be has recently been demonstrated by Guthrie (1963) for the rodents. Within this one order almost all possible variations are present; in some groups both internal carotid (medial) and stapedia (lateral) branches occur; in others one of these is absent, and in yet others both are wanting.

Details of the carotid circulation appear to be of dubious value as an item of evidence for determining higher affinities within the Eutheria.

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(Received 15 December, 1964.)

B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS.

MAY 7, 1965

NUMBER 218

NEW FROGS OF THE GENUS *CORNUFER* (RANIDAE) FROM THE SOLOMON ISLANDS

By WALTER C. BROWN¹

INTRODUCTION

Large collections made by Mr. Fred Parker on Bougainville and neighboring small islands are providing very considerable additions to our knowledge of the fauna of this area. The present paper reports three new species and one new subspecies of the genus *Cornufer* discovered by Mr. Parker. Future papers in this series will describe other novelties in both frogs and reptiles and will record important ecological and behavioral observations.

PLATYMANTIS SYNONYMIZED WITH *CORNUFER*

In my revision of the amphibians of the Solomon Islands (Brown, 1952), I followed Boulenger (1918, p. 372), Noble (1931, p. 522), and Deckert (1938, p. 148) in maintaining *Platymantis* and *Cornufer* as distinct genera. My separation of the two genera was based primarily on the structure of the digital pads, as emphasized by Boulenger (1918, p. 372). On the basis of this character, the Solomon Islands representatives of this group of ranid frogs, which were known at that time, fitted rather readily into one or the other of the two categories. Inger (1954, p. 348), on the basis of his experience with the Philippine ranid frogs, again placed *Platymantis* in the synonymy of *Cornufer*. In so doing, he pointed out the difficulty of maintaining a separation of these two genera when a majority of the species is considered and the apparent evolution of the digital pads is taken into account. However, he did note that the species of

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this group do have a number of characters in common, which separate them from *Rana* (*sensu stricto*). As to their relationships with other ranid genera, it has been noted by Noble (1931, p. 520) and Brown (1952, p. 36) that as a group they are probably more closely related to the genus *Discodeles*, which is somewhat intermediate in position when the *Rana-Discodeles-Cornufer-Batrahylodes* series is being considered.

Since 1952 I have worked extensively with this group of ranid frogs (I have now examined 23 of the 28 species referable to the genus), and I agree with Inger that it is indeed difficult to maintain the two genera as distinct entities on the basis of our present knowledge of the digital or other known characters, or on the basis of any great difference in ecological adaptations. Therefore, in the following list I have assigned all of the species previously placed in *Platymantis* to the genus *Cornufer* and noted their distribution. However, a thorough study of these frogs in terms of their morphology and life histories is much needed in determining relationships within the group.

<i>Cornufer aereochordus</i> new species, Pl. 2	Solomon Islands (Bougainville)
<i>Cornufer aculeodaetylus</i> (Brown), Pl. 1	Solomon Islands (Bougainville, Choiseul)
<i>Cornufer beauforti</i> (Van Kampen)	Waigen Island (not seen by me)
<i>Cornufer boulengeri</i> Boettger	Bismark Island (not seen by me)
<i>Cornufer cheesmani</i> (Parker)	New Guinea
<i>Cornufer cornutus</i> Taylor	Philippine Islands
<i>Cornufer corrugatus</i> (Duméril)	Philippine Islands
<i>Cornufer dorsalis</i> Duméril	Philippine Islands
<i>Cornufer gilliardi</i> (Zweifel)	Bismark and Admiralty Islands (not seen by me)
<i>Cornufer guentheri</i> Boulenger	Philippine Islands
<i>Cornufer guppyi</i> Boulenger, Pl. 1	Solomon Islands
<i>Cornufer hazelae</i> (Taylor)	Philippine Islands
<i>Cornufer ingeri</i> Brown and Aleala	Philippine Islands
<i>Cornufer maerops</i> new species, Pl. 1	Solomon Islands (Bougainville)
<i>Cornufer moszkowski</i> (Vogt)	New Guinea (not seen by me)
<i>Cornufer myersi</i> (Brown), Pl. 2	Solomon Islands (Bougainville)
<i>Cornufer neckeri</i> Brown and Myers, Pl. 1	Solomon Islands
<i>Cornufer p. papuensis</i> (Meyer)	New Guinea, Bismarks
<i>Cornufer papuensis weberi</i> (Schmidt), Pl. 2	Solomon Islands
<i>Cornufer p. parkeri</i> new species, Pl. 1	Solomon Islands (Bougainville)
<i>Cornufer parkeri bukacensis</i> new subspecies,	Solomon Islands (Buka)
<i>Cornufer pelowensis</i> (Peters)	Palau Islands

<i>Cornufer polillensis</i> (Taylor)	Philippine Islands
<i>Cornufer punctata</i> (Peters and Doria)	New Guinea (not seen by me)
<i>Cornufer rubistriatus</i> (Barbour)	Roon Island
<i>Cornufer solomonis</i> Boulenger, Pl. 2	Solomon Islands
<i>Cornufer subterrestris</i> Taylor	Philippine Islands
<i>Cornufer unicolor</i> Tschudi	New Guinea
<i>Cornufer vitianus</i> (Duméril)	Fiji Islands
<i>Cornufer vitiensis</i> (Girard)	Fiji Islands

When considered from a zoogeographical point of view, as shown by this list of species, *Cornufer* appears to represent a relict, peripheral group of ranid frogs with the greatest number of species occurring at present in the fringing Philippine and Solomon archipelagos, and a smaller remnant in New Guinea and related islands, as well as in the Palau and Fiji Islands in the outer Pacific.

NEW SPECIES

The new species collected by Mr. Parker are all relatively small and have been compared directly with the type of *C. aculeodactylus* (USNM 119769) and with a paratype of *C. chccsmani* (MCZ 26501). (The relative sizes at maturity of the several species known from the Solomon Islands are given in Table 1.)

*CORNUFER PARKERI PARKERI*¹ sp. and subsp. nov.

This diminutive frog with its rough, tuberculate skin superficially resembles some of the small Oriental bufonids. However, its firmisternal girdle, well developed omosternum, undilated sacral diapophyses, teeth only on the upper jaw, reduced webs and united outer metatarsals place it in the ranid genus *Cornufer*.

Holotype: MCZ 36923, a mature female collected at Kunua area, Bougainville Island, Solomon Islands, on July 10, 1962, by Fred Parker.

Paratypes: MCZ 36911-18, 36921-22, 38194, 41860, 41866-69, 42524-31, 43741-44, Stanford University Nos. 21773-74, AMNH 70069-71, collected from the same general locality as the holotype, during 1962-1963.

Diagnosis: A diminutive *Cornufer*, largest available mature female measuring 18.5 mm, and largest male 15.9 mm from snout

¹ Named for Mr. Fred Parker.

to vent; skin with numerous warty tubercles on dorsum, lateral surfaces and limbs; first finger shorter than the second; tips of fingers blunt or slightly pointed, occasionally a circummarginal groove faintly indicated; tips of toes scarcely dilated, rather pointed, a shallow groove, most prominent laterally, separating the dorsal from the ventral portions; diameter of eye usually greater than, rarely equal to, length of snout.

Description: A very small *Cornufer*, snout-vent length of 16 mature females 15.1 to 18.5 mm, of 8 mature males 14.0 to 15.9 mm, habitus slender; hind limbs long, the snout-vent length ranging from 60 to 72 per cent of the length of the hind limb for 10 specimens; head about as broad as long; snout round-pointed, upper jaw scarcely protruding; eye large, its diameter somewhat greater than the length of the snout (rarely equal to); tympanum distinct, large, its diameter about 50 to 70 per cent of the diameter of the eye, and usually almost 25 per cent of the breadth of the head; canthus rostralis rounded; loreal region concave, only slightly oblique; a moderately to faintly distinct, oblique fold dorsal and posterior to the tympanum; forelimbs well developed, fingers relatively uniformly slender, bluntly round or slightly pointed, occasionally with a very faint groove separating a ventral pad laterally from the dorsal portion; without webs; subarticular and metacarpal tubercles large and well developed; first finger shorter than the second which is about equal to the fourth (Pl. 1, fig. 3); hind limb long; toes very slender without web, rather pointed with the ventral pad delimited by a shallow groove except at the tip (the fifth toe is more blunt and usually lacks the groove); subarticular and both inner and outer metatarsal tubercles well developed.

Skin of dorsum and dorsolateral surfaces marked by scattered, moderate-sized, round, oval or oblong tubercles; ventral and distal posterior part of the thighs granular; the proximal posterior part of thighs marked by elongate folds.

Color (in preservative): dorsum and lateral surfaces from grayish brown, through brown, to brownish black, the lighter shades with irregular darker blotches; several of the specimens exhibiting a tan, silvery or whitish middorsal band, wider anteriorly than posteriorly, and beginning anteriorly on the posterior part of the head or the pectoral region; lower limbs and edge of jaws with wide, dark transverse bars; venter rather heavily mottled with dark brown.

TABLE 1
 Size at maturity of the species of *Cornufer* known from the Solomon Islands
 (R = range, N = number)

Shout-vent length at maturity in mm	Species									
	<i>C. aculeodactylus</i>	<i>C. guppini</i>	<i>C. macrops</i>	<i>C. mayeri</i>	<i>C. neckeri</i>	<i>C. papuensis neckeri</i>	<i>C. parkeri bukacensis</i>	<i>C. parkeri parkeri</i>	<i>C. solomonis</i>	<i>C. acrochordus</i>
MALES	R = 22.5- 26.8	R = 50.0- 70.4	R = 23.6- 25.9	R = 53.5- 69.3	R = 37.4- 47.2	R = 35.0- 40.0	R = 14.9- 15.4	R = 14.9- 15.9	R = 45.0- 49.0	R = 24.8- 27.1
	N = 6	N = 7	N = 3	N = 4	N = 17	N = 22	N = 2	N = 4	N = 6	N = 4
FEMALES	R = 25.0- 31.1	R = 85.9- 98.0	R = 26.0- 28.5	R = 58.0- 80.0	R = 49.7- 62.0	R = 48.0- 63.6	R = 15.9	R = 15.3- 18.5	R = 60.0- 87.0	R = 37.1- 39.3
	N = 4	N = 7	N = 2	N = 2	N = 10	N = 14	N = 1	N = 11	N = 13	N = 6

Measurements of holotype (in mm): Snout-vent length 18.5; length of head to posterior edge of tympanum 6.8; breadth of head 6.9; diameter of eye 2.4; diameter of tympanum 1.7; length of snout 2.4; length of hind limbs 27.5; length of tibia 8.1.

Ecological note: Parker (personal communication) states that the specimens of this small frog were found under stones and logs in lowland secondary growth areas.

Comparisons: This *Cornufer* is much smaller at maturity than any other known species of the genus. In the warty nature of the skin it is most similar to *C. aereo chordus*.

CORNUFER PARKERI BUKAENSIS subsp. nov.

Holotype: MCZ 35777, a mature female, collected in lowland forest at south end of Buka Island, Solomon Islands, on January 28, 1962, by Fred Parker.

Paratypes: AMNH 69314-15, same locality as holotype.

Diagnosis: The Buka population is distinguishable from the nominate subspecies by the much less warty skin (both dorsal and ventral surfaces); the larger eye as measured by the ratio of eye diameter to breadth of the head and the relatively broader head as measured by the ratio of the length of the head to its breadth (Table 2).

Because of their obvious close affinities, and the fact that the observable morphological differences between individuals of these populations of diminutive *Cornufer* are based upon a very small sample of the Buka population, I prefer to regard these two populations as geographic subspecies of a polytypic species. Were these populations overlapping in range and were there no intergradation, they would be recognized as full species. As pointed out by Mayr (1963, pp. 481-515), geographically isolated populations such as these island populations are certainly incipient species whether or not marked by pronounced morphological differences. If the isolation is relatively complete for a sufficiently long period of time, true reproductive isolates (distinct species) may arise.

Color (in preservative): Dorsum and upper lateral surfaces more or less uniformly purplish brown or with lighter blotches; lower fore limbs and to some degree the thighs marked with dark transverse bands; venter with a reticulate pattern of brown and grayish white.

Measurements of holotype (in mm): Snout-vent length 15.9; length of head to posterior edge of tympanum 5.9; breadth of head 6.4; diameter of eye 2.1; diameter of tympanum 1.2; length of snout 2.3; length of hind limb 23.5; length of tibia 7.2.

(TABLE 2)

Ratios of diameter of eye to breadth of head, and length of head to breadth of head, for *C. parkeri parkeri* and *C. parkeri bukaensis*
(R = range; M = mean; N = number)

	$\frac{\text{Diameter of eye}}{\text{Breadth of head}}$	$\frac{\text{Length of head}}{\text{Breadth of head}}$
<i>C. parkeri parkeri</i>	R = 0.339-0.405 M = 0.376 N = 20	R = 0.966-1.050 M = 1.003 N = 20
<i>C. parkeri bukaensis</i>	R = 0.318-0.328 M = 0.323 N = 3	R = 0.922-0.952 M = 0.937 N = 3

*CORNUFER MACROPS*¹ sp. nov.

Holotype: MCZ 41864, an adult female, collected at 3000 to 4000 feet, in mountains of Aresi area, south of Kunua, Bougainville Island, Solomon Islands, 1963, by Fred Parker.

Paratypes: MCZ 38195-96 and 43740 in mountains of Kunua area, Bougainville Island; Stanford University No. 21795, Kieta area, Bougainville Island, collected by Fred Parker, 1962.

Diagnosis: A small *Cornufer*, largest available mature female measuring 28.5 mm, and largest male 25.9 mm from snout to

¹ From the Greek meaning "large eye."

vent; second finger longer than first; slightly dilated disks at the tips of the fingers and toes; the ventral pad separated from the dorsal by a circummarginal groove; eyes relatively large, diameter of eye greater than length of snout (Table 3), about 40 per cent of head breadth.

Description: A moderately small *Cornufer*, snout-vent length 26.0 to 28.5 mm for the two females; 23.2 to 25.9 mm for the three adult males; habitus slender, tapering from head to groin; hind limbs long; the snout-vent length about 65 per cent of the length of the hind limb; head about as broad as long; snout rounded, upper jaw not protruding; eye very large, its diameter about 16 to 17 per cent of the snout-vent length, greater than the length of the snout (Table 3); tympanum distinct, its diameter slightly more than 20 per cent of the breadth of the head; canthus rostralis rounded; loreal region oblique, concave; a relatively inconspicuous fold above and posterior to the tympanum; fingers relatively long, slender, without web; finger tips slightly dilated and more or less rounded, the ventral pad separated from the dorsal portion by a shallow marginal groove, first finger much shorter than the second which is shorter than the fourth; distal subarticular tubercles large and strongly protruding, basal and metacarpal tubercles less protruding (Pl. 1, fig. 5); hind limb long; toes slender, without web; tips of toes slightly dilated, round or round-pointed, the ventral portion separated from the dorsal by a circummarginal groove; subarticular tubercles moderately large and strongly protruding; inner metatarsal tubercle large and broadly oval, the outer small and round.

Skin of dorsal and dorsolateral surfaces of body and upper surfaces of limbs without prominent tubercles or folds; skin of ventral abdominal region with faint small granules.

Color (in preservative): Dorsal and lateral surfaces blotched light and dark brown; hind limbs with dark crossbars; ventral surfaces heavily flecked with brown.

Measurements of holotype (in mm): Snout-vent length 26.0; length of head to posterior edge of tympanum 10.7; breadth of head 11.1; diameter of eye 4.9; diameter of tympanum 2.3; length of snout 3.9; length of hind limb 44.9; length of tibia 13.6; length of third finger 4.3; diameter of third finger disk 0.8.

Comparisons: *Cornufer macrops* is distinguished from *C. myersi* by its smaller size at maturity and relatively larger eye, diameter of eye greater than length of snout (not less as for *myersi*). It is distinguished from *C. parkeri* by its larger size.

TABLE 3

Significant proportional differences for *C. acrochordus*,
C. aculcodactylus, *C. gillardi*, *C. macrops*
 (R = Range; M = Mean; N = Number)

	Length of third finger Breadth of head	Diameter of eye Length of snout	Breadth of head Snout-vent length	Diameter of eye Snout-vent length
<i>C. acrochordus</i>	R = 0.252-0.312 M = 0.283 N = 13	R = 0.939-1.068 M = 0.993 N = 13	R = 0.427-0.460 M = 0.443 N = 11	R = 0.148-0.166 M = 0.157 N = 13
<i>C. aculcodactylus</i>	R = 0.242-0.304 M = 0.282 N = 10	R = 0.902-0.977 M = 0.948 N = 10	R = 0.381-0.423 M = 0.396 N = 10	R = 0.135-0.143 M = 0.139 N = 10
<i>C. gillardi</i> ¹			R = 0.390-0.410 M = 0.396 N = 4	R = 0.132-0.140 M = 0.137 N = 4
<i>C. macrops</i>	R = 0.387-0.443 M = 0.424 N = 5	R = 1.167-1.312 M = 1.229 N = 5	R = 0.386-0.427 M = 0.398 N = 5	R = 0.161-0.188 M = 0.173 N = 5

¹ After Zweifel, 1960 (Information for first two ratios not available).

In size, *C. macrops* is most similar to the Papuan-Solomon species *C. aculcodactylus*, *C. acrochordus*, n. sp., *C. cheesmanae*, *C. gilliardi* and *C. unicolor*. It differs from *C. aculcodactylus* in its much less pointed fingers; the first finger shorter than the second (not longer) and the fingers longer relative to other measurements, length of third finger to base of second subarticular tubercle about 40 per cent of breadth of head as compared to 25 to 32 per cent in *C. aculcodactylus* (Table 3); smaller, rounded, outer metacarpal tubercle; and eye larger relative to length of snout (Table 3). It differs from *C. gilliardi* in that the first finger is shorter than the second (not longer); head narrower; dorsal folds absent. It differs from *C. acrochordus* in having the skin much less warty; the fingers less pointed; the fingers longer (differences for third finger length relative to breadth of head are shown in Table 3); and the eye larger relative to length of snout (see also Table 3). *C. macrops* differs from *C. cheesmanae* in the larger eye (diameter of eye greater than length of snout, not less than, and more than 35 per cent of breadth of head, not less than as for *cheesmanae*); and the more granular posterior venter. It differs from *C. unicolor* in the absence of a web at the base of the toes, the relatively longer hind limbs; and the relatively broader head.

CORNUFER ACROCHORDUS¹ sp. nov.

Holotype: MCZ 44264, a mature female collected at Aresi Mountain region, south of Kunua, between 2000-4000 feet, Bougainville Island, Solomon Islands, on 6 September 1963, by Mr. Fred Parker.

Paratypes: MCZ 44256-63, 44265-66, same general area as the holotype; MCZ 41871-2 and Stanford University 21832, Aresi area south of Kunua (elevation about 3000-4000 feet), Bougainville Island, Solomon Islands.

Diagnosis: A moderate-sized *Cornufer*, largest available mature female measuring 39.3 mm and largest male 27.1 mm from snout to vent; dorsal surfaces of limbs and body with scattered, prominent, roundish tubercles, dorsum also with some elongate folds, venter with coarse, rounded granules; fingers short; first finger longer than the second; fingers and toes distinctly pointed; subarticular and inner metacarpal and metatarsal tubercles very large and strongly protruding.

¹ From the Greek for "warty."

Description: A moderate-sized *Cornufer*, snout-vent length about 25 to 28 mm for mature males (4 measured); 37.0 to 40.0 mm for mature females (6 measured). (Two females about 30 mm in length have undilated, straight oviducts.) Habitus moderately broad and depressed; hind limbs long, snout-vent length 60 to 70 per cent of the length of the hind limb; head broader than long; snout broadly rounded; upper jaw not or scarcely protruding; eye moderately large, its diameter slightly less to slightly greater than the length of the snout and about 15 to 16.5 per cent of the snout-vent length; tympanum distinct, its diameter about 50 to 70 per cent of the diameter of the eye and 19 to 24 per cent of the breadth of the head; canthus rostralis broadly rounded; loreal region strongly oblique and only slightly concave; a prominent fold above and posterior to the tympanum; fingers slender, round-pointed to pointed, ventral pad lacking, without web or lateral fringe; first finger usually longer than second (rarely equal to); second finger about equal in length to the fourth; subarticular tubercles very large and protruding but not pointed (Pl. 2, fig. 4); metacarpal tubercles large, the inner protruding laterally; hind limb relatively long; toes slender, tips of toes slightly dilated, pointed, the ventral portion separated from the dorsal by lateral grooves; subarticular tubercles moderate, strongly protruding, distally pointed; inner metatarsal tubercle large, strongly protruding; the outer a rounded cone; solar and palmar tubercles small but prominent; skin of dorsal and lateral surfaces of head, body and limbs with numerous small to moderate, prominent, rounded or elongate tubercles; dorsum also marked with relatively short folds, the longest pair forming an urn-shaped pattern between the post-orbital and the axillary levels; venter posterior to the fore limbs, and the posterior surface of the thighs marked by prominent, relatively large, rounded tubercles.

Color (in preservative): Dorsum variable, grayish to black, mottled usually with a broad occipital blotch; fore and hind limbs marked by light and dark transverse bars of about equal width; lips with dark bars; venter with brown flecks, heavily concentrated anterior to the fore limbs; areolated light-dark pattern on inner and usually lower surface of thighs.

Measurements of holotype (in mm): Snout-vent length 37.7; length of head to posterior edge of tympanum 15.1; breadth of head 16.5; diameter of eye 5.6; diameter of tympanum 3.3; length of snout 5.9; length of hind limbs 60.5; length of tibia

18.0; length of third finger to base of second subarticular tubercle 5.0.

Eggs: A small clutch of 10 eggs, stated to be of this species by Parker, were measured. In the preserved state they measure 3 or 4 mm in diameter. They are creamy white, without any indication of pigment.

Comparisons: *Cornufer acrochordus* is intermediate in size at maturity between *C. macrops* and *C. papuensis weberi* of species known from the Solomon Islands, and closest to *C. macrops* (Table 1). When compared with extraterritorial species it is of about the same size as *C. dorsalis* from the Philippines and slightly smaller than *C. gilliardi* from New Britain. The sharply pointed and relatively short fingers distinguish *C. acrochordus* from known species of the genus other than *C. aculeodactylus* and possibly *C. gilliardi*. It differs from *C. aculeodactylus* in its larger size (Table 1), much more warty skin, color pattern, larger eye relative to length of snout, and the broader head relative to snout-vent length (Table 3). It differs from *C. gilliardi* in its smaller size, more pointed fingers, more warty skin, broader head, and larger eye (Table 3); the differences from *C. macrops* have been discussed in the section on that species (p. 10).

ARTIFICIAL KEY TO SPECIES OF *CORNUFER*
KNOWN FROM THE SOLOMON ISLANDS

1. Tips of fingers broadly dilated, breadth of disk of third finger more than 30 per cent of the length of the third finger as measured to the base of the second subarticular tubercle 2
 Tips of fingers not or scarcely dilated, breadth of disk of third finger, if dilated, less than 20 per cent of the length of the third finger as measured to the base of the second subarticular tubercle 3
2. Head relatively narrow, its breadth usually less than 40 per cent snout-vent length; loreal region slightly or moderately oblique; eye large, its diameter nearly equal to length of snout *neckeri*
 Head relatively broad, its breadth usually greater than 40 per cent snout-vent length; loreal region strongly oblique; eye moderate, its diameter equal to or slightly greater than the distance from eye to nostril *guppyi*
3. First finger distinctly shorter than the second 4
 First finger longer than (occasionally about equal to) the second 5
4. Snout-vent length of adults 20 to 30 mm; tips of fingers and toes round, with moderately dilated disks; fourth finger longer than second *macrops*

- Snout-vent length of adults less than 20 mm; tips of fingers and toes blunt or slightly pointed, scarcely dilated; fourth finger usually shorter than or about equal to second *parkeri*
5. Tips of fingers sharply pointed; fourth finger usually shorter than the second when adpressed 6
 Tips of fingers blunt or rounded; fourth finger usually longer than the second when adpressed 7
6. Skin with numerous prominent warts and dorsal folds; solar area with numerous tubercles *achrochordus*
 Skin relatively smooth; solar area without tubercles *aculcodactylus*
7. Tips of fingers bluntly swollen, lacking a marginal groove delimiting a ventral pad; length of tibia usually less than 50 per cent of snout-vent length *solomonis*
 Tips of fingers with slightly dilated disks, a marginal groove delimiting a ventral pad; length of tibia usually greater than 50 per cent of snout-vent length 8
8. Solar area with prominent tubercles; web at base of toes not reaching proximal edge of subarticular tubercle on inner margin of second toe; dorsum, especially of adults, with numerous narrow folds *papuensis weberi*
 Solar area lacking prominent tubercles; web at base of toes reaching midpoint of subarticular tubercle on inner margin of second toe; dorsum lacking numerous narrow folds *myersi*

ACKNOWLEDGMENTS

I wish to thank Dr. Alan Leviton, California Academy of Sciences, Dr. Doris Cochran, United States National Museum (USNM), Dr. Richard Zweifel, American Museum of Natural History (AMNH), Dr. Alice Grandison, British Museum (Natural History), Drs. L. D. Brongersma and M. Boseman, Leiden Museum, for the opportunity of examining pertinent materials in the collections of their institutions; and Dr. Ernest Williams, Museum of Comparative Zoology, for suggesting that I describe these interesting frogs.

The study of this genus of frogs is part of the author's program concerned with herpetofauna of the Pacific Islands. This program is sponsored by the National Science Foundation grant no. GB-409.

Drawings are by Mr. Walter Zawojski, Stanford University.

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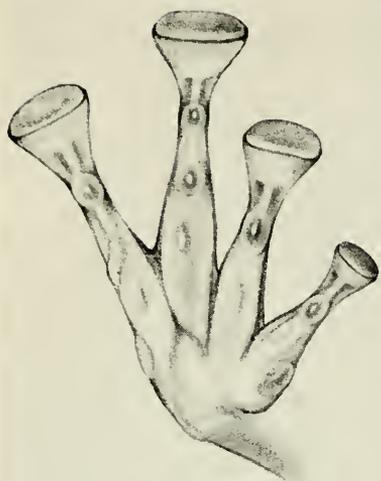


FIGURE 1



FIGURE 2



FIGURE 3



FIGURE 4



FIGURE 5

PLATE 1

- FIG. 1. *Cornufer guppyi*, inferior view of hand.
 FIG. 2. *Cornufer neckeri*, inferior view of hand.
 FIG. 3. *Cornufer p. parkeri* n. sp., inferior view of hand.
 FIG. 4. *Cornufer aculeodactylus*, inferior view of hand.
 FIG. 5. *Cornufer macrops* n. sp., inferior view of hand.

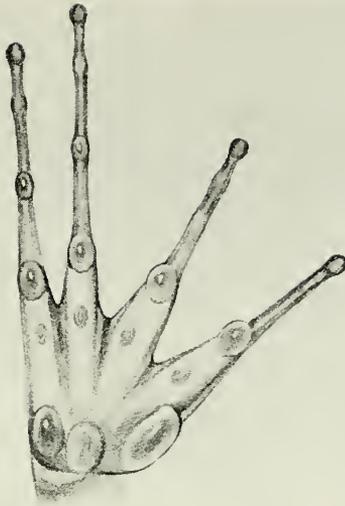


FIGURE 1



FIGURE 2



FIGURE 3



FIGURE 4

PLATE 2

FIG. 1. *Cornufer myersi*, inferior view of hand.

FIG. 2. *Cornufer papuensis weberi*, inferior view of hand.

FIG. 3. *Cornufer solomonis*, inferior view of hand.

FIG. 4. *Cornufer acrochordus* n. sp., inferior view of hand.

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Museum of Comparative Zoology

CAMBRIDGE, MASS.

MAY 7, 1965

NUMBER 219

THE EARLY EVOLUTION OF THE ECHINOZOA

By H. BARRACLOUGH FELL
Museum of Comparative Zoology

INTRODUCTION

The phylum Echinodermata is customarily considered to embrace two contrasted subphyla. One of these, the Pelmatozoa, comprises forms which are attached to the substrate for part or the whole of the life history, and which have a U-shaped gut, with the mouth and anus both directed upwards. The other, the Eleutherozoa, comprises free-living forms in which the mouth is directed downwards, and the anus (if present) is normally placed on the upper surface. The best known members of the Eleutherozoa are the sea urchins, the sea cucumbers, the starfishes and the brittlestars. However, these included forms differ so widely that it has been a difficult task to elucidate their interrelationship and the probable nature of their presumed common ancestor. Further, there are strong grounds for suspecting that the subphylum Pelmatozoa includes some forms which are really related more closely to certain Eleutherozoa than they are to other members of the Pelmatozoa. These grounds are here set out, and it is proposed to abandon the Pelmatozoa as a formal classificatory division, and to adopt patterns of body symmetry as the main criteria for defining subphyla, instead of using habit and attitude.

Recent morphological and paleontological studies have led to the conclusion (Fell, 1962, 1963a, 1963b) that the star-shaped members are interrelated and comprise a single grouping which may be regarded as a subphylum, and for which the name Asterozoa is already available. Similarly, other evidence implied that the globoid members were probably interrelated, and these have been associated as another subphylum, Echinozoa. Consequently, the so-called Eleutherozoa proved to be a polyphyletic

assemblage, and the name should therefore be abandoned. The present contribution is aimed principally at clarifying the inferred interrelationships between the various classes of Echinozoa, and adapting the current classification to reflect these relationships.

The discovery of the hitherto unknown class *Helicoplacoidea* (Durham and Caster, 1963) has shown that primitive, free-living echinoderms, with characters intermediate between those of Echinozoidea, *Holothuroidea* and *Edrioasteroidea*, had already differentiated in early Cambrian times. The morphological characters of the *Helicoplacoidea* suggest a relationship to some common ancestral stock from which arose, on the one hand, the eleutherozoan Echinozoidea and *Holothuroidea*, and on the other hand, the pelmatozoan *Edrioasteroidea*. Hitherto, the pelmatozoan echinoderms have generally been thought to represent a single natural assemblage, the subphylum *Pelmatozoa*, but this concept now becomes suspect. Further grounds for doubting the validity of subphyla based on eleutherozoan or pelmatozoan habit are provided by recent work on Paleozoic sea-stars, from which it has become evident that the subphylum *Eleutherozoa*, erected to comprise the free-living echinoderms, consists actually of two entirely separate stocks, the Echinozoa and *Asterozoa* (Fell, 1962, 1963a). The Echinozoa represent an ancient, pre-crinoid stock, of which the modern representatives are the Echinozoidea and *Holothuroidea*; whereas the *Asterozoa* are of relatively late origin, derived from a pinnulate pelmatozoan stock, provisionally identified with *Crinoidea*. Some analogous results emerge from recent work by Ubags (1961), from which it is apparent that the lower Paleozoic *Homalozoa* comprise a stock of asymmetrical, or bilaterally symmetrical, echinoderms, some members of which were free-living (i.e., eleutherozoan), while others were stalked and attached to the substrate (i.e., pelmatozoan). Lastly, data given later in this paper imply the essentially archaic character of the dendrochirote orders of *Holothuroidea*, and point to possible relationships between these forms and the Cambrian *Helicoplacoidea*. Certain parallels between the dendrochirote psolid holothurians, on the one hand, and the *Edrioasteroidea*, on the other, serve also to reinforce suspicions that the *Edrioasteroidea* should be classified with the echinozoan echinoderms, and not with the so-called *Pelmatozoa*, where they are commonly placed. Indeed, this inference is already implicit in a phylogenetic diagram published by Fell (1962).

PATTERNS OF SYMMETRY

Four structural patterns may be contrasted in echinoderms; these are:

(1) **Homalozoan pattern**, seen in those early Paleozoic echinoderms in which the skeletal plates are arranged either asymmetrically, or with more or less bilateral symmetry. These forms have been assigned to a separate subphylum, the Homalozoa (Whitehouse, 1941; Ubaghs, in press).

(2) **Echinozoan pattern**, seen in the Helicoplacoidea, Holothuroidea, Echinoidea, Ophiocistioidea and Edrioasteroidea, all essentially globoid forms lacking arms, with meridional symmetry. The Echinoidea and Holothuroidea were placed by Zittel (1895) and Jaekel (1918) in a subphylum Echinozoa, and the same name may be retained in a more extended sense, to comprise all the classes listed here.

(3) **Crinozoan pattern**, seen in the pelmatozoan classes Eocrinoidea, Paracrinoidea, Cystoidea, Blastoidea, Edrioblastoidea, and Crinoidea, initially globoid forms with partial meridional symmetry, but acquiring radially divergent systems of ambulacral feeding appendages (brachioles or arms). These groups, together with the Edrioasteroidea and some dendrochirote Holothuroidea, exhibit a sessile habit, involving certain morphological features normally utilized in defining a subphylum Pelmatozoa. However, although the sessile holothurians have never been grouped, the so-called Pelmatozoa cannot be defined so as to include the one without the other. It is evident that two categories of diagnostic criteria have been intermingled, and a more critical definition is required.

(4) **Asterozoan pattern**, seen in the Somasteroidea, Asteroidea and Ophiuroidea, in which radial divergent axes of symmetry produce arms, and the earliest morphological features of the arms correspond to those seen in pinnulate Crinoidea. These taxa fall within the subphylum Asterozoa, as defined by Zittel (1895), Jaekel (1918), and at greater length by Fell (1963a).

It will be noted that whereas categories (1), (2), and (4) above appear to be natural groupings, and offer no diagnostic difficulties, some unsatisfactory features arise under category (3). These are now examined, in the light of evidence supplied by the other three groupings.

ELEUTHEROZOAN AND PELMATAZOAN TRENDS

In each of the subphyla Homalozoa, Echinozoa and Asterozoa, irrespective of the pattern of symmetry adopted, two mutually opposed evolutionary trends may be observed, fundamentally governed by the attitude which the animal adopts with respect to its habitat. These are:

(a) **Eleutherozoan tendencies**, that is, adoption of a free-living habit, in which the animal acquires locomotor mechanisms permitting it to seek out food wherever it is to be found, by browsing on available algae, preying upon other animals, or swallowing large quantities of mud for the sake of its slight organic content. Such tendencies are invariably accompanied by the evolution of jaws, or of some special oral appendages adapted to gross (macrophagous) feeding. The anus, if developed, tends to lie on a part of the body remote from the mouth.

(b) **Pelmatazoan tendencies**, that is, adoption of a sessile habit, by which the animal becomes attached more or less permanently to the substrate, either by the aboral surface itself or by an aboral stalk. Locomotor organs are atrophied or lost altogether, and the animal is then dependent upon such planktonic sources of food as the sea-currents may provide. It secures the food by some ciliary or comparable advective mechanism mediated by the tube-feet, the food particles being conveyed to the mouth by food grooves on the upper surface, the nutrition being therefore, of the microphagous type. The mouth and anus necessarily both lie on the upper surface, and the alimentary canal is consequently bent into a U-shape in the vertical plane. Although the modifications are here considered only in the context of echinoderms, analogous features, of course, occur in other phyla with sessile members. It may be noted here that radial symmetry is by no means a consequence of the adoption of sessile habits. On the contrary, echinoderms which already possess radial symmetry, if they adopt a sessile habit, may acquire a strongly marked bilateral symmetry, very similar to that acquired by the sessile tunicates, for example, with which the psolid holothurians were once confounded. Further, the discovery of *Helicoplacus* (Durham and Caster, 1963) implies that the echinozoan echinoderms were already free-living forms *before* radial symmetry was fully developed, and that no subsequent sessile stages supervened between the Cambrian *Helicoplacoidea* and

their presumed Ordovician successors, which include the earliest known echinoids and holothurians.

It would appear that cleutherozoan and pelmatozoan tendencies are not directly related to the pattern of symmetry of the body in echinoderms, and that the two categories of evolutionary change, namely body symmetry and habit, have operated as simultaneous variables. This may be illustrated by reference to the echinozoan classes.

EVOLUTION OF THE ECHINOZOA

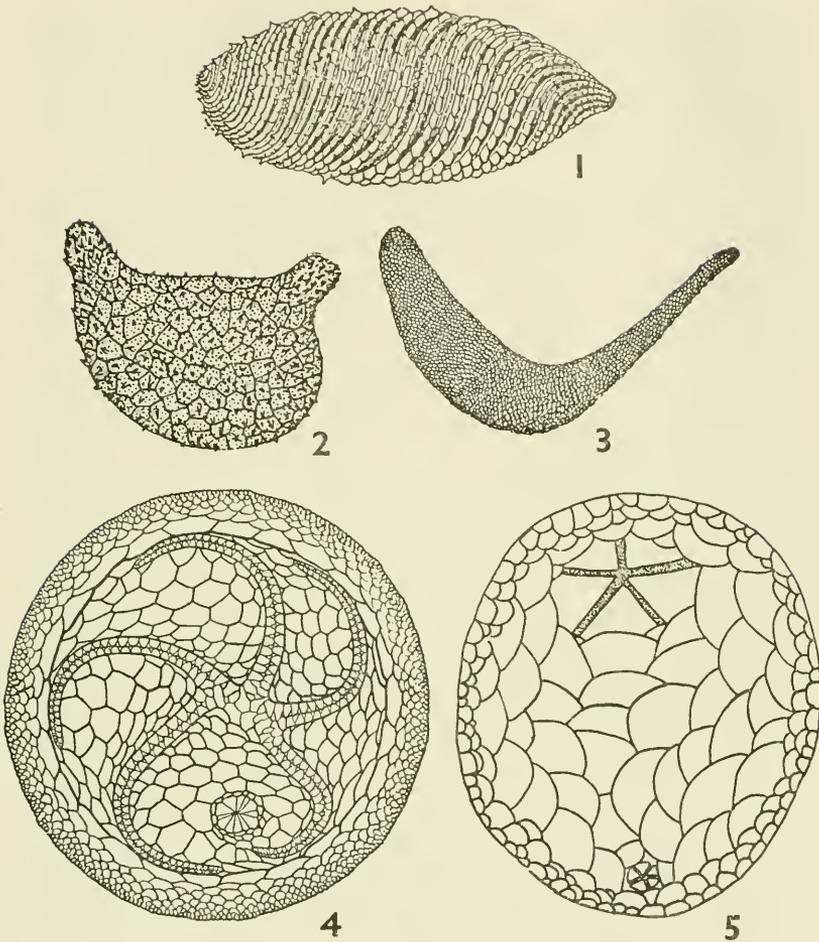
The oldest known echinozoan is the lower Cambrian *Helicoplacus*, in which the body is fusiform in shape, with the mouth at a broad anterior end, and the anus at the tapering opposite extremity (Fig. 1). The skeleton comprises numerous quadrangular or lozenge-shaped plates, sometimes bearing a rigid, erect spine, and disposed in counter-clockwise helical series. A single band of smaller platelets winds in a helix (sometimes bifurcated) around the body, and evidently indicates the position occupied by a single external ambulacral water-vessel. The symmetry would appear to be bilateral, therefore, but distorted by the counter-clockwise torsion, and combined with an apparent radial symmetry displayed by the arrangement of the thecal plates. Similar torsion is observable in the earliest Echinoidea, notably *Eothuria* in the Ordovician; here, however, the symmetry is overtly radial, or more correctly meridional, for there are now five ambulacra, disposed at regular intervals of 72° , forming twisted meridians. Analogous torsion is seen in the Edrioasteroidea, but has not yet been reported from Holothuroidea or Ophiocystioidea. The torsion was eventually lost in the echinoid line, but it persisted in the edrioasteroids until their extinction in the Carboniferous.

As already noted above, cleutherozoan and pelmatozoan trends have arisen independently from time to time in the various groups of echinoderms. Within the Echinozoa, the classes Echinoidea and Ophiocystioidea are not yet known to have produced any sessile forms. The initial echinozoan stock, to judge by the Helicoplacoidea, was itself free-living, too. *Helicoplacus* must have been a motile, bottom-feeding echinoderm, resembling a plated dendrochirote holothurian, as suggested below. The skeletal plates formed a complete, robust though flexible test. The

varying degrees of expansion and contraction reported in fossils by Durham and Caster (1963) imply an underlying musculature, able to operate concertinawise. Thus, *Helicoplacus* probably crept over the sea floor, like an annelid. The fossils occur in a fine elastic matrix, implying that the habitat was mud; *Helicoplacus* was probably a gross mud-swallower, like many aspidochirote holothurians. The primitive state of the ambulacrum suggests that the organ may have carried, at best, only rudimentary tube-feet, which could hardly have been more than respiratory organs, and probably were only sensory tentacles, like the dorsal tube-feet of many holothurians. The complete plating of the body-wall, and the probably rudimentary form of the tube-feet, imply the lack of an effective respiratory mechanism on the outer surface of the body. If this is correct, then it may be inferred that rectal respiration was required, either of the pulsatory crinoid type, or by means of respiratory trees, as in holothurians. Study of the distribution of respiratory trees among holothurian orders suggests a direct relationship to the habits of these animals, and also implies that the earliest holothurians had already developed these structures. It therefore seems likely that respiratory trees of a rudimentary type were present in Helicoplacoidea.

The earliest Echinoidea, such as *Eothuria*, possessed a multi-plated, flexible, spirally twisted body wall, similar to that of the Helicoplacoidea, and perhaps inherited from a helicoplacoid ancestry. They, however, had five well-developed ambulacra, on which the meridional water-vessels lay as external structures, though with internal ampullae for the tube-feet. Structural details of the ambulacral pores show that the tube-feet were large, and probably suctorial — certainly extensile and muscular. They would, therefore, serve the double function of locomotor organs and respiratory organs, as in modern echinoids. The fossils exhibit a developed jaw mechanism, showing that the early echinoids were already capable of feeding in the manner of their extant endocyclic descendants, that is to say, by biting and grinding organisms in the substrate, and chewing algae. This type of feeding demands an eleutherozoan habit, and contraindicates any pelmatozoan tendencies, since an animal with such feeding mechanisms would rapidly starve if it adopted a sessile manner of life.

The Ophiocistioidea developed a rigid skeleton by soldering of adjacent plates of the test, in much the same manner as in the



FIGURES 1-5. Archaic types of placoid echinozoans. 1, *Helicoplacus* lateral aspect, X 3. 2, *Ypsilothuria* lateral aspect, X 3. 3, *Placothuria* lateral aspect, X 2. 4, *Isorophus* actinal aspect, X 3. 5, *Lepidopsolus* actinal aspect, X 2. Fig. 1 from Durham and Caster, 1963; Figs. 2, 3, 5, drawn by D. L. Pawson, Fig. 4, from Kesling and Mintz, 1960.

later echinoids. Locomotion, however, was effected by the use of the grossly enlarged and plated oral tube-feet, so characteristic of the class. The enlarged oral tube-feet on the lower surface would also subserve the function of nutrition, by sweeping up detrital

material, and cramming it into the mouth, which was directed downwards. The anus, as in the endocyclic echinoids, lay on the upper surface, though not at the apical pole. Here, as in the endocyclic echinoids, the feeding and locomotor habits imply an eleutherozoan mode of life, and no sessile forms are known to have developed.

The early Holothuroidea are known at present only from isolated skeletal plates. However, on the basis of recent studies by Pawson (1965) it would appear extremely probable that the Ordovician and later Paleozoic holothurians resembled the extant Ypsilothuriidae (Fig. 2). Further, when once the dendrochirote tentacle had been evolved, they would resemble the extant genus *Paracucumis*, or *Placothuria* (Fig. 3). These are all heavily plated forms, with a complete test, flexible, made up of large plates with or without rigid spinous processes. The early holothurians would also be comparable with *Helicoplacus*, and with the flexible-bodied Ordovician echinoids, such as *Eothuria* (the latter genus having originally been regarded as a holothurian). Suctorial tube-feet may have been lacking from the earliest holothurians, to judge by their rudimentary state in extant plated genera, though this is uncertain. If they were initially lacking, then locomotor movements would have been effected by contraction and expansion of the body wall and its flexible test. Once suctorial tube-feet had developed, locomotion on the echinoid plan would be possible. There is morphological evidence that some kind of jaw apparatus, resembling the echinoid lantern, was developed early in the holothurians. Apparently it was abandoned once the dendrochirote tentacle had developed, but the skeletal elements of the presumed lantern acquired a new purpose — the attachment of the radial (and retractor) muscles — and hence the organ persisted in later holothurians as the calcareous ring on the pharynx.

It is probable, especially from data given by Pawson (1965), that the dendrochirote tentacle evolved from a formerly simple oral tube-foot. Repeated dichotomy led to the complex dendritic tentacle of the Dendrochirotida. This is an efficient collecting organ for planktonic material which is conveyed to the mouth by the contractions of the tentacles, ciliary action, and the "spooning" action of two ventral tentacles. Dendrochirote holothurians, whether motile or not, are able to trap sufficient nourishment by filtering the surrounding sea water, provided there are currents replacing the surrounding water, and bringing fresh

supplies of food particles. From such dendrochirote holothurians more than one line of evolution is possible, for they have the means of adopting either eleutherozoan or pelmatozoan habits. If the locomotor system is retained, the oral tentacles can be adapted to serve as food-collecting organs operating in various ways. In the Cucumariidae, for example, the body may be held erect, attached only by the posterior tube-feet, whilst the tentacles are spread out in a ring around the mouth, which is directed upwards, so that the habit of the animal resembles that of a sea anemone. In holothurians which adopt the horizontal attitude (lying on the ventral side where the tube-feet are retained), the tentacles can readily evolve from dendrochirote to aspidochirote forms, thus permitting gross mud-swallowing, and a markedly eleutherozoan habit.

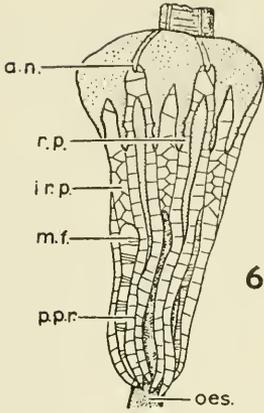
A further possibility is for the locomotor system to fulfill a purely adhesive role, leading to a sessile (pelmatozoan) habit. This is illustrated by the psolid dendrochirotes, in some genera of which the body is converted into a flattened, limpet-like form, adhering by a broad, flattened ventral surface, applied to a firm substrate (Fig. 5). The exposed dorsal and lateral surface is covered by a test of imbricating, robust plates. The mouth and anus lie on the upper surface, often protected by valvate plates, similar to those of cystoids or edrioasteroids. The whole body, in fact, is comparable to that of an edrioasteroid, the only distinction being the lack of external ambulacral plates (Figs. 4, 5). Thus the psolids are actually closer to edrioasteroids in morphological features than to many holothurians, or even to echinoids, and the only character by which they differ from edrioasteroids is the same as that which distinguishes them from echinoids — namely, the fact that the water-vessels are internal, and the test consequently does not form ambulacral plates. Hence a comparison of *Psolus* with an edrioasteroid illustrates two important features: (1) Edrioasteroids have the same pattern of symmetry as Echinozoa, and have evidently arisen from an early echinozoan stock similar to that which gave rise to the dendrochirote holothurians, of which the psolids are obvious members. (2) The pelmatozoan characters of edrioasteroids and of psolid holothurians have arisen as a direct habit response to adoption of a sessile mode of life, and do not indicate any near relationship to such pelmatozoan groups as are customarily included in the subphylum Pelmatozoa.

Comparative study of the internal skeleton of the pharyngeal

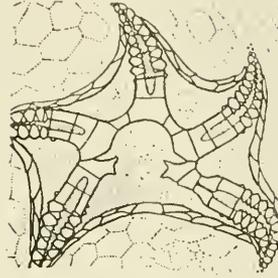
region of dendrochirote holothurians suggests to me that the original holothurians must have had external ambulacra formed by modified plates of the test and similar to those seen in the fossil edrioasteroids and illustrated by Kesling and Mintz (1960) (Fig. 7). Apparently, when once evolved, the large dendrochirote tentacles required a protective mechanism, by which they could be withdrawn into the body. The protection was achieved by telescoping of the anterior end (termed the introvert), capable of retraction under the action of muscles derived from the radial muscle group. The evolution of the introvert, in turn, implied the conversion of the original external ambulacral areas of the test into internal structures, surrounding the pharynx, and serving for the insertion of the retractor muscles. In primitive dendrochirotes the pharyngeal skeleton is still recognizable as equivalent to the ambulacral plates of an edrioasteroid, but in most surviving holothurians the mechanism is very reduced or vestigial. Stages in the reduction are illustrated in Figures 6 and 8 to 12. Inferred homologies of edrioasteroid and dendrochirote skeletal elements are indicated in the captions to these figures.

The Edrioasteroidea (Figs. 4, 7) adopted a similar habit to that of psolid Holothuroidea, but the ambulacra remained external, instead of sinking inwards, and this permitted an alternative method of feeding, suited to a pelmatozoan way of life. The feeding mechanism was provided by the whole complex of tube-feet. The five ambulacra grew outwards from the mouth as meridians, but only on the upper surface. Each ambulacrum

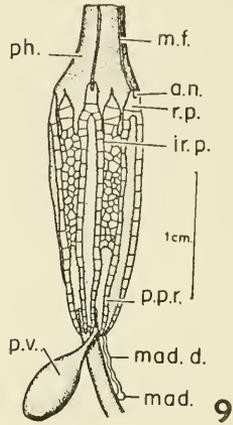
FIGURES 6-12. Ambulacral plating systems and calcareous ring elements in holothurians (6, 8-12), and an edrioasteroid (7), considered in this paper to be homologous structures. 6, *Pentadactyla* (Dendrochirotida), X 3. 7, *Isorophus* (Edrioasteroidea), X 4. 8, *Placothuria* (Dendrochirotida), X 4. 9, *Neothyonidium* (Dendrochirotida), X 2. 10, *Psolus* (Dendrochirotida), X 3. 11, *Euthyonidiella* (Dendrochirotida), X 3. 12, *Mitsukuriella* (Dendrochirotida), X 4. *Abbreviations*: *a.n.*, anterior notch of radial plate; *g.d.*, gonoduct; *ir.p.*, interradial plate; *mad.*, madreporite; *mad. d.*, stone canal; *m.f.*, radial water-vessel; *oes.*, esophagus; *p.p.r.*, posterior process (considered in this paper to be the distal ambulacral plates); *ph.*, pharynx; *p.v.*, polian vesicle; *r.m.*, retractor muscle; *r.p.*, radial plate (here considered to be an ambulacral element). Figs. 6, 8, 9, from Pawson, 1963; 7, from Kesling and Mintz, 1960; 10, drawn by D. I. Pawson; 11, 12, redrawn from Hedging and Panning, 1954.



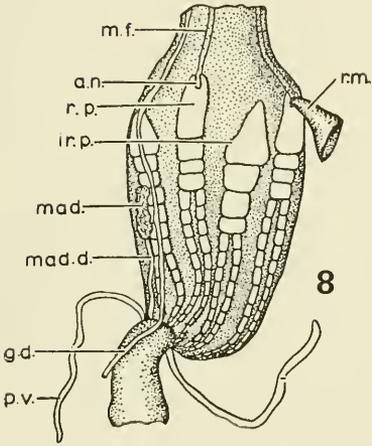
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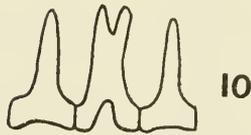
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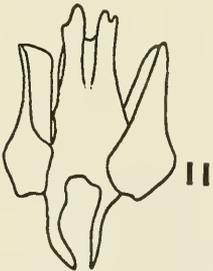
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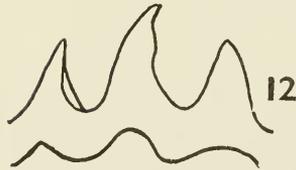
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11



12

carried a median groove, bordered on either side by the tube-feet. The latter must have functioned in a manner similar to the tube-feet of sea lilies, that is, they would wave about in the water, trapping small plankton and organic particles on their mucous surface, and sweeping them inwards towards the mouth, along the food-groove on the ambulacrum. Evidently no introvert evolved, and this implies that dendrochirote tentacles never developed.

It may be inferred that the Edrioasteroidea, soon after their differentiation from the initial echinozoan stock, adopted the sessile habit but, unlike the dendrochirote holothurians, had no oral tentacles on which to rely for nutrition. The ambulacra as a whole, therefore, took on the function of nutrition, mediated by the tube feet; and the advective food grooves, and the ambulacral plates on which they were carried, were a natural consequence. In the holothurian line, the radial water vessels were early converted into internal canals, as also occurred in the post-echinocystitoid echinoids. Hence the adoption of pelmatozoan habit inevitably demanded a pre-existing dendrochirote nutritive mechanism, and never involved external ambulacra in holothurians. As Bassler (1935) has pointed out, the earliest (i.e. mid-Cambrian) edrioasteroids retain a fully-plated ventral sole, unlike their later derivatives, and this may be taken as evidence that the test was originally spherical in edrioasteroids. The ambulacra in the early edrioasteroids were also more simple than in later forms, and most of the so-called pelmatozoan features, such as cover-plates, may well be later specializations, analogous to the development of cover-plates in crinoids and somasteroids.

Comparison of dissections of psolids with edrioasteroids suggests certain inferences as to the internal anatomy of edrioasteroids. In the absence of any evidence to the contrary, we may assume that the edrioasteroids had a gonad placed in the dorsal interradius. In psolids the gonopore lies on the introvert, just posterior to the mouth. The corresponding position on an edrioasteroid would be that in which a pore is known to occur, but the pore has hitherto been supposed to be a hydropore. Psolids, however, respire (at least in part) by rectal respiratory trees. It seems probable that respiratory trees would be required by edrioasteroids also, and that the hydropore would have been internal, as it is in dendrochirote holothurians.

Irrespective of these latter inferences, the main conclusion emerges that edrioasteroids should be treated as members of

the Echinozoa and that their pelmatozoan features are no more fundamental than the same features in psolid holothurians, being purely secondary responses to the demands of sessile habit.

The Echinozoa have here been selected to illustrate an argument which could also be developed on the basis of evidence provided by other groups of echinoderms. The hitherto puzzling features of Homalozoa, for example, some being apparently pelmatozoans, others eleutherozoans, would appear to be no more unusual than the circumstances found within the Echinozoa. Without prolonging the discussion at this stage by reference in detail to other subphyla, the inference may be drawn that the eleutherozoan and pelmatozoan characters have arisen independently, and at different times, in various echinoderm groups, and it is not possible to devise a natural classification on the basis of such characters alone. A revised classification now emerges in which the Edrioasteroidea are transferred to the subphylum Echinozoa. When this transfer is made, the residual pelmatozoan classes prove to comprise a much more uniform assemblage which may be defined, not in terms of their habit, but in terms of their morphological symmetry, as follows:

Subphylum **Crinozoa** Matsumoto, 1929 (redefined)

Fundamentally globoid echinoderms with partial meridional symmetry tending to produce an aboral calyx, the ambulacra developing as aboral semi-meridians later forming radially divergent systems of ambulacral feeding appendages which take the form of brachioles or arms.

Included classes: Cystoidea, Eocrinoidea, Paracrinoidea, Blastoidea, Edrioblastoidea and Crinoidea.

The following extended diagnosis of the Echinozoa also emerges:

Subphylum **Echinozoa** Zittel, 1895 (redefined)

Fundamentally globoid echinoderms which never develop arms. In earliest members mouth and anus lay at opposite ends of the body, but in some later forms these have become secondarily displaced. Meridional water-vessels traverse the body wall in the direction of the anus, the vessels lying originally on the surface, but sinking into its substance in later Paleozoic and all post-Paleozoic groups. Skeleton, nervous system, reproductive organs and muscular system tend to differentiate into meridional systems, although an underlying bilateral symmetry is always evident.

Included classes: Helicoplacoidea, Edrioasteroidea, Ophioeistioidea, Holothuroidea, Echinoidea.

We can now set out a general classification of the phylum Echinodermata, incorporating the proposals relating to the eleutherozoan groups already made in an earlier paper (Fell, 1963a), together with the results of the present investigation. These are given in Table 1. It will be noted that uniform terminations in -zoa are adopted for subphylum categories, whilst class names end in -oidea.

Conventional Classification	Classification Herein Adopted
Subphylum Pelmatozoa	Subphylum Homalozoa
Class Carpoidea	Class Carpoidea
	Subphylum Crinozoa
Class Cystoidea	Class Cystoidea
Class Eocrinoidea	Class Eocrinoidea
Class Paracrinoidea	Class Paracrinoidea
Class Blastoidea	Class Blastoidea
Class Edrioblastoidea	Class Edrioblastoidea
Class Crinoidea	Class Crinoidea
—*	Subphylum Echinozoa
Class Edrioasteroidea	Class Helicoplacoidea*
	Class Edrioasteroidea
Subphylum Eleutherozoa	
Class Ophiocistioidea	Class Ophiocistioidea
Class Echinoidea	Class Echinoidea
Class Holothuroidea	Class Holothuroidea
	Subphylum Asterozoa
Class Asteroidea	Class Stelleroidea (including
Class Ophiuroidea	the subclasses Somasteroidea,
	Asteroidea and Ophiuroidea)

*Helicoplacoidea unknown before 1963.

TABLE 1. Comparison of the conventional classification (left) of Echinodermata with that herein adopted (right). The new arrangement of the classes in four subphyla is believed to avoid the polyphyletic categories which have been demonstrated in the conventional classification, and it attempts to reconcile the systematic treatment with the evidence of the fossil record.

ACKNOWLEDGMENTS

In preparing this paper I was assisted by having access to then unpublished data on the morphology of dendrochirote holothurians assembled by Dr. David L. Pawson, at the time when

we were working together on South Pacific echinoderms; these data are presented elsewhere (Pawson, 1965). A revised classification of Holothuroidea recently proposed (Pawson and Fell, 1965) synthesizes the systematic outcome of our separate contributions. A further contribution, incorporating some material

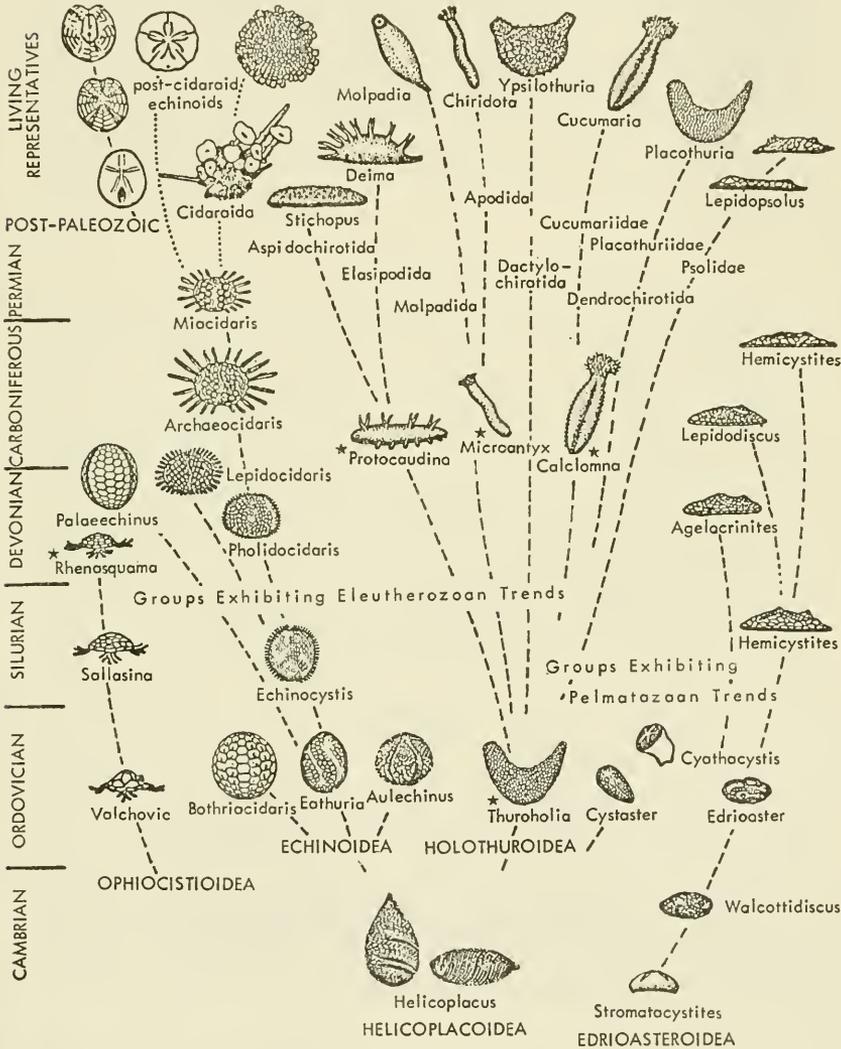


FIGURE 13. Approximate inferred phylogeny of the Echinozoa as deduced from evidence discussed in this paper.

added by Professor Raymond C. Moore, University of Kansas, will be given in the forthcoming Treatise on Invertebrate Paleontology, volume U, where the material of this paper is given a formal text-book presentation (Fell and Moore, 1965); for assistance in re-lettering Figure 13, I am grateful to Dr. Moore. I have to thank Dr. Ernst Mayr for reading and criticizing the manuscript, and for suggesting the inclusion of Table 1; Dr. David Pawson for assistance in illustrating holothurians, and for permission to use Figures 2, 5, 6 and 8; Dr. Porter M. Kier for some suggestions; and other colleagues and students who have discussed the interpretations offered here, and who have all to some extent influenced the manner of presentation here adopted.

SUMMARY

The morphology of fossil and extant Echinodermata implies that pelmatozoan and eleutherozoan characters must have arisen independently in the various classes at several different times since the Pre-Cambrian. Hence it is not possible to base a natural classification on these two categories of contrasting characters alone; for sessile and free-moving echinoderm assemblages each comprise two or more unrelated stocks, the similarities of which are due only to convergent evolution. At least four subphyla may be defined on the basis of four recognized patterns of growth and symmetry, mediated by the hydrocoel, evidently as innate trends initially independent of the environment. At least three of the four subphyla include pelmatozoan and eleutherozoan stocks, which are here regarded as arising as simple habit responses to the habitat.

Edrioasteroidea are interpreted as members of the subphylum Echinozoa, and should be removed from their present conventionally accepted position among the so-called Pelmatozoa. The latter assemblage, after removal of the Edrioasteroidea, is redefined and assigned the rank of subphylum, under the name Crinozoa. The so-called calcareous ring of holothurians is here interpreted to be the homologue of the ambulacral plating system of edrioasteroids, telescoped within the body, following the evolution of the introvert.

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(Received 18 January, 1965.)

B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS.

MAY 7, 1965

NUMBER 220

A NEW SPECIES OF *ELEUTHERODACTYLUS* FROM GUADELOUPE, WEST INDIES

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The numerous Greater Antillean frogs of the genus *Eleutherodactylus* have, for the most part, been studied as groups and in faunal studies. Cochran (1941) studied the forms occurring on Hispaniola, and Lynn and Grant (1940) studied the Jamaican forms. In a series of papers, Schwartz (1957, 1958a-d, 1959a, b, and 1960) has clarified the status of the forms occurring on Cuba.

The frogs of this genus in the Lesser Antilles are less well understood. Five names have thus far been applied to the frogs occurring there. These are: *E. martinicensis* (Tschudi), *E. johnstonei* Barbour, *E. lentus* (Cope), *E. antillensis* Reinhardt and Lutken, and *E. barbudensis* (Auffenberg). The last form was described as an extinct *Hyla* by Auffenberg (1958) but I have recently shown (Copeia, in press) that it is an *Eleutherodactylus* and is probably not extinct. My studies on the osteology of these frogs and the researches of Albert Schwartz, who is currently revising the Lesser Antillean *Eleutherodactylus*, show that in reality there are numerous forms of this genus occurring on the Lesser Antilles.

James Lazell, Jr. and Patrice Barlagne collected two forms at Matouba, north of Basse Terre, La Guadeloupe, which they could distinguish by voice and habit of calling. On external features, however, they are nearly identical. But from Lazell's field notes and discussions with him it appeared that two species were involved. Inasmuch as I had had good fortune in separating some of the other *Eleutherodactylus* on neighboring islands by the structure of their pelvic osteology, specimens of these

forms were macerated, and strong differences were found between the ilia of the two forms. These differences are as great or greater than those between any other of the forms of this genus occurring on Antigua, Barbuda, Martinique, St. Kitts or Grenada. In view of this, as well as the minor external differences, and the call difference (which must be an important isolating mechanism), it is evident that there are two species occurring in the vicinity of Matouba.

One of these, the larger, also occurs on Martinique and is very probably *E. martinicensis*. The second species is apparently cryptic (although not sibling). It is here named for M. Patrice Barlagne, who collected the majority of the specimens and aided Lazell in collecting on the Souffriere-Sans Toucher massif of La Guadeloupe.

ELEUTHERODACTYLUS BARLAGNEI sp. nov.

Holotype. Adult female, MCZ 35334, collected by Patrice Barlagne and James Lazell, Jr., at Matouba, La Guadeloupe, ca. 700 meters elevation, on 17 August, 1961.

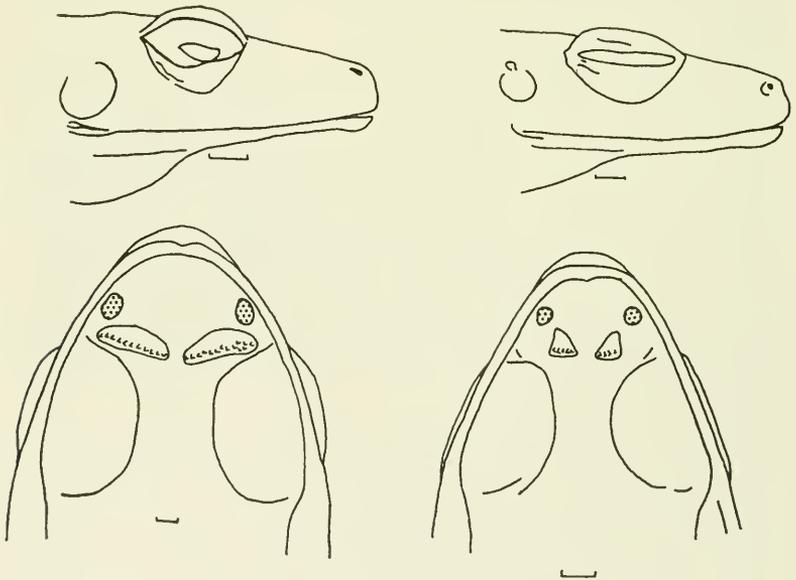


FIGURE 1. (Left) *Eleutherodactylus martinicensis* MCZ 35322; top, side of head; bottom, roof of mouth. (Right) *Eleutherodactylus barlagnei* sp. nov., holotype MCZ 35334; top, side of head, bottom, roof of mouth.

Paratypes. MCZ 35330-33 (4), same data as for holotype. MCZ 35331 is a skeleton.

Diagnosis. An *Eleutherodactylus* apparently related to *E. martinicensis* and separable from that species and all other Lesser Antillean species of the genus by the following combination of characters: head narrow, not wider than body; tympanum small, hidden dorsally, a small tubercle in the area of the hidden tympanic membrane; tympanum separated from commissure of jaws by three-quarters to more than the horizontal diameter of the tympanum; choanae completely visible from below; vomerine tooth bosses triangular in outline, within the borders of and posterior to the choanae; the voice assumed to be that of the new form (since the species could not be separated on other bases in the field) is described by Lazell as "Teecn."

Description of holotype. Adult female (see Fig. 1): head very slightly broader than long; head not broader than body; eyes small, width of eyelid less than interorbital distance; canthus rostralis distinct, not sharp; loreal region slightly concave, sloping sharply to lip; nostrils closer to tip of snout than to eye, area around them swollen; length of eye greater than distance from eye to nostril; tympanum small, about one-third diameter of eye, upper portions hidden, not distinguishable; tubercle present in area where upper rim of tympanum should be; distance from tympanum to commissure of mouth slightly greater than horizontal length of tympanum; anterior edge of tympanum from eye about one and one-half times horizontal width of tympanum; no supra- or post-tympanic fold present.

Tongue oval, free for about one-half its length; no vocal sac or slits; choanae not concealed by rim of upper jaws, small, round, slightly smaller than area of a vomerine tooth boss; vomerine tooth bosses between and posterior to choanae, triangular in outline, separated by a distance about equal to width of a single boss.

No axillary membrane; no tubercles or ridges on arm; palmar tubercles small; supernumerary tubercles on palms very faint or lacking; subarticular tubercles large, rounded, simple; lateral fringe present on fingers; no webbing between fingers; order of finger length, shortest to longest, 1, 2, 4, 3; circular disks on fingers, somewhat like pads of hylids in lateral view, notch present; no tarsal fold or tubercles; inner metatarsal tubercle small, elongate; outer metatarsal tubercle faint, but large; no supernumerary tubercles on soles; subarticular tubercles large, round,

simple; lateral fringes on toes; pads on toes like those on fingers, but smaller; faint webbing on toes except for web between toes 3 and 4 which is clearly visible for about one-half of toe 3; legs short, heels do not overlap when flexed legs are held at right angles to body; heel of adpressed hind limb extends to mid-eye.

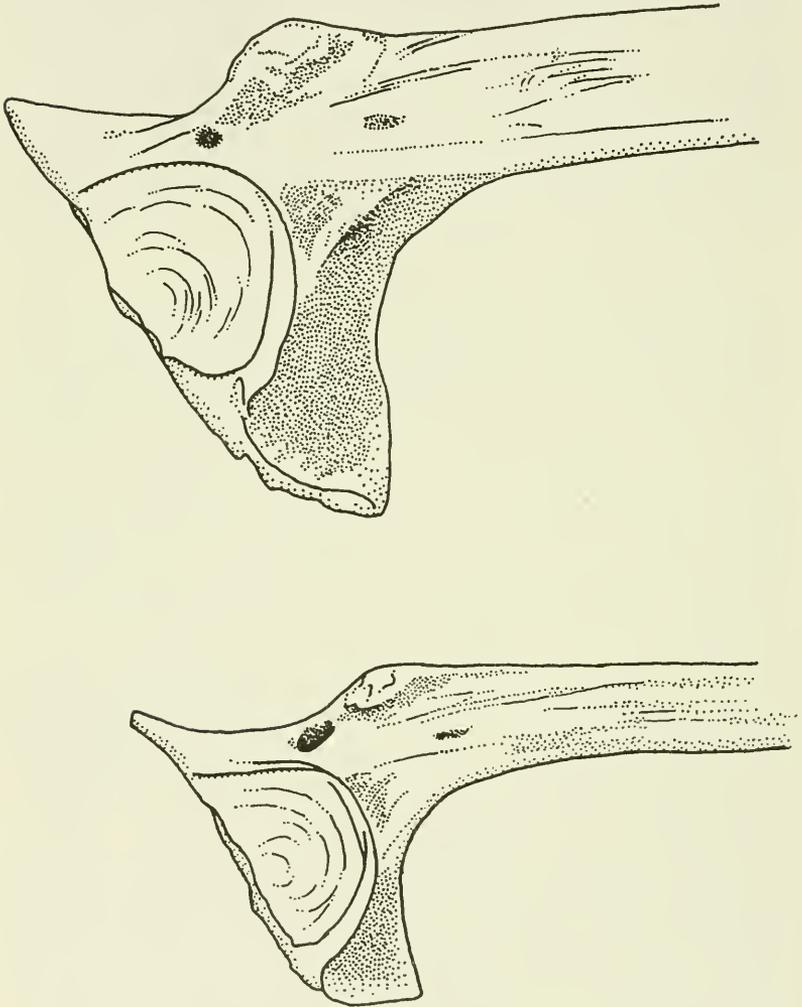


FIGURE 2. (Top) Right ilium of *Eleutherodactylus martinicensis*, MCZ 35321. (Bottom) Right ilium of *Eleutherodactylus bartagnei* sp. nov., paratype, MCZ 35331.

Skin of dorsum and sides smooth, that of belly and ventral and posterior surface of thighs granular.

Color in alcohol. Dorsum nearly uniform red-brown with scattered faint reticulations of black. Bands are evident on the limbs. Those of thigh are broad, three on each side. Those of tibia are narrower and three on each side. Two bands are present on tarsus and foot and two on the forelimbs. The venter is a dusky brown with small lighter spots. The undersurfaces of the forelimbs and the area across the chest lack the dusky brown pigment and are yellow.

Measurements in mm. Snout to vent 33; width of head 10.2; length of head 9.8; horizontal length of tympanum 1.2; length of eye 3.6; eye to nostril 3.2; eyelid width 2.2; interorbital distance 2.6; length of tibia 13.0.

Variation. The four paratypes are quite similar in appearance. In all specimens the venter is grey-cream with cream spots on chin and throat. The legs are flecked with brown pigment giving the appearance of cream flecks. All specimens have a light triangular interorbital spot, although it is weak in the holotype. Two specimens have a dark chevron on the dorsum (MCZ 35330, 35333). None of the type-series shows the wide or narrow vertebral stripe, although this variation is seen in examples of *E. martinicensis* collected with the type-series.

This species has a narrower head than does *E. martinicensis*. The head width/body length ratio ranges from 0.27 to 0.32 with a mean of 0.30, whereas of twenty-four *E. martinicensis* taken at the type locality by Barlagne and Lazell, the ratio varies from 0.32 to 0.41 with a mean of 0.33.

Comparisons. While morphologically *E. barlagnei* is quite similar to *E. martinicensis*, there are several differences. *E. barlagnei* has a dark venter, the tympanum appears smaller and is farther from the mouth and the vomerine tooth bosses are triangular in outline, not elongate, and do not extend laterally beyond the inner borders of the choanae (in *E. martinicensis* the bosses extend laterally as far as the outer borders of the choanae).

E. wrichi has less prominent vomerine tooth patches which are round. *E. johnstonei* has shorter limbs and the choanae are not completely visible when the roof of the mouth is viewed from directly below. *E. barbudensis* has elongate vomerine tooth patches.

A further difference can be noted between these frogs. In

connection with a study regarding the identity of *Hyla barbudensis* (= *Eleutherodactylus barbudensis*), I prepared skeletons of the two species found at Matouba. *E. barlagnei* is very dissimilar to *E. martinicensis* with regards to the form of the ilium. These differences are readily apparent in Figure 2. *E. barlagnei* has a thinner ilial shaft, smaller angle of ventral acetabular expansion, less elevated ilial prominence and a very short

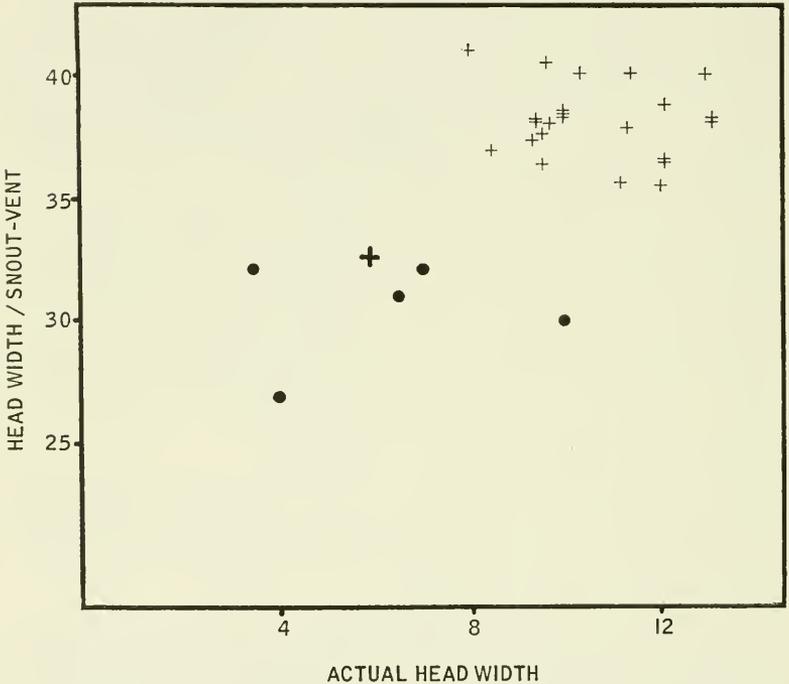


FIGURE 3. Head width in per cent of snout-vent length vs. actual head width in mm. Crosses are *E. martinicensis*, circles are *E. barlagnei* sp. nov. Large cross is a small *E. martinicensis* with a narrow head; in other features it is typical of its form.

crest beginning at the anterior edge of the ilial prominence and extending anterad about one and one-half times the length of the prominence. There is also less of a ventral acetabular expansion in *E. barlagnei*.

Acknowledgment. The collections on which this study was based were made under the auspices of National Science Foundation Grant NSF-G 16066.

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(Received 22 January, 1965.)

B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS.

MAY 7, 1965

NUMBER 221

NEW MELANESIAN ANTS OF THE GENERA *SIMOPONE* AND *AMBLYOPONE* (HYMENOPTERA- FORMICIDAE) OF ZOOGEOGRAPHIC SIGNIFICANCE^{1,2}

By ROBERT W. TAYLOR
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The two ants described below are of special zoogeographic interest. *Simopone gressitti* sp. n. (subfamily Cerapachyinae) is the second species of its genus recorded from the Indo-Australian area, and the first east of the Philippines. *Amblyopone noonadan* sp. n. (subfamily Ponerinae) is the first apparently endemic *Amblyopone* to be described from Western Melanesia.

Simopone Forel includes ten described Ethiopian and Malagasy species: *S. grandidieri* Forel, 1891 (in Grandidier, Hist. Nat. Phys. Madagascar, 20: 141, pl. 4, fig. 8, Imerina, Madagascar); *S. emeryi* Forel, 1891 (*ibid.* 247, Anosidé, Madagascar); *S. conradti* Emery, 1899 (Ann. Soc. ent. Belg., 43: 475, Cameroon; 1911, Genera Insect., 118: 16, pl. 1, fig. 7); *S. (?) mayri* (Emery), 1900 (Bull. Soc. ent. Ital., 31: 264 (*Cerapachys*); 1911, Genera Insect., 118: 16, Antongil Bay, Madagascar); *S. marleyi* Arnold, 1915 (Ann. S. Afr. Mus., 14 (1): 20, Stella Bush, South Africa); *S. grandis* Santschi, 1923 (Rev. Zool. Afr., 11 (3): 259, Kungu, Congo); *S. schoutedeni* Santschi, 1923 (*ibid.*: 260, fig. 1 a-c, Kamaiembi, Congo); *S. fulvinodis* Santschi, 1923 (*ibid.*: 262, fig. 1d, Kidaba [Kitabola], Congo); *S. wilburi* Weber, 1949 (Am. Mus. Novit., 1396: 7, figs. 6, 7, N. of Beni, Congo); *S. laevissima* Arnold, 1954 (Ann. Mus. Congo, n.s., 4°, Zool., 1:291, figs. 1, 1a, Zika Forest, Uganda). An eleventh species, *S. bakeri* Menozzi, 1926, was described from Singapore (Atti Soc. Nat. Mat. Modena, (6) 4: 92 (1925)). All these species are known only from the worker, except *S. mayri*, which

¹ Research supported by U.S. National Science Foundation Grant No. GB. 1634.

² The specimens discussed here were provided by Drs. J. L. Gressitt (Bishop Museum, Honolulu) and Børge Peterson (Universitets Zoologiske Museum, Copenhagen), whose assistance is gratefully acknowledged.

is based on a unique male and may not really belong in *Simopone*.

Simopone workers are small to medium sized slender ants (length about 5.0-8.5 mm), usually dark brown or black in color, with very weak to moderately intense sculpturation and pilosity. The head is elongate-subrectangular, prismatic behind, with a transverse occipital carina. Frontal carinae horizontal, diverging posteriorly and obscuring the antennal insertions in facial view; fused anteriorly with the median part of the clypeus, and forming with it and the frontal area a continuous planar surface, thus producing an anterior cephalic structure much as in the aberrant Indo-Australian myrmicine genus *Metapone*. Eyes very large (maximum diameter about 0.3 to 0.5 x the head width), situated at or just behind the middle of the sides of the head. Ocelli present, usually minute and closely approximated. The 11-segmented antennae have flattened stubby scapes (usually only about 3 x as long as broad) which lie at rest in well developed preocular antennal scrobes, each of which is enclosed dorsally by the frontal carina and ventrally by the characteristically cerapachyine genal carina. These carinae usually reach the eye posteriorly and may become continuous with a very fine postorbital carina, so that the eye is essentially enclosed within the scrobal area. Mandibles obtusely triangular, strongly arched ventrally; masticatory border with a number of small regular teeth. The palpal formula of a single African specimen (species evidently undescribed) in the MCZ collection is *maxillary* 6 : *labial* 2, possibly 3 (inspected).

The structure of the mesosoma is generally like that of *Phyracaces mayri* Forel, with its dorsolateral borders broadly or narrowly rounded, sometimes angled but never carinate. Pronotum prismatic anteriorly, with a transverse carina between the humeri. A similar carina may separate the dorsal and declivitous faces of the propodeum and the declivitous face may be laterally margined. Sutural traces on mesosomal dorsum weak or vestigial, the mesometanotal suture sometimes lacking. The leg segments, especially the femora, are often inflated, the fore and hind tibiae each bear a single pectinate spur, and the pretarsal claws are toothed or pectinate.³ The posterior flange of the hind coxa may be produced dorsally as a more or less raised lamella

³ The characters of the tibial spurs and the pretarsal claws have been seldom mentioned in specific descriptions. All specimens which I have seen lack tibial spurs on the middle legs, and have a single median tooth on each tarsal claw.

(another character common to many cerapachyines). Petiole longer than broad, subrectangular-trapezoidal in dorsal view, the dorsolateral margins acarinate, though sometimes angled; there is usually a transverse anterior carina, and sometimes a posterior one. Postpetiole strongly constricted behind, subrectangular in dorsal view, about equal in size to the petiole or larger. Pygidium flattened at its apex, with a full or reduced complement of bristle-like marginal setae, the presence of which indubitably establishes the cerapachyine affinities of this genus (see Brown, 1954).

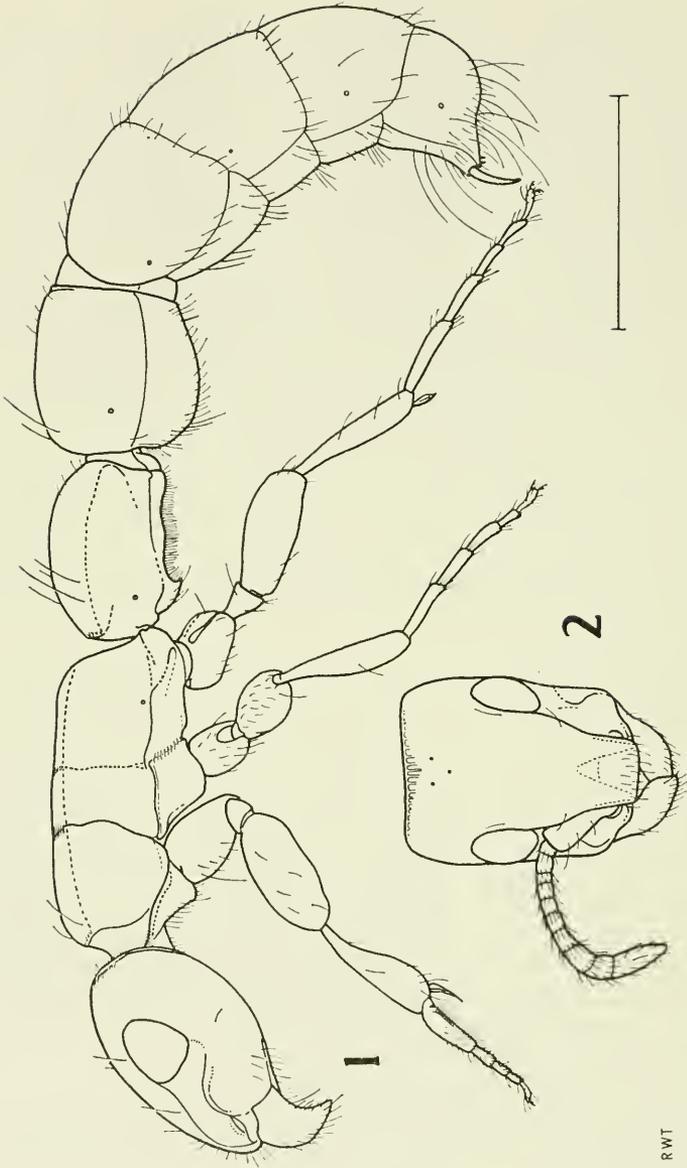
Little is known of the biology of *Simopone* but its general habitus strongly implies that it is arboricolous; several of the older types were collected on vegetation and one species (*S. marleyi*—see Arnold, 1915) has been taken in hollow twigs. Specimens in the MCZ collections are either labeled as having been swept from foliage, or else carry adherent moth wing scales, an almost sure sign that they were collected by sweep-net. The genus is apparently an aberrant arboricolous offshoot from *Phyracaces*-like stock. The feeding biology needs study, especially since many cerapachyines, including some *Phyracaces* species, are apparently specialized myrmecophagous feeders (Wilson, 1958).

Amblyopone Erichson is an almost cosmopolitan genus now containing 50 described and apparently valid species, including 31 from the Indo-Australian area. The world fauna was extensively reviewed by Brown (1960), and one subsequently described species is known (Brown, 1962). *A. noonadan* sp. n. is a member of the Indo-Australian *luzonica* group, which includes the following species: *luzonica* (Wheeler and Chapman) 1925, Philippines (= *williamsi* (Wheeler and Chapman) 1925; synonymy by Brown, 1960); *silvestrii* (Wheeler) 1928, Japan; *amblyops* (Karawajew) 1935, Indo-China; and probably also *celata* (Mann) 1919, Solomon Islands (see Brown, 1960, for details and references). The features distinguishing *noonadan* from these species and others present in Melanesia are given below.

SIMOPONE GRESSITTI Taylor, new species

Type locality. NEW GUINEA (WEST): Hollandia-Binnen, 100 m. The unique holotype worker was collected on November 1, 1958, by Dr. J. L. Gressitt for whom this species is named.

Type deposition. Holotype deposited in the Bernice P. Bishop Museum, Honolulu, Hawaii.



RWT

FIGS. 1 AND 2: *Simopone gressitti* sp. n. Fig. 1. Lateral view, left antenna omitted. Fig. 2. Frontal view of head, left antenna omitted. Scale line 1 mm. Holotype worker.

Description. Dimensions (in mm): Total length (TL) 6.4; head length at midline (HL) 0.98; maximum head width (HW) 0.79; maximum pronotum width (PW) 0.70; Weber's length of mesosoma (WL) 1.4; petiolar node length at midline 0.72; maximum petiolar node width 0.69; postpetiolar length at midline 0.70; maximum width of postpetiole 0.75. General form as shown in Figures 1 and 2. Mandibles small, their outer borders sinuate, convex basally; angle between masticatory and posterior borders broadly rounded; dentition worn, almost effaced, probably originally like that of *S. bakeri*. Head 0.81 x as broad as long; sides almost parallel, slightly concave before eyes, slightly convex behind; occipital border feebly concave; occipital carina well developed, ribbed along its anterior edge, enclosing the occiput laterally as well as dorsally, its ventral traces extended forwards for a short distance on each side, along the sides of the postgenae. Eyes large, maximum diameter 0.30 mm (0.38 x the head width), separated by a distance of 0.46 mm (1.53 x their maximum diameter); ocelli minute. Scapes barely reaching anterior margins of eyes, flagellar proportions as in Figure 2. Anterior clypeal border feebly convex. Frontal carinae diverging posteriorly, on each side meeting the postorbital carina, which is very fine and continuous below the eye with the genal carina.

Mesosoma twice as long as broad in dorsal view, its dorsolateral borders approximately right-angled but acarinate; transverse pronotal carina well developed; angle between dorsal and declivitous propodeal faces abruptly rounded, acarinate. Sutura-tion of mesosomal walls as shown in Figure 1; promesonotal and mesometanotal sutures represented by transversely ribbed traces on mesosomal dorsum, mesometanotal suture weakest. Femora and tibiae moderately inflated (Fig. 1); posterior edge of hind coxa raised but not lamellate; pretarsal claws each with a single median tooth. Petiole trapezoidal in dorsal view, broader behind than in front, with a distinct ribbed transverse anterior carina; lateral borders strongly angled at about 60 degrees, but not carinate; profile as in Figure 1. Sides of postpetiole slightly convergent posteriorly in dorsal view. Pygidial spines reduced to a single minute pair on each side, at the extreme apex.

Mandibles smooth and shining, with a few minute piligerous punctures. Entire body strongly shining, virtually lacking sculpturation except for scattered minute piligerous punctures, and some effaced longitudinal rugosity along the sides of the pronotal dorsum and on the metepisternum, which is in part coarsely punctate-rugose. Pilosity reduced. A few moderately long

suberect to reclinate hairs on mandibles, clypeus and underside of head, propleurae, coxae, and undersides of petiole and gaster; hairs most abundant on the propleurae and coxae, and on the petiolar sternite where they form a peculiar brush-like series behind the subpetiolar process. Single, slightly longer erect hairs in the following positions: at the midlength of each frontal carina, above eyes, on pronotal humeri, on the anterior half of the sides of the node (2 pairs) and the anterodorsal corners of the postpetiole. Similar, but slightly less erect hairs increasingly long and abundant towards the gastric apex, which is surrounded by very long arched hairs. Pubescence virtually absent. Color very dark brown, almost black, the following areas weakly infuscated with reddish brown: mandibles and front of head, anterior parts of each gastric tergite, gastric apex and legs, especially the tibiae and tarsi; antennae medium dull reddish brown.

Diagnosis. According to Menozzi's description (Menozzi, 1926) *S. bakeri* is smaller than *gressitti*, with a narrower head and petiolar node. I have tentatively identified as *S. bakeri* a specimen in the J. W. Chapman collection (MCZ) from the Philippine Island of Negros (Horns of Negros 3,600 ft., J. W. Chapman).

This individual agrees well with Menozzi's description, and resembles *gressitti* in color and habitus, but has very different cephalic, ocular and petiolar proportions as follows: TL *c.* 5 mm; HL 0.91 mm; HW 0.68 mm (head 0.75 x as broad as long); PW 0.55 mm; WL 1.2 mm; petiolar node length at midline 0.68 mm; maximum petiolar node width 0.56 mm (node 0.52 x as broad as long); postpetiolar length at midline 0.64 mm; maximum width of postpetiole 0.61 mm. The maximum diameter of the eyes is 0.30 mm (0.44 x head width) and they are separated by a distance of 0.34 mm (1.14 x their maximum diameter). Apart from these proportional differences the post-cephalic structure is similar to that of *gressitti*. The pilosity is similarly distributed but less abundant, and the subpetiolar "brush" is lacking.

AMBLYOPONE NOONADAN Taylor, new species

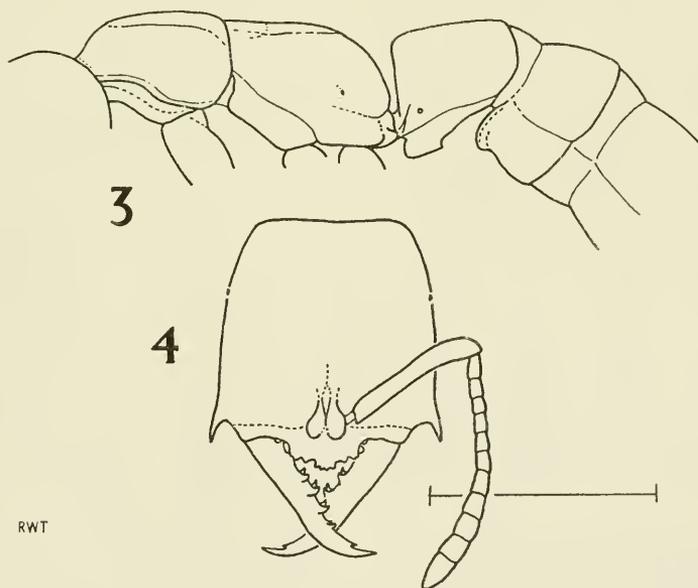
Type locality. TERRITORY OF NEW GUINEA: *New Britain*: Yalom, 1,000 m, May 19, 1962 (Danish Noona Dan Expedition). The types were collected "in or on the ground in newly cleared secondary growth," no collector specified.

Type deposition. The holotype is deposited in the Universitetets Zoologiske Museum, Copenhagen, Denmark; the paratype is in the Museum of Comparative Zoology (Type No. 31148). The species is named, in apposition, for the Danish expedition vessel *Noona Dan*.

Worker. The following description is based on the holotype and single paratype.

Dimensions (in mm, holotype cited first). TL *c.* 5.5, 6 mm; HL (including clypeal denticles) 1.04, 1.12; HW (immediately behind genal teeth) 0.96, 1.04; maximum scape length (excluding articular condyle) 0.64, 0.68; outside total length of mandible 0.85, 0.90; PW 0.58, 0.65; WL 1.38, 1.42; midline length of petiolar dorsum 0.49, 0.55; maximum petiolar node width 0.50, 0.57; postpetiolar length at midline 0.36, 0.40; maximum width of postpetiole 0.65, 0.73.

General habitus as in Figures 3 and 4. Head with occipital border feebly concave, sides feebly convex, converging posteriad;



FIGS. 3 AND 4: *Amblyopone noonadan* sp. n. Fig. 3. Lateral view of mesosoma and node. Fig. 4. Frontal view of head, right antenna omitted. Scale line 1 mm. Holotype worker.

anterior corners with strong acute genal teeth, the inner edges of which are about as long as the maximum width of the mandibular shafts. Frontal lobes approximate, separated by a deep linear groove. Clypeal apron strongly convex, with eight small denticles; the four median ones closely approximate, less deeply separated from each other than from the more lateral denticles, their apices diverging from the midline; the innermost of the two lateral denticles on each side moderately large, triangular, separated from the median quartet by a gap equal to its width at base; the outer tooth large and blunt, its apex jagged, forming two or three indistinct cusps. Mandibles slender, their external margins feebly concave, each bearing ten acute, slightly recurved teeth. The two basal teeth simple, conical, the basalmost blunt, the second acute; the eight apical teeth arranged in four more or less separated pairs, in typical "stigmatommine" fashion; the dorsalmost tooth of each pair lies slightly distal to its partner; a distinct low reclinate tooth is present on the inner edge of the strong acute mandibular apex. The mandibular apices cross when the jaws are closed, leaving a triangular gap between the mandibular and clypeal teeth. Palpal formula *maxillary* 4: *labial* 3 (paratype dissected). Scapes slender, slightly incrassate; funiculus with 11 segments proportioned as in Figure 4. Eyes small, variable in size, maximum diameter 0.02 mm in holotype, 0.06 mm in paratype, with four and nine or ten indistinct facets, respectively.

Mesosomal profile as in Figure 3. In dorsal view this tagma is widest at the pronotum and strongly narrowed at the base of the propodeum. Pronotal dorsum almost flat, with marginate lateral borders; inferior angles of pronotum broadly rounded. Promesonotal suture flexible; mesonotum transverse; mesometanotal suture vestigial, represented only by a sculptural break between the subopaque mesonotum and the moderately shining propodeum. Propodeal dorsum about as long as broad, its sides diverging posteriad; declivity feebly concave, rounding into dorsum, its lateral edges slightly raised, forming angles of a little more than 90 degrees in dorsal view.

Petiole sessile, its profile as in Figure 3; subpetiolar process afenestrate; nodal dorsum slightly wider than long in dorsal view, the anterior border with a slight median emargination, the sides converging slightly anteriad. Postpetiole wider but shorter than node, and also shorter than the succeeding segment which is of about the same width. Gastric apex laterally compressed,

sting stout. Tibial spurs vestigial on middle legs; posterior tibiae each with a broad flat pectinate spur and a more slender simple conical one.

Mandibles and frontal lobes obscurely longitudinally striate. Clypeal apron with somewhat radial longitudinal striae; lateral parts of clypeus similarly sculptured, the striae on each side radiating back from a focal point at about the level of the inner basal edge of the mandible. These lateral clypeal striae arch back over the cheeks, where those nearest the midline are almost longitudinal, reaching back to the base of the frontal carinae; the cheek striae become increasingly divergent towards the sides of the head and the most lateral ones gather apically, at the base of the genal tooth. Remainder of head coarsely and roughly punctate-rugose; the sculptural trend faint, mainly longitudinal, but transverse across a narrow posterior strip. Scapes finely shagreened. Postgenae somewhat obscurely and irregularly longitudinally striate, the striae diverging posteriad. Lateral parts of the dorsa of the pronotum and propodeum with scattered punctures, about 0.02 mm in diameter, separated by about twice this distance on pronotum and more widely spaced on propodeum; a narrow longitudinal median strip on these sclerites lacks punctures, the surface here is shining, with a very fine superficial scale-like surface pattern which is also present on the interpunctural areas of the lateral strips, and which has a transverse trend on the posterior propodeal dorsum. Mesonotum subopaque, coarsely and irregularly shagreened.

Sides of mesosoma, except metepisternal area, subopaque, bearing somewhat effaced and polished, almost vertical fine striae, which are slightly curved (concave anteriorly) and slope posteriorly; sculptural intensity diminishing posteriad, with striae virtually absent behind the propodeal spiracle. Metepisternal area longitudinally striate. Declivity of propodeum shining, with very superficial, minutely scale-like transverse sculpturation. Petiolar dorsum subopaque, with scattered fine piligerous punctures; gastric tergites similar, the punctures finer and more abundant.

Pubescence adpressed and subadpressed, generally distributed over body except for the post-pronotal sides of the mesosoma and the sides of the petiolar node. Erect pilosity moderately abundant, especially on the dorsum of the body and towards the gastric apex, where the hairs are longest. Ground color dark

chocolate brown, with the following areas infuscated with reddish brown: clypeus, frontal lobes, anterior corners of head, including genal teeth, pronotal collar, area of mesosomal-petiolar junction, subpetiolar process, posterior edges of gastric tergites, and gastric apex. Mandibles, antennae, legs and sting rich golden brown.

Diagnosis. *A. noonadan* is readily distinguished from the only other known western Melanesian *Amblyopone*, *A. australis* Erichson, by the characters of its "stigmatommine habitus" (i.e., "double ranked" mandibular dentition and enlarged clypeal teeth, etc., — see Brown, 1960). In addition, *australis* is larger (minimum known HW on New Guinea about 1.5 mm), and has an acute tooth on each inferior pronotal angle. The third known Melanesian species, *A. celata* Mann (Solomon Islands), is much smaller (3 syntype workers in the MCZ collection have HL 0.69-0.71 mm; HW 0.60-0.63 mm) with minute genal teeth (maximally only about as large as the median clypeal denticles) and with the head evenly and rather finely shagreened.

The other *luzonica* group species have reduced genal teeth, as in *celata*, and most specimens (MCZ collection) are somewhat smaller than the *noonadan* types: 3 *silvestrii* syntypes have HL 0.87-0.92 mm; HW 0.76-0.81 mm; the *luzonica* female holotype from Los Baños (Luzon) has HL 0.82 mm, HW 0.74 mm; and six *luzonica* workers from Dumaguete (Negros) have HL 0.85-0.90 mm, HW 0.74-0.80 mm. Three *williamsi* syntype workers from Baguio (Luzon) are somewhat larger with HL 1.03-1.09 mm, HW 0.91-0.97 mm, and Karawajew (1935) gave similar measurements for his *amblyops* type — HL 1.05 mm, HW 0.98 mm. These "species" differ among themselves in the conformation of the clypeal denticles and in the sculpturation (Brown, 1960, p. 196), but they may ultimately prove to be geographical variants of a single species, especially considering the extensive variation known in other members of the genus. Notwithstanding, there can be little doubt that *noonadan* and *celata* are good "species."

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B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS.

MAY 28, 1965

NUMBER 222

THE GENUS *LEPTOTYPHLOPS* IN THE WEST INDIES WITH DESCRIPTION OF A NEW SPECIES FROM HIS- PANIOLA (SERPENTES, LEPTOTYPHLOPIDAE)

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Three specimens of *Leptotyphlops* were collected in the summer of 1964 in the vicinity of the town of Pedernales, Dominican Republic, by Mr. David C. Leber and myself. These snakes appear most closely related to *L. bilineata* Schlegel which they resemble in the failure of the ocular to reach the labial border. No snakes of the genus *Leptotyphlops* have previously been definitely noted from the island of Hispaniola.

Boulenger (1893), however, recorded a specimen of *Leptotyphlos albifrons* Wagler from Santo Domingo de Guzmán collected by Dr. A. C. Buller. It so happens that the name of the capital city of the Dominican Republic, rarely referred to in its entirety, is Santo Domingo de Guzmán. The question of the provenance and relationships of the Buller specimen might therefore be important. Thanks to Miss A. G. C. Grandison, I have been able to examine this specimen (BM 90.10.10.73) and can confirm its affinities with the *albifrons* group of the genus. It appears to agree most closely with *L. phenops bakewelli* Oliver although the rostral-prefrontal fusion is apparently lacking. (Dunn and Saxe, 1950, regard *phenops* as a race of *albifrons*; but I here follow more recent authors such as Peters, 1954, and Duellman, 1961, in giving *phenops* specific rank.) Miss A. G. C. Grandison writes (*in litt.*) that "Dr. Audley C. Buller . . . made quite extensive collections in Mexico in 1891 and 1892, travelling from L. [Lago] Chapala and Guadalajara . . . to Bolaños and back to Ixtlán and later . . . to an area west of Guadalajara." Examination of a recent map of Mexico shows that roughly 200 km to the south of the city of Guadalajara in the state of Jalisco is a Ciudad Guzmán, which may well be another case of the unwieldy Santo Domingo de Guzmán having been shortened. Smith

and Taylor (1945) list *L. phenops bakewelli* from the states of Colima, Guerrero, Jalisco, Michoacán, and Oaxaca. That identity, collector, locality and time should all approximately coincide seems too remarkable for mere coincidence. This specimen (BM 90.10.10.73)¹ is here considered to be close to *L. p. bakewelli* from what is now Ciudad Guzmán, Jalisco, Mexico, and hence irrelevant to the Hispaniolan problem.

The specimens from Pedernales, however, are distinct from other species and apparently represent an endemic form, here named in allusion to the type locality² :

LEPTOTYPHLOPS PYRITES new species

Holotype: MCZ 77239, collected at the southern outskirts of the town of Pedernales, approx. 1 km from the center of town, Pedernales Province, Dominican Republic, 3 July 1964, by Richard Thomas.

Paratypes: USNM 152452, same locality as type, 26 June 1964, Richard Thomas; ASFS V2601, 9 km N Pedernales, Pedernales Province, Dominican Republic, 26 June 1964, David C. Leber.

Diagnosis: A species of *Leptotyphlops* of closest affinities to *bilineata* in that the second and third upper labial scales exclude the ocular from the labial border. It is further characterized by considerable attenuation, a high number of middorsal scales (from rostral to tail spine), 12 scale rows around the base of the tail, and 15 to 16 subcaudals, a trilineate dorsal pattern and unicolor, dark sides and venter.

Distribution: Known presently only from the northwestern lowlands of the Barahona peninsular region of Hispaniola.

Description of holotype (Fig. 1) : Head rounded, of same width as neck. Rostral at widest point slightly less than width of head at eyes, broadly truncate posteriorly at contact with prefrontal. Nasals separated by a transverse suture proceeding from first labial diagonally upward across naris to rostral; dorsal half of nasal also in contact with rostral, prefrontal, supraocular, ocular,

¹ BM 90.10.10.73: Total length ca. 151 mm; tail 7.6 mm; middorsal scales about 246; subcaudals 16; scale rows 14; 10 scale rows around tail. Rostral extends posteriorly to slightly beyond level of eye, does not contact supraoculars. Suture completely divides nasals; supraoculars elongate, slanting sharply forward. One supralabial between oculolabial and nasal, one behind oculolabial. Light spot on rostral scale and on underside of tail from 13th scale anterior to caudal spine and including caudal spine. Dorsum dark, light scale edges form lines; anterior venter light, becoming darker posteriorly.

² "Pedernales" means "flints," in Spanish, hence "pyrites," the Greek equivalent.

and first and second supralabials. Four supralabials, first smallest, second and third of about equal size, fourth largest; second and third supralabials in contact with ocular, occluding it from contact with labial border. Prefrontal, frontal and interparietal (third middorsal scale) increase in size in that order; middorsal

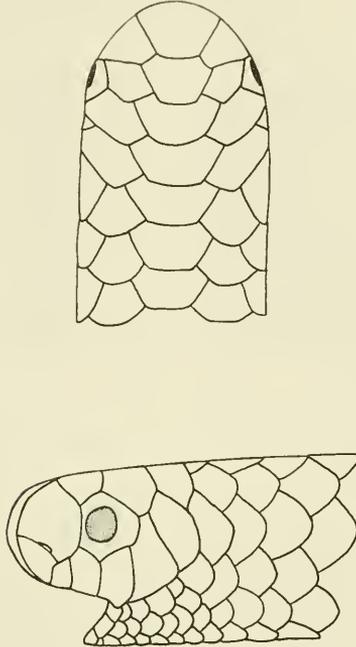


Fig. 1. Dorsal and lateral views of the head of the type specimen of *Leptotyphlops pyrites* (MCZ 77239).

scales posterior to the interparietal decrease gradually to standard body scale size. Parietal and fourth upper labial in broad contact behind ocular. Parietal and postparietal distinctly enlarged, parietal the larger. Supraocular about equal in size to prefrontal. Middorsal scales 273 from rostral to caudal spine; 14 scales around body; 12 around base of tail; subcaudals 15. Anal scale enlarged and shield shaped, tri-lobate posteriorly. Body very slender, of nearly uniform diameter throughout; total length 133 mm; diameter at midbody (2.0 mm) into total length about 67 times; length of tail into total length 24 times.

Coloration (Fig. 2): Ground color of body chestnut; mid-dorsal scales from prefrontal back, chestnut with faint lighter (tannish brown) lateral corners. First paramedian dorsal rows (including supranasals, supraoculars, parietals and postparietals) plus dorsal third of second paramedian rows tannish brown. Central axis of first paramedian dorsal rows suffused with darker brown forming a thin darker line on these rows,

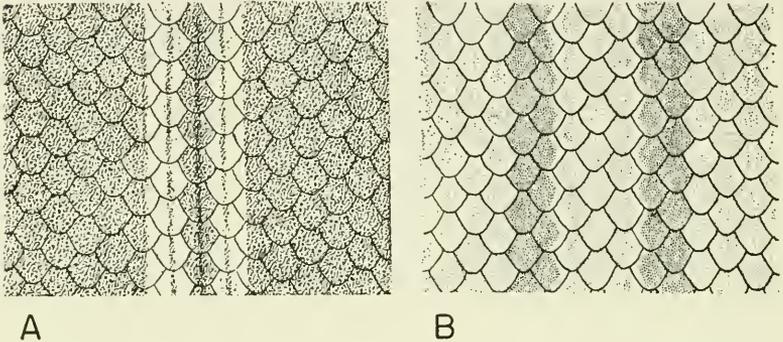


Fig. 2. A, color pattern at midbody of *L. pyrites*; B, color pattern at midbody of *L. bilineata*.

resulting pattern trilineate on light middorsal zone (Fig. 2A); middorsal stripe slightly club-shaped anteriorly because of enlargement of median cephalic scales. Upper and lower labial margins light, nearly continuous with light areas on top of head flanking median dark stripe; paramedian dark lines commence on first scale behind second parietal; rostral faintly suffused with brown.

Variation: Head scalation in the two paratypes is much the same as that of the type. Total length of each paratype 123 mm; diameters at midbody (1.9 and 2.0 mm) go into total length 65 and 61 times; tail lengths into total lengths go 21 times for each specimen. Middorsal scales 269 and 283; 15 and 16 subcaudals; 14 scale rows and 12 scales around the base of tail in both paratypes. Color patterns the same as that of the type.

Comparisons and discussion: As noted previously, *L. pyrites* is most closely related to *bilineata*, described by Schlegel from Martinique; *bilineata* is additionally recorded from Guadeloupe (Duméril and Bibron, *vide* Barbour, 1914), Barbados (Boulenger, 1893), and St. Lucia. (See also below, specimens examined.)

Underwood (1962) indicated that *bilineata* occurs on the mainland of South America, but he has informed me (*in litt.*) that this was a mistake. There appear to be no other records of *bilineata* from the mainland. The Guadeloupe record has not been substantiated in recent years. Dr. Guibé of the Muséum National d'Histoire Naturelle, Paris, writes (*in litt.*) that there are no specimens from Guadeloupe in that institution, and that he has not been able to find any indication of specimens from Guadeloupe. All of the specimens collected by Guyon and Plée have the locality indicated as Martinique. It seems best, therefore, to regard the Guadeloupe record as erroneous.³

Of the eight specimens of *bilineata* examined from Martinique, St. Lucia and Barbados, middorsal scales range from 170 to 189, in the neighborhood of one hundred scales lower than the counts for *pyrites* (269-283); scale rows are 14 in all cases, although two specimens reduce to 12 and 13 just anterior to the vent. Subcaudals range from 12 to 14 (15-16 in *pyrites*); scale rows around the base of the tail are 10 (11 in one) in all specimens from Martinique and St. Lucia versus 12 for *pyrites*. The Barbados specimen has 12 scale rows around the tail. Total lengths for the *bilineata* specimens 60-108 mm, for *pyrites* 123-133 mm. The ratio of midbody diameter into total length ranges from 34.6 to 43.2 in *bilineata*, 61.0-66.5 for *pyrites*. The ratio of tail length into total length varies from 15 to 18 for *bilineata*, 21-22 for *pyrites*. It can be seen that the two species differ abundantly in body scalation and proportions. In head scalation there are no constant differences between the two. In coloration, once again, the differences are striking (Fig. 2B). The unicolor middorsal zone, dorsolateral light lines, dark sides and light venter of *bilineata* contrast strongly with the more complex dorsal pattern and uniformly dark sides and venter of *pyrites*. *L. bilineata* also has a rather large patch of light (cream or yellow) scales surrounding the cloacal opening, while *pyrites* does not (the lips of the cloaca are light, but the scales surrounding it are not). In addition to having 12 scales around the tail, the Barbados specimen also has the highest middorsal scale count (189). Klauber (1940) has found the number of scales around the tail to be a useful differential character; it is possible that the

³ Mr. James D. Lazell, Jr. states (pers. comm.) that the natives of Guadeloupe spoke of two kinds of "two-headed" snakes (i.e. *Typhlops* or *Leptotyphlops*), of which one was said to have a lineate pattern and to inhabit the hotter, dryer parts of the island — a rather accurate and concise characterization of *L. bilineata*.

Barbados snakes are distinct from those of Martinique and St. Lucia.

Leptotyphlops albifrons Wagler has been recorded from Antigua, Grenada (Boulenger, 1893), and from Swan Island (Dunn and Saxe, 1950) in the West Indies; it also occurs on the South American mainland. This species (and its relatives in the *albifrons* group) is quickly distinguished from *pyrites* and *bilineata* by the extension of the ocular scale to the labial border; it is also characterized by a finely lineate dorsal and ventral pattern, and a light spot on the rostral and one on the tip of the tail. The name "*albifrons*" is used here with some reservations. I have examined a number of *Leptotyphlops* from South America pertaining to this group, but unfortunately none from the type locality of *albifrons* (Pará, Brazil). There is obviously more than one species involved in the material I have seen, but I have not tried to determine which of the profusion of available names applies to which forms except where West Indian specimens are concerned.

Examination of the specimen of *albifrons* recorded by Boulenger from Antigua shows it to agree closely, both in coloration and supraocular-first labial contact, with specimens from Trinidad to which the name *L. tenella*⁴ has been given (Klauber, 1939). No further specimens of *Leptotyphlops* from Antigua have come to light, not even under the more intensive herpetological collecting of the region in recent years. The locality for the specimen is possibly incorrect; it is probably best to regard the Antiguan record for *Leptotyphlops* as problematical until specimens are obtained or the negative evidence becomes stronger. Mr. Wayne King has informed me (pers. comm.) that the record of *Leptotyphlops* from the nearby island of Barbuda (Auffenberg, 1958) is in error and was due to an incorrectly identified *Typhlops*.

The record of *L. albifrons* from Grenada (Boulenger, 1893) is based on two specimens in the British Museum. Miss Grandison has advised me that the correct datum for these specimens is New Granada. As New Granada is the old name for the South

⁴ Subsequent to its proposal, the name *tenella* has been regarded variously as applying to a distinct species with specimens reported from as far south as the Brazilian state of Mato Grosso (Bailey and Carvalho, 1946) or as a race of *albifrons* inhabiting northeastern South America (Rozé, 1952). It is my feeling that *tenella* represents either a subspecies of a wide-ranging South American form (presumably true *albifrons*) or a variant (supraoculars and first labials in contact) which occurs throughout much of the range of *albifrons* (as far south as Mato Grosso) but is of particularly high frequency in the northeast. However, my knowledge of the complex of forms in the *albifrons* group is too meager to venture a solution to the problem at this time.

American country of Colombia, these specimens can no longer be regarded as pertaining to the Lesser Antillean island of Grenada.

The New Granada specimens are indeed of the *albifrons* group but do not pertain to that species. They have uniformly dark colored tails (with the exception of the terminal light spot) and relatively high middorsal scale counts (245, 253); they possibly pertain to a form or complex of forms including *margaritae* Rozé (1952, described as a subspecies of *albifrons*) from Isla Margarita, off of Venezuela, and *melanoterma* Cope (1862) described from Corrientes, Argentina.

L. albifrons magnamaculata Taylor is known from Swan Island in the West Indies and additionally from San Andrés, Providencia, and the Bay Islands of Honduras, including Utila (type locality). It is supposedly distinguished by a larger white spot on the snout and a more extensive spot under the tail (Taylor, 1940), and more vivid markings (Dunn and Saxe, 1950).

Leptotyphlops columbi Klauber is known only from Watlings Island in the Bahamas, over 400 miles from its nearest congener. The Bahamas are as a whole poorly collected, and it may well be found to occur on other islands. *L. columbi* too can be distinguished from *pyrites* in the possession of an oculo-labial contact; it is further distinguished by a high subcaudal count (22-25: Legler, 1959), and a nearly uniform dark dorsal coloration but paler venter (*op. cit.*). Klauber used the coloration and the high subcaudal count to distinguish it from forms of the *albifrons* group (however, Legler's new data indicate an overlap with the highest "*albifrons*" counts of 23 noted by Klauber, 1939, and myself).

Key to the West Indian *Leptotyphlops*

1. Ocular excluded from labial border 2
 Ocular extends to labial border 3
2. Middorsal scales (between rostral and terminal spine) 170-189,
 venter light *bilineata*
 Middorsal scales 269-283, venter dark *pyrites*, n. sp.
3. Light spot on snout and tip of tail 4
 No light spot on snout and tip of tail, coloration generally dark above,
 lighter below *columbi*
4. Supraoculars contact first supralabials *tenella*
 Supraoculars not in contact with first
 supralabials *albifrons magnamaculata*

The strange apparent distribution of *Leptotyphlops* in the West Indies should be noted (Fig. 3). There has been a tendency to dismiss the erratic insular occurrence of these small snakes as due in large part to introduction by man, both pre- and post-Columbian. While it must be admitted that their small size and burrowing habits make them likely candidates for artificial transportation, we have no evidence that this has occurred. Such thinking is an easy way out of facing what might well be a real but complex zoogeographic problem. To begin with, the distribution of *Leptotyphlops* in the Lesser Antilles is perhaps no more unusual than the non-uniform distribution of several other forms in this region (cf. *Leptodactylus*, *Ameiva*, *Gymnophthalmus*, *Bothrops*, *Constrictor*). The non-uniform distribution of other forms is attributable in part to the erratic nature of natural dispersal across water and in part perhaps to selective extinction on some islands; in the case of creatures like *Leptotyphlops* some of the gaps may be more apparent than real due to incomplete collecting.

Not all cases are, in any event, erratic. *L. a. magnamaculata* occurs on marginal islands (Swan Island) that are close to the mainland; it is closely allied to the mainland *albifrons* representative (Dunn and Saxe, 1950); its distribution, therefore, is not particularly remarkable or unexpected. Although the specimen of Antigua *tenella* is regarded as being of questionable provenance, the occurrence of a form of strong South American affinities so far up the chain would not be unprecedented if this record is verified. Thus, the gecko *Phyllodactylus* occurs on Puerto Rico and the adjacent Caja de Muertos; the nearest records to the south for this genus are Grenada and Barbados. *Leptotyphlops pyrites* and *L. columbi* are the Antillean forms found farthest from the mainland and whose distributions are the most irregular. The fact that *L. pyrites* has an obvious relative in the Lesser Antilles and apparently none on the mainland strongly bespeaks a relict distribution in the West Indies. The exact relationships of *L. columbi* are uncertain; although Klauber suggested a closer affinity with *albifrons* than with other forms, it is apparently not close. *L. columbi* may either represent a fortuitous arrival in the Bahamas or a relict distribution. Its apparent distinctness would seem to speak against its having been artificially introduced, as has been suggested (Darlington, 1957:221).

I wish to express my appreciation to Dr. Albert Schwartz who supported this study and the collecting that resulted in the

acquisition of the form described. I also wish to thank the following people for their help in various ways: Père R. Pinchon of the Séminaire College (SC), Fort-de-France, Martinique, for the loan of specimens and for the donation of a specimen to the ASFS (Albert Schwartz Field Series) collection; Miss A. G. C. Grandison of the British Museum (Natural History) (BM) for the loan of specimens and the biographical information on Dr. A. C. Buller; Dr. James A. Peters of the U. S. National Museum (USNM) for the loan of specimens and help in finding *Leptotyphlops* names and literature; Dr. Ernest E. Williams of the Museum of Comparative Zoology, Harvard (MCZ) for loan of specimens and help in obtaining literature; Neil D. Richmond of the Carnegie Museum (CM) for the loan of specimens; and Mr. David C. Leber for his most able assistance in the field. RT designates specimens in the Richard Thomas private collection.

SPECIMENS EXAMINED

Leptotyphlops pyrites: As listed for the type and paratypes.

Leptotyphlops bilineata: Martinique: BM 53.2.4.36, USNM 119168; Fort-de-France, SC 1; Tartane, Morne Jésus, SC 2-3, ASFS V4150. St. Lucia: MCZ 10693. Barbados: BM 89.7.5.27.

Leptotyphlops "albifrons" (no nomenclatural finality intended): Specimens in the American Museum of Natural History and the University of Michigan Museum of Zoology collections, Brazil (1), Bolivia (7), Perú (16).

Leptotyphlops tenella: Trinidad: St. George Co.: Mt. St. Benedict, CM 4888-89, 4892, 6612 (paratypes); El Dorado, CM 4893 (paratype); Arima Ward, Santa Cruz Valley, 7.5 mi. N San Juan, RT 1186. ?Antigua: BM 50.4.29.3.

Leptotyphlops cf. *margaritae*: New Granada: BM 80.2.26.4-5.

Leptotyphlops phenops cf. *bakewelli*: Santo Domingo de Guzmán, BM 90.10.10.73.

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(Received 16 February, 1965.)

	Total length	Tail length	Mid- dorsals	Sub- caudals	Rows, tail	Midbody diameter
<i>pyrites</i>						
USNM 152452	123	6	283	15	12	1.9
ASFS V2601	123	6	269	16	12	2.0
MCZ 77239	133	6	273	15	12	2.0
<i>bilincata</i>						
MCZ 10693	74	4	182	13	10	1.7
BM 53.2.4.36	108	7	183	14	11	2.5
SC 1	107	6	174	12	10	3.1
SC 2	93	5	181	14	10	2.4
SC 3	60	4	187	14	10	1.6
ASFS V4150	108	6	175	13	10	2.9
USNM 119168	102	7	170	13	10	
BM 89.7.5.27	102	6	189	13	12	

Table 1. Data for individual specimens of *L. pyrites* and *L. bilincata* examined. Measurements are in millimeters.

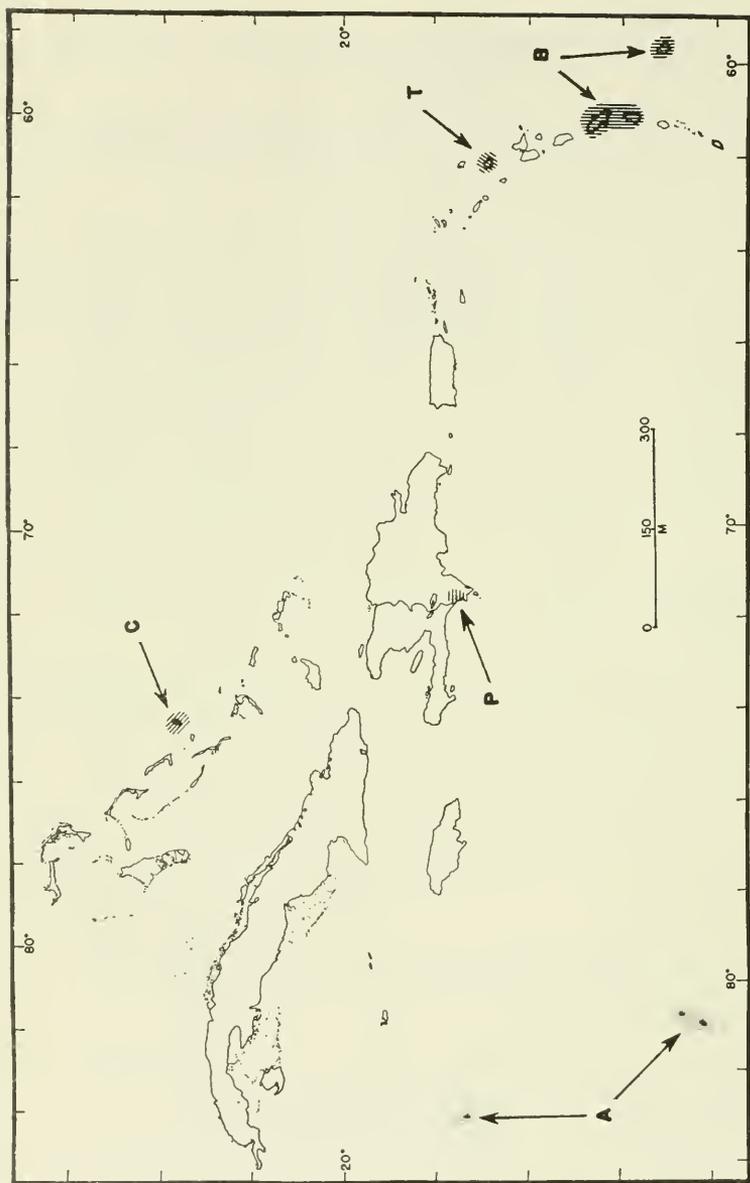


Fig. 3. Map of the West Indies showing the distribution of *Leptotyphlops*. A, *albifrons* (Swan I., San Andrés, Providencia); C, *columbi* (Watlings); P, *pyrites* (Hispaniola); T, *tenella* (Antigua); B, *bilineata* (Martinique, St. Lucia, Barbados).

B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS.

MAY 28, 1965

NUMBER 223

A NEW SUBSPECIES OF *CLELIA CLELIA* (SERPENTES: COLUBRIDAE) FROM THE ISLAND OF GRENADA

BY ALLEN E. GREER

The recent acquisition of two specimens of *Clelia clelia* from the island of Grenada, Lesser Antilles, draws attention to significant morphological and behavioral differences between the island and mainland populations of this species. The population of *Clelia clelia* from Grenada warrants taxonomic recognition and may be known as:

*CLELIA CLELIA GROOMEI*¹ new subspecies

Fig. 1

Holotype. MCZ 79767, adult male, Beausejour, Grenada. Coll. James D. Lazell, Jr., 1 July, 1964.

Paratypes. MCZ 79766, Du Quesne, Du Quesne River Valley, St. Marks, Grenada. Coll. James D. Lazell, Jr., 26 June, 1964. MCZ 4507, Grenada. Coll. Peter Gillinam. Received by the Museum, August, 1880.

Diagnosis. *Clelia clelia groomei* is similar to the mainland populations of *C. clelia* except for the preocular which is either very much reduced in size or united with the supraocular. When present, the preocular does not reach dorsally to the level of the upper edge of the loreal. When the preocular is lacking, the supraocular extends ventrally in front of the eye to touch the third supralabial.

Comments. In all three specimens the reduced preocular is present on the left side of the head and absent on the right.

As only three specimens of *Clelia* are known from Grenada,

¹Grenada is one of the few places in the world where snakes are protected by law. Dr. John R. Groome of Point Salines, Grenada, one of the few zoologists in the Lesser Antilles, has been the primary instigator of this reform. For this, and for his hospitality to Mr. Lazell during his stay on Grenada, the new subspecies is named in Dr. Groome's honor.

it may be objected that the diagnostic head scale characters are nothing more than asymmetrical anomalies. Obviously, only an examination of a larger sample would test this objection satisfactorily. For the present, however, it seems significant to me that the diagnostic characters are found not only in two specimens (MCZ 79766-79767) recently collected in different areas of Grenada (Fig. 2) but also in a third specimen (MCZ 4507)

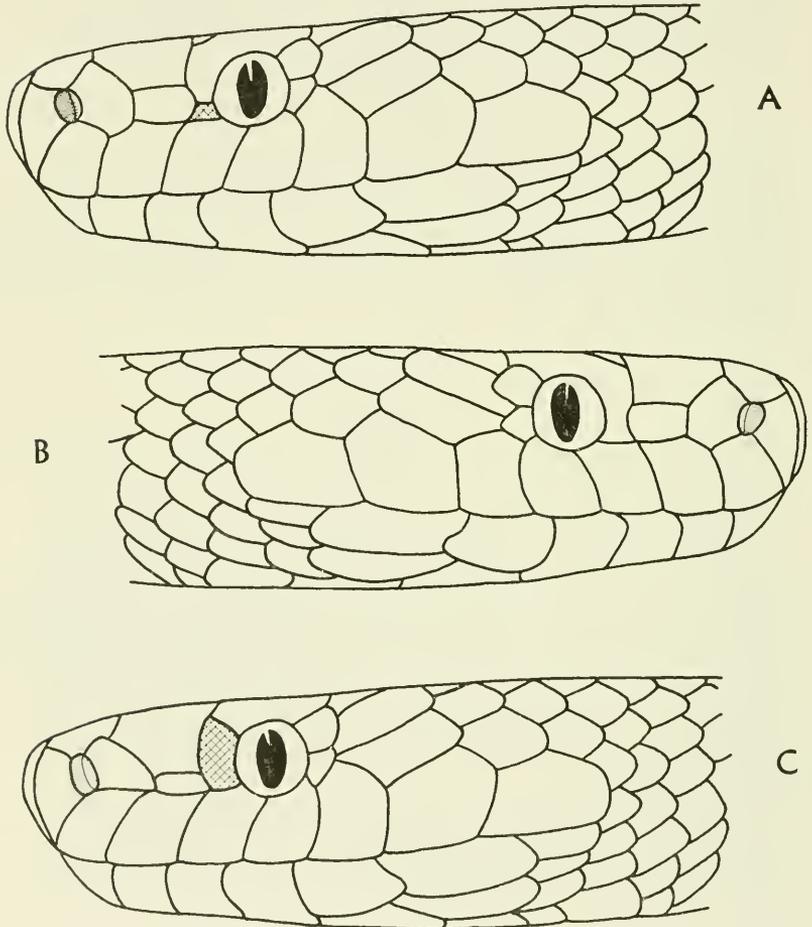


Fig. 1. Side of the head of *Clelia clelia*. A and B, *C.c. groomei* new subspecies, paratype, MCZ 79766, Du Quesne, Grenada; C, *C. clelia* (Daudin), MCZ 19933, Ulna River, Tela, Honduras. Preocular scale is cross-hatched.

collected at probably yet a third locality 83 years previously. These admittedly slight, but constant, morphological differences, together with the behavioral differences alluded to below, indicate that the Grenada population of *Clelia* should be given at least subspecific status.

The holotype (MCZ 79767), a male, has 216 ventral scales, 72 + subcaudal scales, and 19-19-19 longitudinal scale rows. The uniform slate grey color of the dorsum extends ventrally to the lateral quarter of the ventral scales. The chin, throat and entire midventer are white.

MCZ 79766 is a female with 231 ventrals, 81 subcaudals and 19-19-17 longitudinal scale rows. The color is essentially similar to that of the holotype.

MCZ 4507 is a female with 232 ventrals, 44 + subcaudals and 19-19-17 longitudinal scale rows. The distribution of the color is the same as in the holotype, but the dorsum is uniformly brown and the midventer is yellowish brown. The specimen has been long preserved in alcohol.

All three specimens have well-defined paired apical pits on the dorsal scales.

The hemipenes of the holotype (MCZ 79767) agree well with Cope's (1900, pl. 26, fig. 4) figure of *Oxyrrhopus plumbeus* (= *Clelia clelia*) from Brazil.

Field Notes. Mr. James D. Lazell, Jr., who is currently studying the iguanid lizards of the Lesser Antilles, has kindly summarized his knowledge of *C. clelia groomei* for me. The account is presented in its colorful entirety below.

"When I was first in Grenada, in 1959, I heard tales of a snake, supposedly huge and much feared by Grenadians, called 'Cribo.' Underwood (1962, p. 164) having heard the same stories, recorded *Constrictor constrictor* from Grenada; he made the remarkable assumption (pers. comm.) that the stories could only apply to that species. As the distribution of *Constrictor* in the Lesser Antilles was of great interest to me (Lazell, 1964), when I returned to Grenada in June and July of 1964 I made a special effort to find out all I could about the famous 'Cribo.' Primary among my sources of information were Dr. John R. Groome, of Point Salines, Major Francis Power, of Tufton Hall, and Mr. Nick Neckles, of Beausejour. From these and many others, I learned that the 'Cribo' is indeed a large snake (up to ten feet ?), much feared by the local people for its strength (not its venom), restricted in range to the wet portions of the

island (though it is not known to what elevation it occurs), and uniform slate in dorsal color.

"Obviously the 'Cribo' was not a *Constrictor*; I thought, however, that it might be *Clelia clelia*, a species supposedly recorded from Grenada by one specimen (MCZ 4507). I knew from Drs. John Price and Jake Kenny (pers. comm.) and Mr. Michael Dix (pers. comm.) that in Trinidad and Central America, respectively, *C. clelia* was a nocturnal, ophiophagous snake.

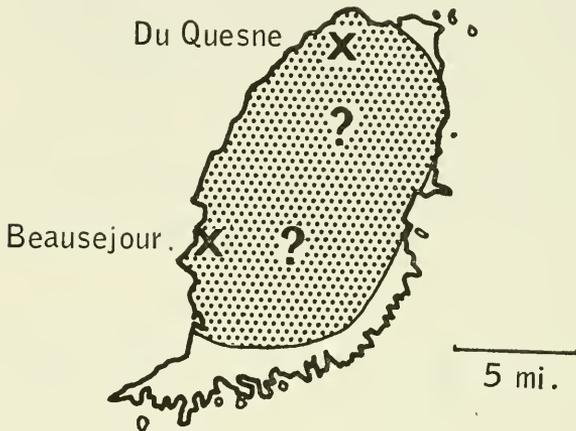


Fig. 2. Grenada. The stippled region indicates the wet portions of the island. *Clelia* is reported not to occur outside this region. X = localities represented by specimens. Question marks are centered on extremely wet, high, montane areas.

I spent seven nights, from dark to dawn, driving north out of St. George's around the coast and back by the Grand Etang road in a fruitless effort to collect specimens. Throughout this time, I learned on the sixth day, people all along my route had been encountering 'Cribos' in the daytime. On 26 June, therefore, I continued on around again after sunrise. At 9:10 A.M., in the Du Quesne Valley in northern Grenada, the car in front of me swerved off onto the shoulder of the road and ran over a 50-inch *Clelia*. This individual (MCZ 79766) was in the process of swallowing a rat (*Rattus rattus*) at the time, and the side of the neck was burst. I took the dead snake on around the island, stopping at villages to ask about it. To the question, 'What is this?' I got the invariable reply: 'a Cribo'; I then asked, 'How

old do you think it is?' and got always a variation on: 'It is *very* young.' I became famous on Grenada, needless to say.

"On the morning of 1 July, I was coming south along the leeward coast road when I was stopped by a man who had just seen a 'Cribo' crossing the road. It was 9:30 A.M. I uncovered the specimen (MCZ 79767) in some bushes alongside the road, where my informant indicated it had gone.

"This specimen was kept alive for several days. It seemed nervous, making abrupt darts with its head when handled, but it never attempted to bite. It was active in the morning, but remained quite dormant at night. It was a powerful constrictor. Fresh dead, it measured 62 inches.

"The people of Grenada confirm my records of the 'Cribo' eating rats, and mention occasional hen house raids as well. This species appears to be strictly diurnal with an apparent activity peak between sunrise and noon. It does not occur in the extremely dry area along the coast of Grenada from Point Salines to Telescope Point; similarly, it is absent from the dry northeast part of the island (Fig. 2). Elsewhere, in the wet lowlands at least, it is apparently fairly common.

"Several people in Carriacou maintain that a 'Cribo' (fitting the general description of the Grenada animal) occurs there; they are not confusing it with the 'serpent' (*Boa* sp.), which is abundant in the Grenadines and Grenada. If *Clelia* does occur on Carriacou, it is remarkable, for that island is drier by far than any habitat occupied by *Clelia* on the Grenada mainland."

Mr. Michael Dix of the Biological Laboratories, Harvard College, has studied the habits of *C. clelia* both in the wild and in captivity. He informs me that in the vicinity of Middlesex, British Honduras, the snake is an inhabitant of the "tropical wet forest" and is strictly nocturnal, being most active between 8-10 P.M. It is both terrestrial and arboreal (one individual having been found 5 feet above the ground), an observation supported by Beebe (1946, p. 23).

Captive individuals from Central America will take birds the size of sparrows and a little larger but prefer their more traditional bill of fare — snakes. Apparently food items are "trailed about the cage by olfaction. Mice, rats and frogs have been offered as food but never accepted. Several successful attempts to escape confinement also attest to the climbing abilities of the species."

Large adults in the vicinity of Middlesex are black dorsally but slate grey when younger.

Discussion. Throughout its range on the mainland from Mexico to Argentina, and on the island of Trinidad, the "Mussurana" is known as a nocturnal, ophiophagous snake. On Grenada it appears as if the "Cribo" is primarily diurnal and not unwilling to make a meal of small rodents. Morphologically, the two populations are separated by what most taxonomists would consider to be subspecific differences, while from the behavioral standpoint, the two populations are distinct to a degree suggesting specific separation. Assigning island populations to the species or subspecies category is largely a matter of personal preference and practicality. In this case our purpose is perhaps best served by recognizing the Grenada "Cribo" as a subspecies of the mainland *C. celia* and thereby acknowledging its close relationship with the mainland population.

Acknowledgments. My thanks go to Mr. James D. Lazell, Jr. for suggesting an examination of the Grenada specimens. The extensive knowledge of the Antillean herpetofauna possessed by both Dr. E. E. Williams and Mr. Lazell made their criticisms of the paper most valuable.

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(Received 10 March, 1965.)

B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS.

JULY 15, 1965

NUMBER 224

NEW SPECIES OF LAND MOLLUSKS WITH NOTES ON OTHER SPECIES FROM THE SOLOMON ISLANDS

By WILLIAM J. CLENCII

The three new species described in this paper were received from James R. Hood of Chattanooga, Tennessee, who was stationed in the Solomon Islands in 1949, and from the Rev. J. Vander Riet, a missionary in Ataa, Malaita. A fine series of land and freshwater shells from this region was received from the latter.

While working up this and other Solomon Island material several systematic problems were encountered and these are discussed in this study.

CAMAENIDAE

The following species, generally placed in the genus *Papuina*, are here placed in *Solmopina* Iredale. They have been confused with one another and are in need of clarification. This confusion resulted from the fact that *Solmopina macfarlanei* (Cox) had not been figured, and the island in the Solomons from which it came was unknown until the locality was published by Rensch in 1934.

SOLMOPINA MACFARLANEI (Cox)

Pl. 1, figs. 1-2

Helix (Geotrochus) macfarlanei Cox 1873, Proc. Zool. Soc. London, p. 567
(Solomon Islands).

Helix (Papuina) macfarlanei Cox. Pilsbry 1891, Manual of Conchology
(2) 7:13 (Solomon Islands).

Papuina macfarlanei (Cox). Rensch 1934, Amer. Mus. Novit. No. 763:7
(Kieta, Bougainville, Solomon Islands).

Measurements

Height	Greater diameter	
mm	mm	
23	25	near Buin, Bougainville
23	24.5	near Buin, Bougainville
21	22	near Buin, Bougainville

Description: Shell trochiform, imperforate, smooth, and reaching 25 mm in greater diameter. Color a pale ivory with a dark brown band at the whorl periphery and a broad circular area of the same color on the base of the shell. In addition, there are numerous irregular spots of brown both above and below the periphery. These brown bands and spots are translucent. The somewhat lighter brown spots are a little more translucent than the bands. Whorls $5\frac{1}{2}$ and convex. Spire somewhat extended and produced at an angle of about 70° . Aperture subquadrate with the lip slightly reflected and cast at an angle of about 42° from the base. Columella at an angle from the umbilical area to the base. Suture indented. Sculpture consisting of fine and irregular growth lines. Protoconch of $1\frac{1}{2}$ whorls, white and smooth.

Remarks: This species differs from *S. coriana* (Angas) by being larger, having more convex whorls, and in having the peripheral band of brown. The shell of *S. coriana* is more delicate in structure and the brown coloration is considerably lighter in color. The brown spots in *coriana* are also translucent. I do not agree with Rensch that these two species may be only geographic races. They appear quite distinct. In 101 specimens examined only a single specimen lacked the peripheral band. Rensch has recorded this species from Kieta, Bougainville.

Specimens examined: BOUGAINVILLE: Buin (MCZ).

SOLMOPINA COXIANA (Angas)

Pl. 1, fig. 3

Geotrochus coriana Angas 1867, Proc. Zool. Soc. London, p. 889, pl. 43, figs. 7-8 (Ysabel Island, Solomon Islands).

Helix (Papuina) coriana (Angas). Pilsbry 1891, Manual of Conchology (2) 7:13, pl. 3, figs. 36-37.

Papuina coriana (Angas). Rensch 1934, Amer. Mus. Novit. No. 763:8.

Measurements

Height	Greater Diameter	
mm	mm	
17	20	Ysabel Island

Description: Shell trochiform, imperforate, smooth and reaching 20 mm in greater diameter. Color a pale ivory with a broad circular area of light brown on the base of the shell, and, in addition, a few brownish spots irregularly disposed over the shell. Both the basal band and the spots are translucent. Whorls 5, slightly convex. Spire somewhat extended and produced at an angle of about 70°. Aperture subquadrate with the lip slightly reflected, colored brown and cast at an angle of about 40° from the base. Columella white and at an angle from the umbilical area to the base. Suture slightly indented. Sculpture consisting of very fine and irregular growth lines. Protoconch of 1½ whorls, white and smooth.

Remarks: See *Remarks* under *S. macfarlanei*.

Specimens examined: YSABEL.

Specimens recorded: CHOISEUL: Luti and Tauro (Rensch).

ARIOPHANTIDAE

TROCHOMORPHA VANDERRIETHI new species

Pl. 2, figs. 1-2

Holotype: MCZ 251176, from Ataa, Malaita Island, British Solomon Islands. Rev. J. Vander Riet, collector, 1964.

Paratypes: Figured paratype, MCZ 251177; additional paratypes, MCZ 247959, all from the same locality as the holotype.

	Greater	Lesser	
Height	diameter	diameter	
mm	mm	mm	
11	26.5	22	Holotype
10	27	22	Paratype MCZ 251177 (figured)
11.5	26	20.5	Paratype MCZ 251177
11.5	25	20.5	Paratype MCZ 251177
10	28	21	Paratype MCZ 247959 (figured)

Description: Shell reaching 27 mm in width, subdepressed, finely carinated and umbilicated. Color a dark, yellowish brown, unicolorous below the thread-like carina and flecked with numerous narrow, straw-colored patches in axial arrangement above the carina. The brown coloration is in the shell; the straw coloration is invested in the periostracum. Whorls 5 to 5½, convex, and the last whorl with a fine, thread-like carina. Spire depressed, dome-shaped and forming an angle of about 135°. Aperture subovate, with the outer lip slightly depressed near its juncture with the whorl above. Outer lip narrowly reflected

along the basal area. Umbilicus rather narrow and very deep, and is $\frac{1}{6}$ the width of the shell in greater diameter. Suture slightly indented and well defined. Sculpture consisting of numerous oblique and fine costae above the whorl periphery and nearly smooth below.

Remarks: In relationship, this species is nearest to *Trochomorpha aukiensis* Clapp, also from Malaita. *Trochomorpha vanderrichti* differs from *R. aukiensis* by being larger, not being spirally banded and in having a narrower umbilicus, being $\frac{1}{6}$ of the greater diameter, while in *aukiensis* the umbilicus is $\frac{1}{4}$ of the greater diameter and there are no straw-yellow flecks above the whorl periphery.

Including *T. vanderrichti*, there are seven species of *Trochomorpha* now known from Malaita Island. These are:

Trochomorpha aukiensis Clapp 1923, Bull. Mus. Comp. Zool., **65**:361, pl. 2, figs. 10-15 (Auki, Malaita). [Holotype, MCZ 32535].

Trochomorpha belmorci (Cox) 1871, Proc. Zool. Soc. London, p. 647, pl. 52, fig. 12 (Solomon Islands).

Trochomorpha concava Clapp 1923, Bull. Mus. Comp. Zool., **65**:363, pl. 3, figs. 1-3 (Auki, Malaita). [Holotype, MCZ 32523].

Trochomorpha crustulum (Cox) 1873, Proc. Zool. Soc. London, p. 150 (Solomon Islands).

Trochomorpha flava Clapp 1923, Bull. Mus. Comp. Zool., **65**:366, pl. 3, figs. 4-6 (Auki, Malaita Island). [Holotype, MCZ 32521].

Trochomorpha melceni Clench 1959, Natural History of Rennell Island, British Solomon Islands, Univ. Copenhagen, Denmark, Vol. **2**:179, pl. 17, fig. 6 (10 miles inland from Suu, Malaita Island). [Holotype, Amer. Mus. Nat. Hist. 79016].

ASSIMINEIDAE

SETAEPOMA Clench

Setaepoma Clench 1955, Nautilus, **63**:134 (type species, *Japonia* (?) *hedigeri* I. and B. Rensch).

SETAEPOMA HOODI new species

Pl. 2, fig. 3

Holotype: MCZ 251309, from the west side of the Tenaru River, about one-half mile above the Catholic Mission, Guadalcanal, Solomon Islands. James R. Hood, collector, 1949.

Measurements

Height	Width	
mm	mm	
8.2	7.9	Holotype

Description: Shell turbinate, thin, umbilicate and having numerous, spiral rows of bristle-like processes of periostracum. Color a golden brown. Whorls 6 and tubular. Spire moderately extended and produced at an angle of about 60° . Aperture nearly circular, holostomatous and with a thin, simple lip. No columella; umbilicus narrow and deep. Suture deeply indented. Periostracum thin, shining, and with numerous, spiral and axial ridges which support a bristle-like process at each intersection. Protoconch of about 2 whorls which are smooth and shining. Operculum calcareous, multispiral and dished. Inner surface with a papilliform central nucleus, smooth, shining, and with faint indications of the outer sculpture.

Remarks: This species is distantly related to *Sctaeopoma hedigeri* I. and B. Rensch (Bougainville Id.) and *S. mayri* Clench (Ysabel and Choiseul Ids.). It differs from both by being more attenuated, having fewer spiral ridges and a much narrower umbilicus.

This present new species is the third known from the Solomon Islands. The other two are:

Sctaeopoma hedigeri (I. and B. Rensch) 1936, Revue Suisse de Zoologie, **43**:678 (Bougainville Id., Solomon Ids.).

Sctaeopoma mayri Clench 1959, Natural History of Rennell Island, British Solomon Islands, Univ. Copenhagen, Denmark, Vol. **2**:168, pl. 17, fig. 5, text fig. 1 (Fulakora, Ysabel Id., and the Wurulata River, Choiseul Id., Solomon Ids.).

CYCLOPHORIDAE

PALAINA (PALAINA) BRAZIERI (Cox)

Pl. 2, fig. 4

Diplommatina brazieri Cox 1870, Proc. Zool. Soc. London, p. 84 (Wanga, San Christoval Id., Solomon Islands).

This species has not been figured previously. The specimen we figure came from Kira Kira, San Christoval Id., collected by the Whitney Expedition in 1929.

PALAINA (PALAINA) DELLI new species

Pl. 2, fig. 5

Holotype: MCZ 258017, from one-half mile above the Seventh Day Adventist Mission Station on the west side of the Lunga River, Guadalcanal Island, Solomon Islands. James R. Hood, collector, 1949.

Paratypes: Five paratypes, MCZ 258018, from the same locality as the holotype.

Measurements

Height	Width	
mm	mm	
4.5	2	Holotype
4.7	2.2	Paratype
4.5	2	Paratype
4.5	2.1	Paratype
4.3	1.8	Paratype

Description: Shell reaching 4.7 mm in height, dextral, imperforate and sculptured. Whorls $6\frac{1}{2}$ and convex. Color a dull grayish brown. Spire attenuate and straight. Aperture circular, with a broadly reflected lip, and attached at the parietal area. No columellar tooth. Suture impressed. Sculpture consisting of numerous, diagonal riblets which are very irregular as to number on the different whorls and between different specimens. These riblets may be single or in groups of 2 to 5 and varying from whorl to whorl. Protoconch of 2 whorls, smooth and rather dull. Operculum with a vertical, spiral lamella.

Remarks: This species is nearest in relationship to *P. brazieri* (Cox) from San Christoval. It differs by being more than twice as large and in having more regular and more numerous axial riblets. Both are dextral and neither has a columellar tooth.

Named for Dr. Richard K. Dell, Dominion Museum, Wellington, New Zealand.

DIPLOMMATINA AERARI Dell

Diplommatina aerari Dell 1955, Pacific Science, 9:425, fig. 1 b (Mono Id., Treasury Group, Solomon Islands).

Three specimens of this species were collected by James R. Hood, one-half mile above the Seventh Day Adventist Mission Station on the west side of the Lunga River, Guadalcanal Island.

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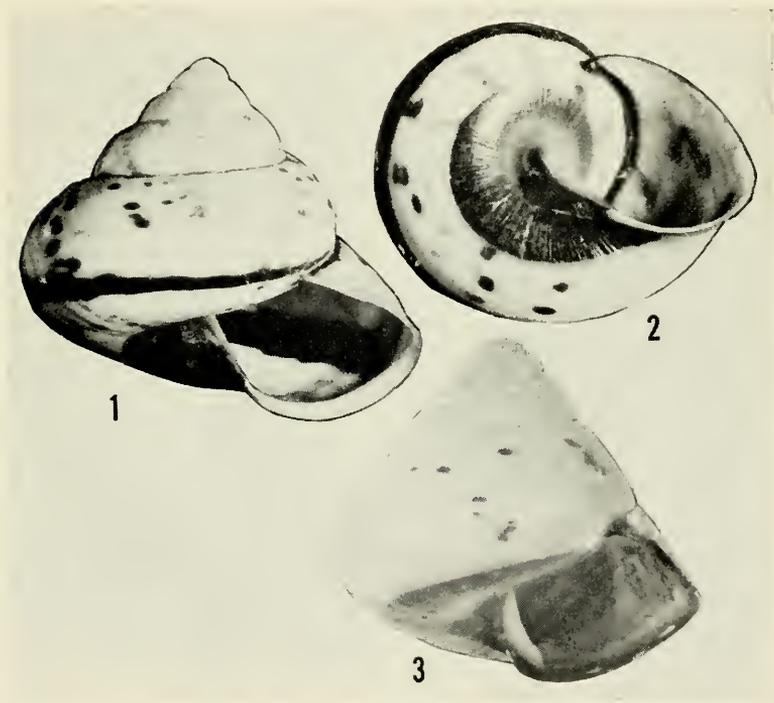


PLATE 1

Figs. 1-2. *Solmopina macfarlanei* (Cox). Buin, Bougainville Id. (about 2 X).

Fig. 3. *Solmopina coriana* (Angas). Ysabel Id. (2.5 X).

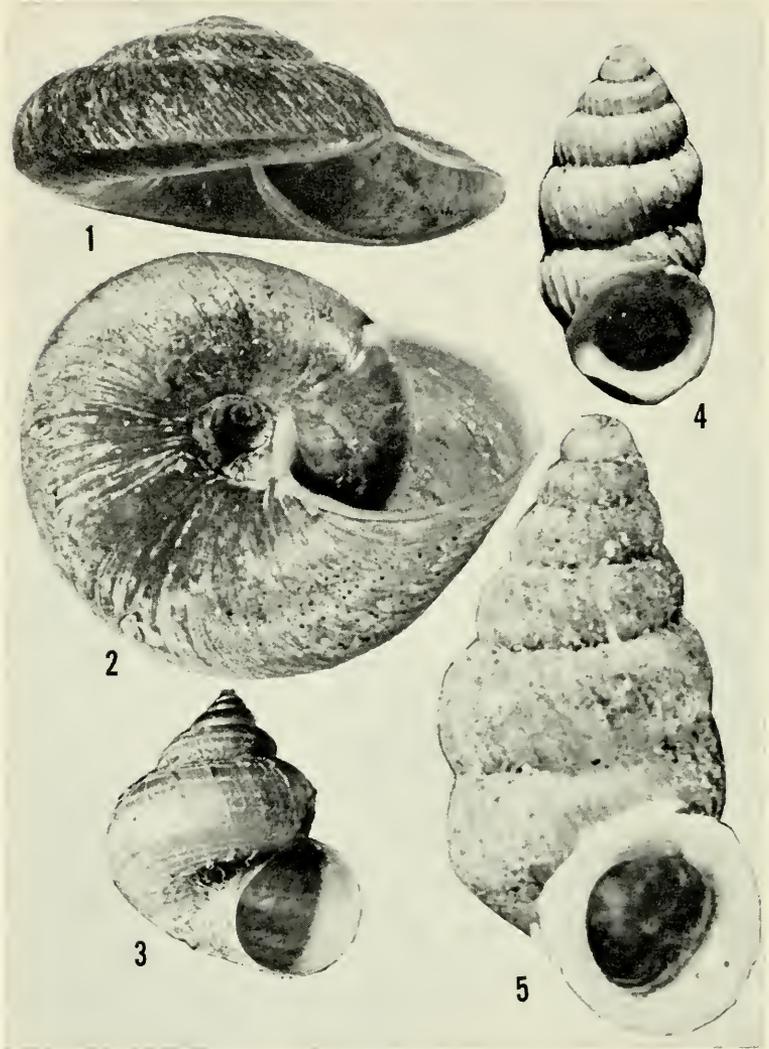


PLATE 2

Fig. 1. *Trochomorpha vanderrieti*, n. sp. Ataa, Malaita Id., Solomon Islands. Holotype, MCZ 251176 (2.4 X).

Fig. 2. *Trochomorpha vanderrieti*, n. sp. Ataa, Malaita Id., Solomon Islands. Paratype, MCZ 247959 (2.4 X).

Fig. 3. *Setaepoma hoodi*, n. sp. West side of the Tenaru River, about one-half mile above the Catholic Mission, Guadalcanal Id., Solomon Ids. Holotype, MCZ 251309 (4.6 X).

Fig. 4. *Palaina (Palaina) brazieri* (Cox). Kira Kira, San Christoval Id. (12.6 X).

Fig. 5. *Palaina (Palaina) delli*, n. sp. West side of the Lunga River, one-half mile above the Seventh Day Adventist Mission, Guadalcanal Id. Holotype, MCZ 258017 (18 X).

B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS.

JULY 15, 1965

NUMBER 225

THE ASIAN SPECIES OF *GALERITULA* STRAND (COLEOPTERA, CARABIDAE)

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Very few attempts have been made to study the relatively few Asian species of *Galeritula*. All these species have been described individually, by separate authors, who usually had very few specimens of each.

Heller (1923:65) was the first to attempt the characterization of species groups when he described *szetschwana* from China. However, the characters he used to divide the Asian species of *Galeritula* into two groups are very variable (posterior constriction of pronotum more or less well developed, and margins of pronotum parallel or divergent behind the constriction), as will be seen below. The failure of this system is evidenced by Heller's separation of *peregrina* Dohrn and *birmanica* Bates into different groups, even though these species were considered synonymous by Andrewes a few years earlier (1919:480).

In 1949 Jeannel assigned the Asian species of *Galeritula* (together with a few African forms) to a new genus, *Galeritella*.

Finally, in 1963, Jedlicka presented a revision of the species found on the Asian Continent. According to this author (1963:474) it is very difficult to separate some species morphologically, since most of them are very similar; Jedlicka separated the species, as did most earlier authors, solely on the basis of color. As pointed out later in this paper, the coloration is a very variable character in *G. orientalis* and for this reason this species has been described several times (eight names are available for *orientalis*). The fact that such variation occurs can, however, only be observed in large series of specimens. No author has yet had many specimens on which to base his studies.

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In the course of my present work on the Neotropical species of *Galeritula*, I have been able to study many types as well as undetermined material of Asian species in the British Museum (Natural History), London, and the Muséum National d'Histoire Naturelle, Paris. In addition, several other museums have provided specimens for identification. Study of this relatively rich collection of 138 specimens has revealed some very interesting facts, and has produced many new distributional records. All this has led to a study of the Oriental species and their relationships, which is reported here.

SOURCES OF MATERIAL, METHODS AND ACKNOWLEDGMENTS

The present study is based on material from the following collections (abbreviations as used in the text):

British Museum (Natural History), London (BM); Mr. Jacques Nègre's collection, Versailles (JN); Institute of Zoology, Polish Academy of Sciences, Warsaw (IZ); Museum of Comparative Zoology, Cambridge, Mass. (MCZ); Muséum National d'Histoire Naturelle, Paris (MNHN); Academy of Natural Sciences, Philadelphia (ANSP), and Senckenberg Museum, Frankfurt am Main (SMF).

The measurements of the specimens have been made with a microruler in the microscope ocular. Comparison is made between measurements of parts of the beetles (expressed in the descriptions by ratios) as follows: *Head* — width/length (width taken at the widest point, including the eyes; length taken from apex of clypeus to constriction behind the eyes, not including the neck); length of eyes/length of occiput (the measurement of the occiput is made parallel to the longitudinal axis of the body, from posterior margin of eye to beginning of neck). *Pronotum* — width/length (width taken at widest point; length along the median line). *Elytra* — width/length (width at widest point; length from base to apex, along suture). Total length of specimens has been measured from the tip of mandibles to apex of elytra, excluding the pygidium.

I am greatly indebted to the curators of the above mentioned collections, without whom this study would have been impossible; special thanks are due to the Evolutionary Biology Committee at Harvard University, which provided the funds for my European studies in June 1964. I am also grateful to Professor P. J.

Darlington, Jr., Dr. E. G. MacLeod and Dr. R. W. Taylor for having read and criticized the manuscript.

GALERITULA Strand, 1936

Galerita Fabricius, 1801, Syst. Eleuth., 1:214 [type, by subsequent designation (Latreille, 1810, Consid. Gen.:426) *Carabus americanus* Linnaeus, 1758]; Jedlicka, 1941, Versuch einer Monographie der Truncatipennen . . . pp. 12, 25 [notes on Asian species]. Not *Galerita* Gouan, 1770.

Galeritula Strand, 1936, Fol. Zool. Hydrobiol., 9:168 [new name for *Galerita* Fabricius, 1801]; Basilewsky, 1963, Ann. Mus. Roy. Afr. Centr., 8°, Sci. Zool., 120:5, 6, 7, 23 [genus restricted to Neotropical species]; Jedlicka, 1963, Ent. Abh. Mus. Dresden, 28:474-475 [revision of continental Asian species].

Galeritina Jeannel, 1949, Faun. Emp. Franç., 11:1058 [new name for *Galerita* Fabricius, 1801].

Galeritella Jeannel, 1949, Faun. Emp. Franç., 11:1058 [type, by original designation, *Galerita orientalis* Schmidt-Goebel, 1846]; Basilewsky, 1963, Ann. Mus. Roy. Afr. Centr., 8°, Sci. Zool., 120:8, 63-64 [revision of African species]. *NEW SYNONYMY*.

Galericeps Jeannel, 1949, Faun. Emp. Franç., 11:1058, 1062 [type, by original designation, *Galericeps pheropsophoides* Jeannel, 1949]; Basilewsky, 1963, Ann. Mus. Roy. Afr. Centr., 8°, Sci. Zool., 120:63, 64 [proposed synonymy with *Galeritella*].

In the revision of the Carabidae from Madagascar, Jeannel divided the pantropical genus *Galerita* into several genera. The new generic groups were based on the following characters: "la forme de la dent labiale et . . . évolutions divergentes de la sculpture élytrale" (1949: 1057). As I have already mentioned in the introduction to this paper, only the Asian forms (which together with some species from Africa and Madagascar have been separated by Jeannel and subsequent authors as *Galeritella*) will be discussed here.

The mouthparts of *G. orientalis* (Fig. 1), type species of *Galeritella*, have been compared with those of *americana* (Fig. 2), the type species of *Galeritula*, and also with other Neotropical species of the genus. No important difference seems to be present, not even in the "dent labiale," the character stressed by previous authors. The same is true for all the other species found in Asia that I have been able to study in detail.

The second character mentioned by Jeannel (1949: 1058), the elytral structure, really seems to be of importance, but no consistent difference between American and Asian species could be

found, as noted by Jeannel himself (1949: 1058, “. . . a développé la même sculpture élytrale”)!

More recently, Basilewsky (1963: 7-8, 63-64) added new characters, which should also be analyzed. He characterized *Galeritella* as having “. . . une membrane apicale transparente aux élytres,” and a more voluminous aedeagus, the latter very often with “partie terminale individualisée” (the latter, however, only in the African species).

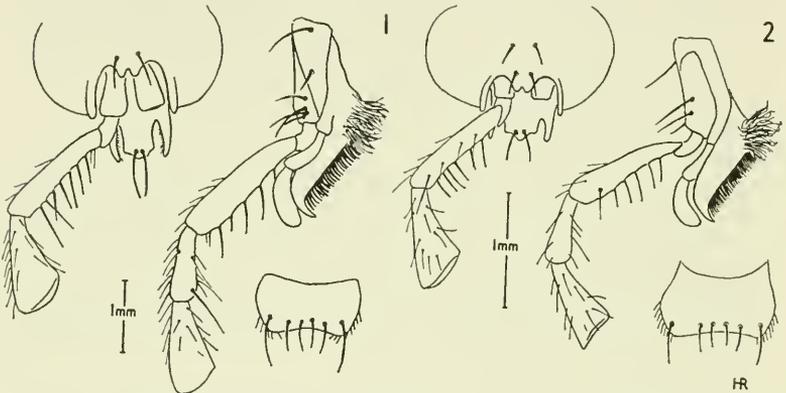


Fig. 1. *Galeritella orientalis*, ♂ from Jabalpur (MCZ), mouthparts.

Fig. 2. *G. americana*, ♂ from Trinidad (MCZ), mouthparts.

As to the first character, Asian species have a membranous apical margin on the elytra (for a width of less than 0.1 mm). This membrane is much less developed in Neotropical species, but it can be found with high magnification and careful examination.

As part of this paper, I have measured and studied the genitalia of the Oriental species which were available (Figs. 4-8). Although the relative size of the aedeagus really seems to be larger in these than in most Neotropical species, it seems also to be true that the Oriental species are larger insects than the average Neotropical species, so that insofar as my investigation goes, the size of aedeagus seems to be directly related to the size of the species. I have not studied the genitalia of any African species of *Galeritella*; however, Basilewsky (1963: 64 and fig. 28) indicates that the African species have a less well developed aedeagus, and this seems to agree with the average smaller size of the African species.

Figure 3 represents the linear regression for total length of aedeagus against total length of specimen in 25 species of *Galeritula* (21 Neotropical, 4 Oriental) and indicates clearly that the size of aedeagus is related to the size of species. Since material available for dissection is not always present in desirable quantities, I have represented in Figure 3 the size of

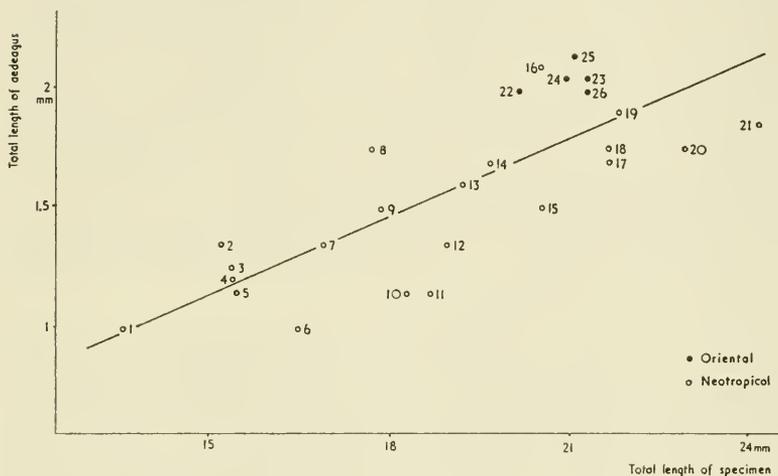


Fig. 3. *Galeritula* species showing linear regression for total length of aedeagus against total length of specimen. 1, *gracilis* Brullé; 2, *unicolor* Latreille and Dejean; 3, *palustris* Liebke; 4, *striata* Klug; 5, *microcostata* Darlington; 6, *lacordairei* Dejean; 7, *coeruleipennis* Chaudoir; 8, *collaris* Dejean; 9, *ruficollis* Dejean; 10, *melanarthra* Chaudoir; 11, *nigra* Chevrolat; 12, *tucumana* Liebke; 13, *americana* Linnaeus; 14, *occidentalis* Olivier; 15, *orbigny* Lucas; 16, *championi* Bates; 17, *brasilienis* Dejean; 18, *bruchi* Liebke; 19, *carbonaria* Mannerheim; 20, *corumbana* Liebke; 21, *ventricosa* Lucas; 22, *orientalis* Schmidt-Goebel, from India; 23, same species from Japan; 24, *carinifrons* Schaufuss; 25, *fae* Bates; 26, *toreuta* Andrewes.

aedeagus in relation to the specimen it comes from, rather than taking mean size of aedeagus against mean size of species in each case. Although variation of aedeagus is not large, in species where I have studied larger series (see for example "22" and "23" in Figure 3, which represent two different sized specimens of the same species, from different localities), it must be kept in mind that the points in Figure 3 do not represent the species, but only one specimen each.

The linear regression for this character shows very clearly that there is no place to objectively draw a line between Oriental and Neotropical species.

As to the apex of genitalia, the aedeagus of Neotropical species shows a large range of variation which includes forms very similar to those of the Asian and African ones.

Thus, a careful study of the two important generic characters given by Jeannel for *Galeritella*, as well as characters added by Basilewsky, leads me to conclude that these are the same as in *Galeritula* and the two genera must be considered synonymous.

The genus *Galeritula*, as considered here, occurs in the Neotropical (50 species more or less, of which several are as yet undescribed), Ethiopian (4 species recently revised by Basilewsky, 1963: 63-72), and Oriental regions (7 species).

It seems unnecessary to give here a full description or even a diagnosis of the genus. The descriptions found in the literature seem to be more than sufficient.

As in my current work on the Neotropical species of the genus, the Asian species of *Galeritula* are here separated into species groups, based on similarities which seem to indicate a phylogenetic relationship. These groups are assemblages of related species, but are not to be considered subgenera. Each group is named after the oldest species. The Oriental species can easily be assigned to two groups, as will be seen below. The African species, although related to Oriental and Neotropical ones, seem to constitute other, distinct groups, as do the Neotropical species.

Key to species

1. Legs black2
 Legs red or yellowish-brown3
2. Head and pronotum more elongate; carinulae-interstices much deeper than carinae-carinulae-interstices; carinae not very high; 21.8 mm; continental species *faeae* Bates
 Head and pronotum less elongate; carinulae-interstices as deep as carinae-carinulae-interstices; carinulae very thin; carinae higher; 21.0-22.0 mm; Java *toreuta* Andrewes
3. Legs completely red; 17.5 mm; India *indica* Chaudoir
 Legs with yellow femora and brownish tibiae; apices of femora darkened4
4. Head with shorter occiput (roughly as long as diameter of one eye); carinae usually less well developed; pubescence in carinae-carinulae-interstices dense, formed by two irregular rows of hairs; head red, clytra usually bluish5

- Head with longer occiput (longer than diameter of one eye); carinae usually well developed; pubescence in carinae-carinulae-interstices less dense, formed by a single row of hairs; head, pronotum and elytra black (or sometimes very dark fuscous) 6
5. Pronotum dark brown; head completely red on superior face; hind wings reduced; 20.0 mm; India *ruficeps* Chaudoir
Pronotum varying from completely red, through red with dark margins, to completely dark brown or black; when completely dark brown, head with frontal ridge and sides of occiput much darkened; hind wings fully developed; 18.5-22.0 mm; India to Japan, Sumatra to Flores *orientalis* Schmidt-Goebel
6. Antennae completely rufous; head, pronotum and elytra dark brownish; humeri very poorly developed, wingless species; 19.5-21.0 mm; Celebes *carinifrons* Schaufuss
Antennae with apex of scape and segments 2-4 darkened; head, pronotum and elytra black; humeri well developed (wings dimorphic?); 21.0 mm; Continental species *batesi* Andrewes

“ORIENTALIS” Group

Characterized mainly by the shape of pronotum, with posterior constriction very basally placed, not well defined; basal angles very rounded; elytra usually with very conspicuous pilosity, formed by two more or less parallel rows of rufous hairs in each carinae-carinulae-interstice.

Three species are known: *orientalis* Schmidt-Goebel, *indica* Chaudoir and *ruficeps* Chaudoir.

GALERITULA ORIENTALIS (Schmidt-Goebel, 1846)

(Figs. 1, 3-5, 9)

Galerita orientalis Schmidt-Goebel, 1846, Faunula Coleopterorum Birmaniae, pp. 26-27 [types, ♂ and ♀, “birmesische Provinzen,” Prague Museum; not examined]; Andrewes, 1923, Trans. Ent. Soc. London: 8 [redescription].

Galerita nigripennis Chaudoir, 1861, Bull. Soc. Nat. Moscow, 31(1):557 [types, ♂ and ♀, “Indes Orientales,” Muséum National d’Histoire Naturelle, Paris; not located]. *NEW SYNONYMY*.

Galerita japonica Bates, 1873, Trans. Ent. Soc. London: 304 [types, Nagasaki, Yokohama; British Museum (Natural History), not located]; Chaudoir, 1877, Bull. Soc. Nat. Moscow, 52(1):255 [synonym of *nigripennis*?]. *NEW SYNONYMY*.

Galerita peregrina Dohrn, 1880, Stett. Ent. Zeit., 41:291 [types, Hong Kong, Stettin Museum; not examined]. *NEW SYNONYMY*.

Galerita ruficeps; Bates [nec Chaudoir], 1889, Ann. Mus. Civ. Genova, 27:109 [Bhamo, Burma].

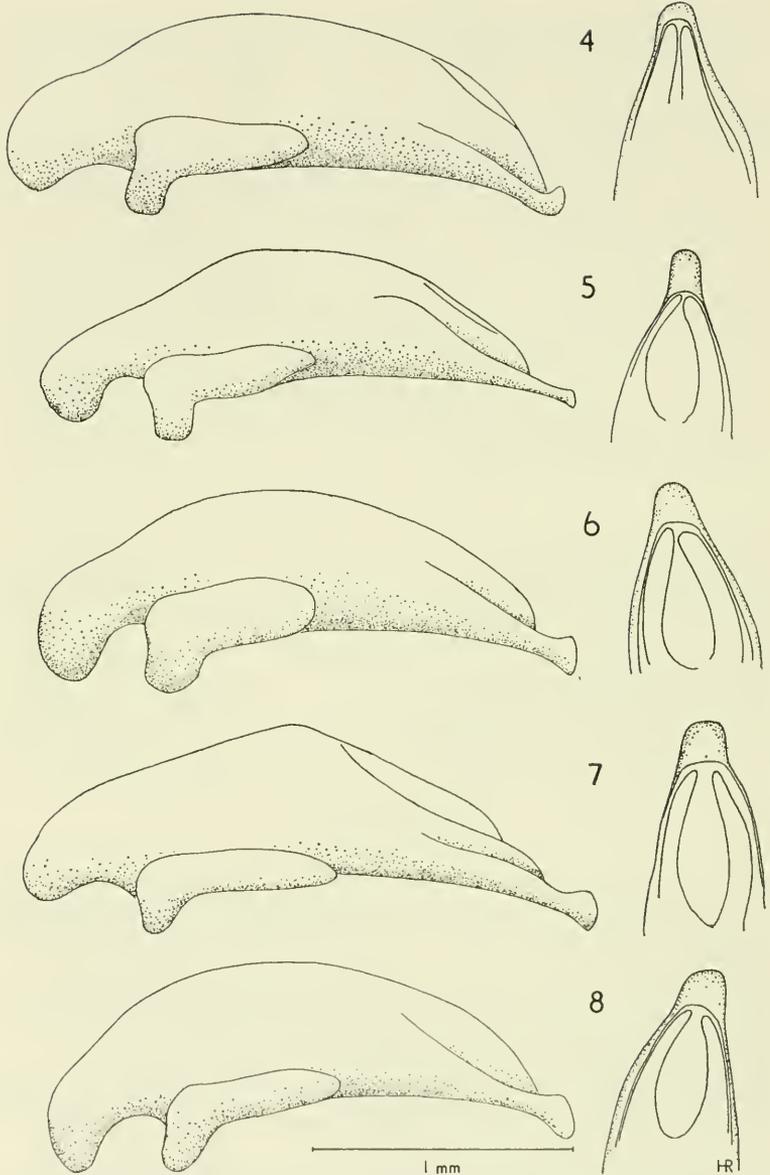


Fig. 4, *Galeritula orientalis*, from Tsushima (SMF C13907), aedeagus; Fig. 5, *G. orientalis* from Jabalpur (MCZ), aedeagus; Fig. 6, *G. carinifrons*, from Bonthain (IZ), aedeagus; Fig. 7, *G. fcae*, from Lambok (SMF C13910), aedeagus; Fig. 8, *G. toreuta*, from Radeng (MCZ), aedeagus.

Galerita birmanica Bates, 1892, Ann. Mus. Civ. Genova, 32:385 [*G. ruficeps*;

Bates, 1889; types, Bhamo, Burma, Genova Museum; not examined].

Galerita szetschwana Heller, 1923, Ent. Blaett., 19:65 [type, "Omisien, Szeschuan," Dresden Museum; not examined]. *NEW SYNONYMY*.

Galerita formosana Kano, 1930, Trans. Nat. Hist. Soc. Formosa, 20:29, fig. 3 [types, 2♀, Taihoku, Urai; Kano collection; not examined]. *NEW SYNONYMY*.

Redescription: Head varying from completely black to completely red, with intermediates where head is red with black frontal ridge and black sides of occiput (typical *peregrina*); pronotum also varying from completely black or bluish (*peregrina*) to completely red (*szetschwana*), with intermediates which have more or less developed black margins (*japonica*, *nigripennis* and *formosana*); elytra blue, sometimes very dark, almost black; antennae and mouthparts rufous; femora yellow with black apices; tibiae and tarsi rufous; inferior side dark brown, almost black on abdomen.

Head longer than wide (1.07) with relatively small eyes; occiput as long as eyes; surface punctate-rugose, with few yellow hairs, mainly in posterior half.

Pronotum wider than head (1.25), slightly longer than wide (1.03); widest slightly in front of the middle; not much narrowed anteriorly or posteriorly; posterior constriction very basal, sides varying from slightly convergent to slightly divergent behind the constriction; surface convex, densely punctate-rugose.

Elytra much wider than pronotum (1.7); 1.73 times as long as wide, almost parallel, slightly widened in posterior half; carinae strong, carinulae very thin, sometimes almost erased; carinulae-interstices with very shallow row of punctures; carinae-carinulae-interstices with dense rufous pilosity, disposed in two somewhat irregular rows. Always fully winged.

Measurements: length, 18.6-22.0 mm; width, 5.9-7.3 mm.

Specimens examined (96): **India**: Kerala, Wallardi, Travancore (10♂, 4♀, MNHN); Madras, Nilgiri Hills (6♂, 7♀, MCZ, BM); Madhya Pradesh, Jabalpur, 480 m (3♂, 1♀, MCZ); Maharashtra, Nagpur (1♀, MCZ); Assam, Patkai Mts. (1♂, BM). **Burma**: Bhamo (2♂, 7♀, BM, MNHN); Tenasserim (1♀, BM); Kachin Hills, Malikha Valley, 300-750 m (1♀, BM); no locality (1♀, SMF C13899). **Vietnam**: Hoabinh (4♂, 2♀, BM, MNHN, IZ); Laetho (1♂, MNHN); Ha Ciang (1♀, MNHN); Tuyenkwan (1♀, MNHN); Hue (1♀, BM); Phue-son (2♀, SMF C13900); Long Chuyan (1♀, BM). **Hong Kong** (1♀, BM). **China**: Kwangsi, Kweiling (1♂, MCZ); Liuchow (1♂,

MCZ); Wuchow (1 ♀, MCZ); *Kiangsu*, Nanking (1 ♀, MCZ); *Tschekiang*, Ning-Po (1 ♀, BM); *Szechuan*, Chungking (1 ♀, MCZ); Kwanshien (1 ♂, SMF C13901); no locality (2 ♂, 2 ♀, BM). **Japan:** Kyoto (1 ♂, SMF C13902, 1 ♀, MNHN); Tokyo (1 ♂, SMF C13903, 1 ♀, MNHN); Saga, Kiushu (2 ♂, SMF C13904, 1 ♀, MNHN); Yuyama (1 ♂, MCZ); Kobe (1 ♂, SMF C13905, 1 ♀, ANSP); Tsushima (3 ♂, SMF C13906-13907); Hiogo (1 ♀, SMF C13908); Osaka (1 ♀, SMF C13909); no locality (3 ♂, MNHN). **Indonesia:** *Sumatra*, Manua (1 ♂, 1 ♀, BM); *Java*, Pelabuhan Ratu (2 ♂, MCZ, MNHN); Buitenzorg (1 ♀, MNHN); no locality (1 ♂, BM); *Sunbawa* (1 ♂, MNHN); *Flores* (1 ♂, MNHN).

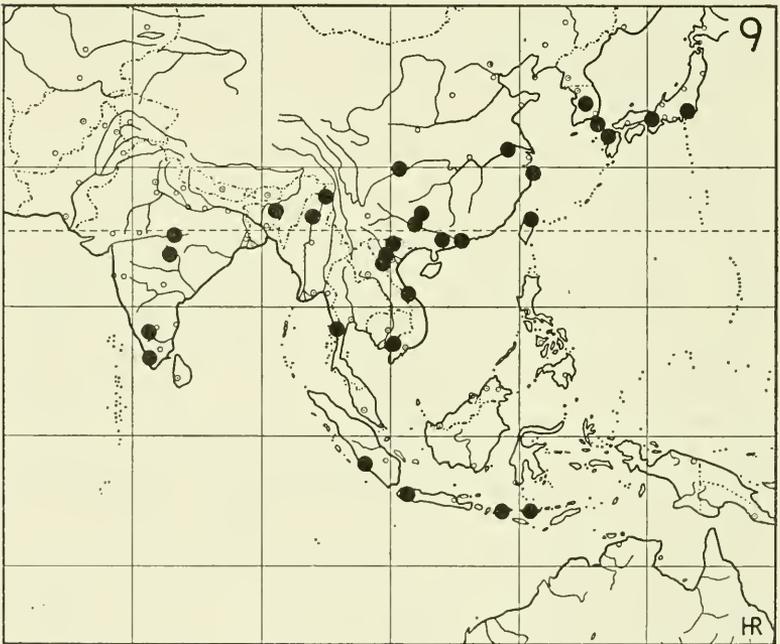


Fig. 9. *Galeritula orientalis*, distribution.

According to the literature, the species is also known from Korea and from Taiwan (*Formosa: formosana*); it was unknown from Indonesia. Its distribution is thus much wider than that of any of the other Asian species (Fig. 9).

The large number of synonyms of this species is due to the variability of the color pattern, which, when only a few specimens are studied (as in all the previous work), seems quite constant. Study of larger series, however, shows that these characters have very little, if any, specific value. With respect to color and pattern, there seems to be no geographic variation in *orientalis*.

The present study also included examination of the male genitalia (aedeagus), which seems to be quite constant in most populations of the species. A different aedeagal shape is, however, found in Indian specimens (described originally as *nigripennis*—see Fig. 5). I have tried to correlate this character with others, but have failed. A series of "*nigripennis*" from Travancore (10 ♂, 4 ♀, MNHN; the genitalia unfortunately could not be studied) shows the same color variation as *orientalis* from elsewhere. For this reason, I think it is not advisable to keep *nigripennis* separated from *orientalis*. There is a complete overlap of the two forms in external characters, mainly in color, and I feel that the difference in aedeagi of Indian *orientalis* is due simply to geographic variation.

The possible synonymy of *nigripennis* and *japonica* was pointed out in 1877 by Chaudoir, who could not find any differences between the two species.

GALERITULA INDICA (Chaudoir, 1861)

Galerita indica Chaudoir, 1861, Bull. Soc. Nat. Moscow, 34(1):557 [Holotype, ♂, "Nord de l'Hindostan," Muséum National d'Histoire Naturelle, Paris; examined].

Only the type specimen of this species seems to be known.

G. indica is very close to *orientalis* but shows a few important differences, and for this reason I consider it separate, at least for the time being. *G. indica* has completely red legs, is a wingless species, and is much smaller than *orientalis* (17.5 mm). More material is essential for a final decision on its status.

GALERITULA RUFICEPS (Chaudoir, 1861)

Galerita ruficeps Chaudoir, 1861, Bull. Soc. Nat. Moscow, 34(1):556-557 [Holotype, ♀, "Nord de l'Hindostan," Muséum National d'Histoire Naturelle, Paris; examined].

Besides the type, I have seen only 1 ♂ from Harki Dun, India (BM). This species, like *indica*, is very close to *orientalis*, and I keep it separate mainly because of reduction of the wings. More material will eventually show its real status.

"CARINIFRONS" Group

Pronotum usually with better defined posterior constriction; this is situated less basally than in *orientalis* group; basal angles sharp; elytra with pilosity less visible, sometimes absent; species with more restricted distribution, some with reduced wings.

Four species are included: *batesi* Andrewes, *carinifrons* Schaufuss, *feae* Bates and *toreuta* Andrewes.

GALERITULA BATESI (Andrewes, 1923)

Galerita batesi Andrewes, 1923, Trans. Ent. Soc. London: 9 [Holotype, ♀, Karin Cheba, Burma, 900-1100 m; British Museum (Natural History); examined].

Galerita orientalis; Bates [nec Schmidt-Goebel], 1889, Ann. Mus. Civ. Genova, 27:109 [pars].

Galeritula batesi is very close to *carinifrons*, distinguished by very few characters, the main ones having been mentioned in the key. These two species are also close to *feae* and *toreuta*, distinguished mainly by the color of the legs.

A superficial examination of the two types in the British Museum (Natural History) (♀, Karin Cheba; ♂, Teinzo), seems to indicate that they have reduced posterior wings. All other examined specimens have normally developed wings. *G. batesi*, however, does not show any reduction of the humeri. The species may be in the process of losing its wings, a process which has already been finished by its close relative, *carinifrons*, probably independently. Cases of wing dimorphism are not common in the genus: the only cases known to me are those of *africana* Dejean from Africa and *forreri* Bates from Mexico.

G. batesi is known only from the mainland, and has a rather restricted area of distribution.

Examined specimens (6): **Burma**: Bhamo (1 ♂, BM); Teinzo (1 ♂, paratype, BM, 1 ♀, MNHN). **India**: Assam, Shillong region (1 ♂, MNHN); Sylhet, Chandkhira (1 ♀, BM).

GALERITULA CARINIFRONS (Schaufuss, 1887)

(Figs. 3, 6)

Galerita carinifrons Schaufuss, 1887, Hor. Soc. Ent. Ross., 21:103-104 [types, Macassar, South Celebes; Zoologisches Museum der Universität Berlin; not seen].

Redescription: Black-brownish, mouthparts and antennae rufous; legs as in *batesi*.

Head large, longer than wide (1.08), with relatively small eyes; occiput slightly longer than the diameter of one eye; surface moderately punctate-rugose, with yellow hairs.

Pronotum wider than head (1.24), longer than wide (1.11); widest in anterior third, as narrowed anteriorly as posteriorly; constriction well developed, sides parallel behind it; surface convex, densely punctate; covered with yellow hairs.

Elytra 1.7 times as wide as pronotum; 1.77 times as long as wide; carinae and carinulae strong, the latter thinner, slightly closer to each other than to next carinae; carinulae-interstices punctate; carinae-carinulae-interstices with single row of yellow hairs; scutellar carina not joining the first; humeri very much reduced; wingless species.

Measurements: length, 19.5-21.0 mm; width, 6.2-6.9 mm.

Specimens examined (3): **Celebes**: Bonthain (3 ♂, IZ, MNHN).

Notes: *G. carinifrons* seems to be restricted to the southern part of Celebes. As already mentioned, it is very close to *batesi*. Both are probably derived from a common ancestor. The loss of wings in *carinifrons* is interesting and may be correlated with the restricted distribution.

GALERITULA FEAЕ (Bates, 1892)

(Figs. 3, 7)

Galerita feae Bates, 1892, Ann. Mus. Civ. Genova, 32:386 [types, Karin Cheba, Burma, 900-1100 m; Genova Museum; not seen].

Redescription: Completely black; antennal segments 5-11, brown.

Head large, longer than wide (1.09), with relatively small eyes; occiput slightly longer than the diameter of one eye; posterior half almost impunctate, anterior half deeply punctate-rugose; covered with few brownish hairs.

Pronotum wider than head (1.21), longer than wide (1.12); form and sculpture as in *batesi* and *carinifrons*, sides slightly divergent behind constriction.

Elytra very similar to those of *carinifrons*, 1.78 times as wide as pronotum; 1.7 times as long as wide; carinae and carinulae well developed; carinulae-interstices very deep, sulciform; carinae-carinulae-interstices with a row of hairs; scutellar carina not joining the first; humeri reduced; wingless species.

Measurements: (♂ from Lambok, SMF) length, 21.8 mm; width, 7.15 mm.

Specimens examined (10): **China:** Yunnan (2 ♀, MNHN). **Laos:** Luang Prabang, Pang Bo (1 ♂, BM); Ban Ban (1 ♂, BM); Xieng Khouang (1 ♂, BM). **Vietnam:** Tam Dao (1 ♀, BM). Localities which I have been unable to locate: "British Bootang" (? = Bhutan) (1 ♂, MNHN); "Pedong" (2 ♂, MNHN); Lambok, Sadjang (1 ♂, SMF C13910).

Notes: *G. feae* is a species which seems to be confined to the Continent. (Lambok has not been located. It may, however, be Lombok. If the species really occurs on Lombok, it should also occur on Java, sympatrically with *toreuta*.) It is very similar to *toreuta* from Java. Both are wingless, with very reduced humeri. One of the best characters to distinguish the two seems to be the carinular interstice (see key). These two forms must also stem from a common ancestor, perhaps the same one from which *batesi* and *carinifrons* have been derived.

GALERITULA TOREUTA (Andrewes, 1933)

(Figs. 3, 8)

Galerita toreuta Andrewes, 1933, *Treubia*, 14:283-284 [holotype, ♀, Idjen Plateau, Java; British Museum (Natural History), examined].

Galerita insulindae Liebke, 1934, *Arb. Morph. Tax. Ent.*, 1:280 [types, Pradjekan, east Java; Deutsches Entomologisches Institut, Berlin; not seen]; Liebke, 1940, *Fol. Zool. Hydrobiol.*, 10:449 [proposed synonymy with *toreuta*].

Galerita fortis Lowerens, 1952, *Treubia*, 21:228 [type, central Java, Mt. Slamet, Kaligua; Lowerens collection (?); not seen]; Lowerens, 1955, *Tijdschr. Ent.*, 98:56 [proposed synonymy with *toreuta*].

It seems unnecessary to repeat a description of this well described species.

Specimens examined (17): **Indonesia:** Java, Soemberwringin, G. Raoeng (1 ♂, BM, 3 ♂, 1 ♀, MCZ); Tengger, Nongokodjadar, 1300 m (1 ♀, BM); Idjes Plateau. Kenedeng Mts. (1 ♀, holotype, 1 ♂, BM); Kawie Mts. (4 ♂, 1 ♀, MNHN); Toegoe (1 ♂, MNHN); Malang Romjer (1 ♀, MNHN); Pradjekan (2 ♀, MCZ).

RELATIONSHIPS AND ZOOGEOGRAPHY OF THE ASIAN SPECIES OF GALERITULA

At present the Asian species of *Galeritula* are completely isolated from the other groups of the genus; however, they must be considered as being relicts of what was probably a more widespread genus in the past, extending from Africa to South America.

The relations of the species groups within the genus are very obscure. According to Jeannel, *Galeritula* must have originated in Africa and from there it must have spread to South America and Asia when the continents were connected. No facts seem to support this view. The presence of two primitive genera of the tribe in the New World (*Progaleritina* Jeannel in North and Central America and *Trichognathus* Latreille in South America), and the immense diversification of the Neotropical species of *Galeritula*, in my opinion suggest a New World origin.

The Asian species have a relatively restricted distribution (see Fig. 9, which represents the distribution of *orientalis*. Inclusion of Celebes shows the limits of the distribution of the genus). In the west these species reach India, in the northeast, Japan; only a few forms have invaded the islands southeast of Asia, where they are found from Sumatra to southern Celebes and Flores. The genus is not known from Borneo, perhaps due to insufficient collecting there. Of the island forms, two are endemic to very restricted areas: *toreuta* is found only in Java, and *carinifrons* in southern Celebes. *G. orientalis*, the third species present on the islands, has the widest distribution of all Oriental species, occurring from India and Japan to Sumatra and Flores. It is a fully winged species, while *toreuta* and *carinifrons* are wingless. The two latter species are closely related to *batesi* (winged) and *faeae* (wingless) from the mainland. There has probably been one ancestral stock, which through isolation (especially on the Indonesian islands) has given origin to the 4 species.

The other Oriental species form the second Asian group of species, that of *G. orientalis*, which is probably also derived from a single common ancestor. As seen above, the taxonomy of these three species is not yet well understood, since of two of them only the types are known.

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(Received 3 May 1965.)

B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS.

JULY 15, 1965

NUMBER 226

THE LARVAL FORM OF THE HETEROMI (PISCES)

By GILES W. MEAD

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The distinctive order Heteromi (Lypomi, Halosauriformes, or Notacanthiformes) includes about 25 species arrayed among about eight genera within the three families Notacanthidae, Halosauridae, and Lipogenyidae. All appear to be bottom fishes which, as adults, live between a few hundred and about 3500 meters. The placement of the order, which has been divided into two by many authors (Gill, 1889; Goode and Bean, 1896:129, 162; Berg, 1940:453; and Lagler, Bardach and Miller, 1962:40), within the teleostean hierarchy has been problematical. The most penetrating study of possible relationships is that of Marshall (1962) who emphasized the unity of the order, and allied it with the true eels or Apodes, chiefly on the basis of significant resemblances in swimbladder structure. The group was also recognized as a distinct order allied to the true eels within their superorder Elopomorpha by Greenwood, Rosen, Weitzman and Myers (1965) — a treatment in which I wholly concur.

The reproductive biology of the group has been a complete enigma. Neither eggs nor larvae have been reported, although Marshall (1962) and Greenwood *et al.* (1965) suggested that if the Heteromi shared common ancestry with the apodal fishes, a leptocephalus-like young should be expected. Similar speculation was included in the review of reproduction in the group provided by Mead, Bertelsen and Cohen (1964:583). It is thus most gratifying to report here on a single, relatively large leptocephalus taken during the midwater trawling program of the International Indian Ocean Expedition. It is broken and badly damaged, but has the typical shape and transparency of a relatively large eel leptocephalus and head structure unmistakably that of a halosaur, probably of the genus *Aldrovandia*. This metamorphosing young was taken as follows:

R/V *Anton Bruun*, Cruise VI, Sta. 351D, APB label 7354; 29 June 1964; Southern Indian Ocean between 31°45'S, 65°08'E and 32°26'S, 65°05'E; 0359 to 1507 hrs.; 10-foot Isaacs-Kidd trawl equipped with Foxton Trousers (Foxton, 1963) set to trip at 350 m; maximum depth of haul 1786 m; probable depth of capture below 125 m; depth of bottom 4480 m. MCZ catalog number 43994.

The body of this specimen which lacks the terminal part is 263 mm long and is composed of 250 somites. It lacks much of its skin, and the anal and the ventral fins are either undeveloped or were lost during capture. The flanks are densely stippled with fine black pigment. The head is similarly but more darkly colored. Along the ventral profile are series of black spots, each continuous with its mate across the ventral midline and connected with the adjacent spots mid-ventrally by a fine line of dense pigment. These spots probably occur throughout the length of the fish, but both skin and pigment are missing in many areas (Fig. 1). Within or surmounting each ventral spot, at least anteriorly, is a pore which may be the precursor of the series of ventral luminous organs seen in *Aldrovandia rostrata* (Günther, 1887, pl. 59, fig. A). Spots and pores occur on every fourth or fifth somite, a relationship similar to that between light organs and rows of scales in certain species. Prior to preservation, the body was nearly as transparent as that of most eel leptocephali. The pectoral fin, which is set close behind the gill opening, is formed of twelve rays. The dorsal fin, badly damaged but including at least eight rays, is short-based and situated relatively far forward compared to that of other halosaurs, suggesting a substantial relative shortening of the post-dorsal part of the body with growth. The anus cannot be found.

The head (Fig. 1) is about as broad as deep and terminates anterior to the gape in a prolonged fleshy snout. The gill openings are broad and continue anteriorly to near the symphysis of the lower jaw. Branchiostegal membranes are free from each other and from the isthmus. The gill membrane is thin and fragile. None of the osteological peculiarities noted by Marshall (1962:253) can be ascertained. Gill rakers are present and lath-like, are about as long as the opposite filaments, and number 4 + 1 + 14 on the first arch.

Jaws are poorly developed and bear teeth only at the tip of the mandible. Upper jaw bones are similar in structure to adult *Aldrovandia*, i.e. a somewhat flattened maxillary bone that abuts anteriorly on the end of the premaxillary which, with its

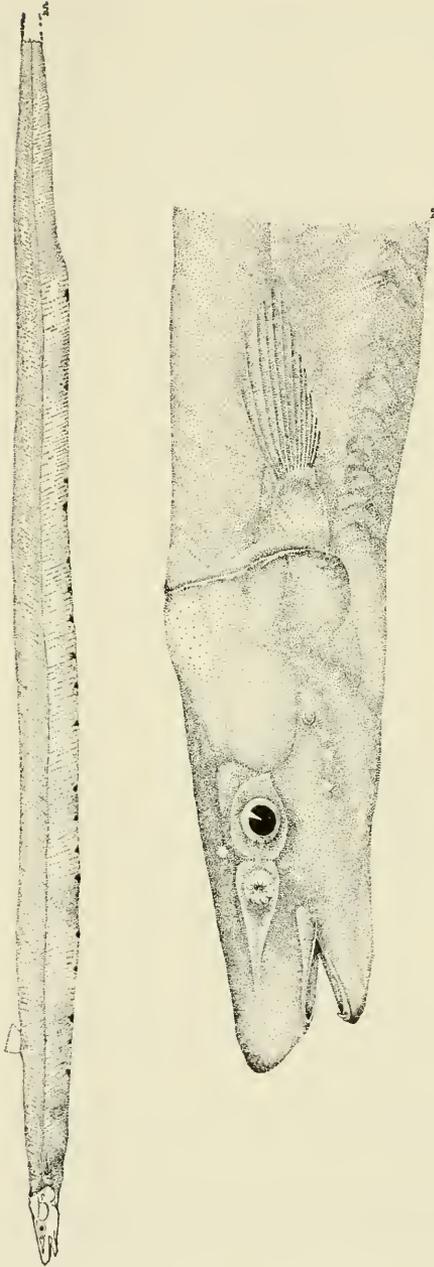


Figure 1. Metamorphosing leptocephalus of *Aldrovandia* sp.

opposite partner, courses transversely across the gape. Pores, presumably sensory, occur on the cheek (Fig. 1) and another pair is situated on the top of the head above the anterior edge of the orbit.

The capture of a specimen, small but of adult appearance, which has been identified provisionally as *Halosaurus nigerrimus* Alcock, 1899, indicates that halosaurus can complete their metamorphosis in midwater. This fish, 185 mm long, was also caught in the more southern latitudes of the Indian Ocean, as follows:

R/V *Anton Bruun*, Cr. VI, Sta. 349B, APB label 7332; 26 June 1964; 26°24'S, 65°02'E to 26°44'S, 65°05'E; 0830 to 1425 hrs.; 10-foot Isaacs-Kidd trawl equipped with Foxton Trousers set to trip at 350 m; maximum depth of haul 1470 m; probable depth of capture below 125 m; depth of bottom 4571 m. MCZ catalog number 43993.

These specimens thus clearly show that heteromous fishes have leptocephalus young so strikingly similar to those of the true eel that a close relationship between the two orders must be recognized, and that the young of at least some of these benthic fishes are pelagic. Thus either a spawning migration of the adults must occur or, less likely, buoyant eggs spawned on the bottom must rise through a water column of substantial height.

ACKNOWLEDGMENTS

I wish to acknowledge, with my sincere thanks, the aid which the National Science Foundation has granted the author through GF 147 and its support of the field work aboard R/V *Anton Bruun*, International Indian Ocean Expedition, which resulted in the capture of the fishes here discussed. I am also grateful to Basil G. Nafpaktitis for the illustrations.

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B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS

SEPTEMBER 10, 1965

NUMBER 227

THE SPECIES OF HISPANIOLAN GREEN ANOLES (SAURIA, IGUANIDAE)

By ERNEST E. WILLIAMS

INTRODUCTION

Certain Hispaniolan anoles of moderate to small size are dwellers in the crowns of trees, green in color, almost without other color or pattern, with short legs and long heads, and with relatively uniform squamation. These seem to be a natural species-group and not an assemblage of forms convergently adapted to the tree-crown niche.

In many external details the Hispaniolan green anoles are strikingly similar; in most squamation characters the several species have overlapping variabilities, and there are only relatively few characters that assist in discriminating fully valid species.

DEFINITION OF THE HISPANIOLAN GREEN ANOLE SPECIES-GROUP

The nearly uniform green color and the tree-crown habitat provide the most immediate diagnostic features of this group. Coinciding with these are a number of morphological characters:

1. Head long ($> 20\%$ snout-vent length).
2. Legs short (80 - 120% head length).
3. Middorsal and flank scales smaller than ventrals, granular, subequal in size or very slightly and *gradually* enlarged in the middorsal line.
4. Ventral scales hexagonal to square, subimbricate or juxtaposed, smooth or weakly keeled but never mucronate.
5. Mental wider than long, 4 scales + 2 sublabials in contact with infralabials. Smallest anterior gular scales not smaller than $1/6$ first sublabial and usually larger.
6. Dewlap small or vestigial.
7. Lamellae under fourth toe always more than 20.
8. Tail round or trigonal, never distinctly compressed; 4-5 dorsal scales per verticil.

SPECIES DIFFERENCES

The green anoles of Hispaniola divide into two subgroups, each a superspecies with two species. The species of the first subgroup (*Anolis chlorocyanus* Duméril and Bibron 1837, and *A. coelestinus* Cope 1862) are widespread and very common in the lowlands and up to at least 1500 meters; those of the second subgroup (*Anolis aliniger* Mertens 1939, and *A. singularis* n. sp.) occur only at elevations well above sea level and appear always to be scarce. The species of subgroup 1 occur sympatrically with those of subgroup 2, but the species within each subgroup are primarily allopatric. The two wide-ranging species of the first subgroup show enough geographic variation to permit description of subspecies; the subspecies will not, however, be discussed in this paper, which is concerned solely with species differences.

In a majority of the characters in which anoles are distinguished by taxonomists, there is conspicuous overlap between these two subgroups and even more overlap between the species of a single subgroup. It is significant that, lacking the distributional evidence that is now available, Mertens (1939) described *aliniger* (of the second subgroup of my terminology) as a subspecies of *chlorocyanus* (of the first subgroup) and was not very sure (p. 62) that *coelestinus* was a species distinct from *chlorocyanus*.

Table 1 shows the extent of this overlap very strikingly. Though in the better represented species of the first subgroup there are evident differences in the means of the several numerical characters, it is quite as evident that there are individuals it would not be possible to place on these characters alone.

Tables 2 and 3 show the very few qualitative characters that seem useful in discriminating the species of Hispaniolan green anoles. Size also differs. *A. chlorocyanus* and *A. coelestinus* may exceed 70 mm in snout-vent length, *A. aliniger* and *A. singularis* do not reach much over 50 mm.

SUBGROUP 1: *A. CHLOROCYANUS* - *A. COELESTINUS*

These two species overlap very little geographically. One has a distribution north, the other south of the Cul de Sac trench (still partly below sea level) which formerly divided Hispaniola into northern and southern islands. At the southern edge of this trench, now dry and very arid land, there is contact and sporadic real sympatry, always it appears, with one species or the other predominating. The actual zone of contact has never been mapped and is known at the moment only from occasional transects. *A. coelestinus* occurs in Port-au-Prince and extends to Damien, but *A. chlorocyanus* occurs in the area too.

Even in this area of contact there is no indication of reinforcement of species differences in body squamation. There are only average differences in the size of the head scales which are reflected in counts of loreal rows, scales across snout, scales between interparietal and supraorbital semicircles, etc. However, the best differences between the two species are in body color (the presence in *coelestinus* of the labial white streak which is continued above the shoulder, and its absence in *chlorocyanus*), and in dewlap color and squamation (very large dewlap scales and black dewlap skin in *chlorocyanus*, small dewlap scales and relatively unpigmented skin in *coelestinus*) (Fig. 1). Thus, in color characters there is some evidence of reinforcement of species difference because of secondary contact.

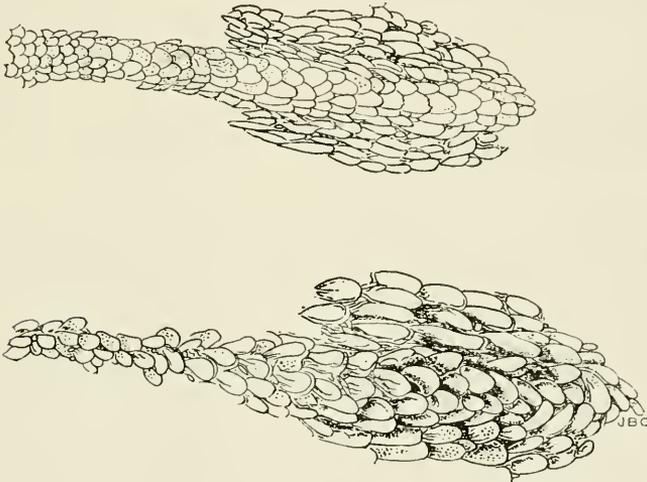


FIG. 1. Scales along edge of dewlap. Above: *Anolis coelestinus*, MCZ 64883, Ça-ira near Leogane, Haiti; below: *Anolis chlorocyanus*, MCZ 80719, Nan Palmiste, Gonave Island, Haiti. Drawn to the same scale; the specimens have the same snout-vent length.

Both body color and dewlap color differences, while they hold over most of the species ranges, are lost or weakened in populations of these species remote from the zone of contact. Thus the Isle Vache population of *coelestinus* lacks the white labial to shoulder streak of other *coelestinus* populations. At least preserved specimens of *coelestinus* remote from the Cul de Sac tend to show darker dewlap, occasionally almost to a degree that

would be confusing were not the dewlap scales consistently small.

In *chlorocyanus* also, geographic variation slightly weakens the diagnostic differences. The population described by Mertens from the vicinity of Santo Domingo City as *A. chlorocyanus cyanostictus* has reduced the black of the dewlap and exhibits a cadmium yellow basal spot.

However, both the Isle Vache population of *coelestinus* and the Santo Domingo City population of *chlorocyanus* are very small segments of the total range of these species. The non-distinctive segment of *coelestinus* is isolated on an island far to the west; the exact range of *chlorocyanus cyanostictus* is very limited and on present evidence very uncertain: typical *chlorocyanus* have been collected in Santo Domingo itself.

Both species are characteristic inhabitants of mesic lowland forests and appear not to extend to the highest peaks. They are, for example, unreported in the Forêt des Pins, Massif de la Selle in Haiti, or at Valle Nuevo in the Cordillera Central in the Dominican Republic. Both these localities have been visited by several investigators and the apparent absences are quite probably real.

SUBGROUP 2: *A. ALINIGER* – *A. SINGULARIS* N. SP.

This pair of species is not known to overlap at all, but they both occur on the Massif de la Selle.

The previously described member of this pair, *A. aliniger*, was until recently known only by the unique type, and was regarded by its describer Mertens as a subspecies of *chlorocyanus*. *A. aliniger* is, however, widely sympatric with *chlorocyanus*. A specimen of *A. aliniger* collected by Clayton Ray and A. S. Rand at 7 km N Carpintero Prov., San Juan, Dominican Republic, was collected on a tree ca. 45 meters from a specimen of *A. chlorocyanus* collected on a pole fence. The head scales of these two specimens are shown in Figure 2. In the Constanza area, La Vega Province, Dominican Republic, natives collecting for Juan Rivero brought in *A. aliniger* and *A. chlorocyanus* at the same time.

A. aliniger is one of the most peculiar of anoles, not indeed in general habitus which is that of a small and somewhat stockier version of *chlorocyanus* or *coelestinus*, but in the singular feature which gives it its name. This is the strange coloration of the axilla, bright orange or yellow followed by a larger or smaller spot of intense black. This is present in both sexes and very conspicuous in freshly preserved specimens, but the yellow or orange is, of course, quickly bleached out by alcohol. There is, however, an

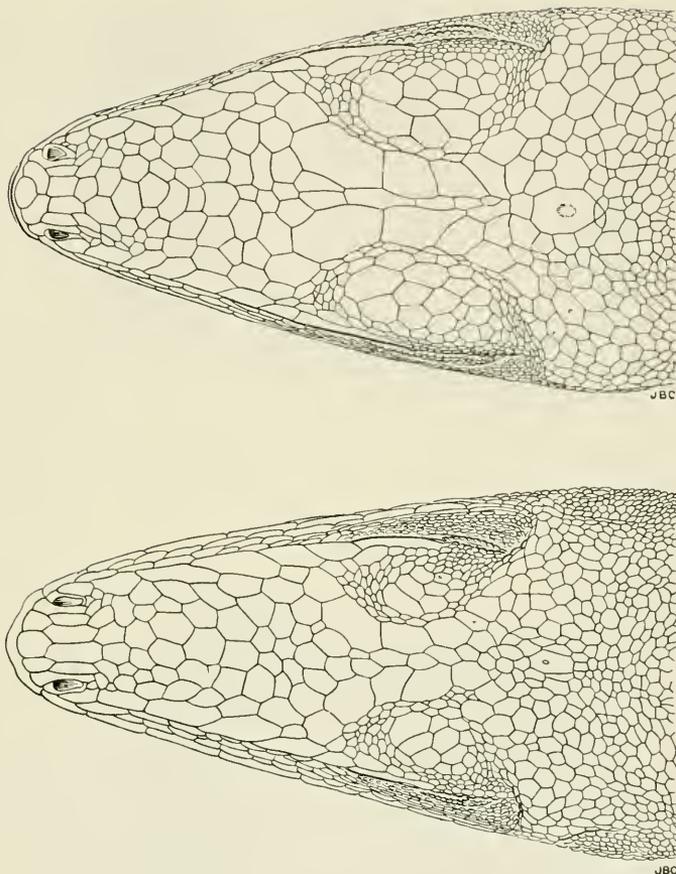


FIG. 2. Head squamation. Above: *A. aliniger*, MCZ 57463; below: *A. chlorocyanus*, MCZ 57473. Both specimens from 7 km N Carpintero, Prov. San Juan, Dominican Republic.

area of scaleless skin which represents the area formerly occupied by the orange spot (Fig. 3). Since the dewlap is hardly developed, almost non-functional, it is very possible that the orange, made more conspicuous by the black behind it, is a flash pattern used in some fashion in high intensity agonistic behavior. This is at present a mere suspicion; the only specimens of *aliniger* seen have been merely captured and preserved, or only very briefly observed.

The best report of the ecology and behavior of *A. aliniger* is that by James Lazell (field notes, December, 1963) at Paraje la Palma near Constanza: "Up in largish trees along the edge of the woods by the stream. Since they retreat upwards, collecting them is merely a problem of having a long enough pole. Just like *coelestinus-chlorocyanus*, therefore, in habits — except for the vertical flattening in display. In display the whole body is vertically compressed — showing much of the venter. Extended, the throat fan is quite small." Lazell's observations were unfortunately terminated by rain which prevented him from seeing any further specimens during the remainder of his stay.

The vertical compression, according to Lazell's sketch from life, emphasizes the yellow color of the belly. Lazell saw, however, no instance of exposure of the black and orange axillary pattern.

A number of descriptions of color in life are available for *aliniger*. They appear to indicate not only that the green of the light phase is different in tone from that of the species of subgroup 1 but also that there is a greater play of patterns and tones in the darker state. (See also *A. singularis* below.) In view of our very inadequate knowledge of the species, I quote these color descriptions in full.

Mertens (1939, translated): "In life this *Anolis* when caught was a uniform chocolate-brown with a large pitch black spot in each axillary region. In the bag in which it was transported the lizard turned blue-green, the black axillary spot remaining unaltered. The dewlap was bright green, the tip of the tail black."

Rand (field notes, 1958). Female — 7 km N of Carpintero: "Gray green above, head grayer, upper lip white, rear of thigh with a dark line, axilla bright yellow with smaller black spot behind it."

Lazell (field notes, 1963): "Duller and bluer green than *coelestinus-chlorocyanus*. Venter, throat fan and frosted spots on sides (especially shoulder region) bright saffron yellow. Orbital skin butter yellow. Axillary spot plain black.

"Changes, when unhappy, to lichenate frosted grey-brown with white. A pattern of large dark bilaterally arranged spots emerges with transverse bands — especially posteriorly. Loreals and irregular stripe through eye emerge slate blackish."

Schwartz (field notes, 1964). ASFS V 1625 — 12 km S of Cabrera de Loma: "Dorsal ground color blackish brown to olive with green sacral 'butterfly' marking and tail banded olive and cream. A white subocular mark. Ventral ground color dull greenish."

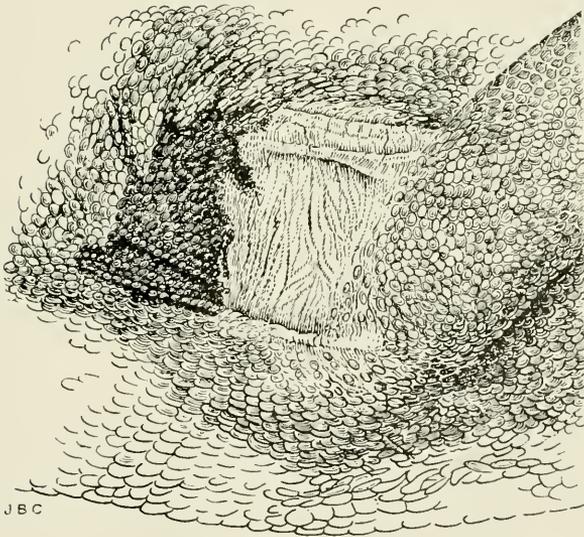
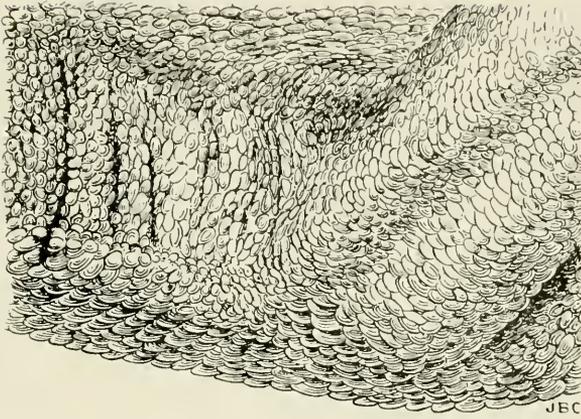


FIG. 3. Axillary squamation. Above: *A. chlorocyanus*, MCZ 57473, 7 km N Carpintero, Prov. San Juan, Dominican Republic; below: *A. aliniger*, MCZ 79341, Paraje La Palma, Municipio Constanza, Prov. La Vega, Dominican Republic.

The type locality of *Anolis chlorocyanus aliniger* Mertens was Paso Bajito on the northern rim of Valle Constanza in La Vega Province, Dominican Republic. Most of the recent specimens have been taken within that valley itself. However, a female has been taken in San Juan Province and a male in Dajabon Province. All specimens are from elevations near or above 600 meters.

These Dominican Republic localities appeared to place *A. aliniger* as an anole of the Cordillera Central or its immediate foothills, present at moderate elevations — within the pine zone — and widely sympatric with *A. chlorocyanus*.

It was with some surprise, therefore, that two specimens were found in a collection of *A. coelestinus* made by the Whiteman brothers at Furey in Haiti. Furey is south of the Cul de Sac trough that separates Hispaniola into northern and southern faunal areas — formerly separate islands.

It is not, of course, especially surprising that a form common in the northern faunal area should sometimes penetrate some distance or even extensively into the southern area. This seems a frequent phenomenon. What is surprising about the discovery of *aliniger* at Furey, Haiti at ca. 1500 meters at the north margin of the Massif de la Selle is that this is not a lowland species, which could without special difficulty cross the dry and hot Cul de Sac Plain, but a creature of higher elevations, cooler temperatures and of quite different floral associations from those which are now seen in either the desertic or mesic habitats of the lowlands. Essentially, the discovery of *aliniger* at Furey is analogous to finding a species of one island present on one cape of a neighboring island.

The ecology of *aliniger* appears to require that at some past time the Cul de Sac gap must have been climatically and floristically passable for the species: the passage from one montane island to the other must have been made at a time of much cooler temperatures — presumably the last cool-wet period of the Pleistocene.

The specimens from Furey remain the only record of the species in Haiti. Doubtless in part this absence of record is an artifact of collecting. A spur of the Cordillera Central enters the northeast of Haiti, but little or no collecting has been done there.

At present the known localities for *aliniger* are: **Dominican Republic.** *La Vega Province.* Below Paso Bajito at about 900 m (type locality), Senckenberg 25825. Valle Constanza, MCZ 56912. Tiroo near Constanza, MCZ 56913–15. Paraje La Palma, east of Constanza, MCZ 75140–41, 79341–43. El Rio, AMNH 44852–53. *San Juan Province.* Seven kilometers north of Carpintero,

MCZ 57463. *Dajabon Province*. Twelve kilometers south of Loma de Cabrera, ASFS V 1625. **Haiti**. *Département de l'Ouest*. Furcy, MCZ 63444-45.

Over most of the southern island of Hispaniola — south of the Cul de Sac trough in both Haiti and Hispaniola — the absence of *aliniger* is plausibly accounted for by the presence of a closely related species — essentially *aliniger* without the axillary light and dark spots. This peculiar species is known from very few specimens, everyone of which is from a different locality. I have, therefore, called this new species by the Latin adjective which means "one at a time."

ANOLIS SINGULARIS new species

Holotype: MCZ 72043, adult male, Pourcine, Massif de la Hotte, Haiti, collected by François Vuilleumier, 31 December 1962.

Paratypes: MCZ 13778, La Gonave Island, Haiti, G. M. Allen coll. 1919; YPM 3229, Nan Cafe, La Gonave Island, P. Humphrey and Sarita Van Vleck coll., March 26, 1959; YPM 3194, Forêt des Pins, Massif de la Selle, Haiti, P. Humphrey and Sarita Van Vleck coll., February 19, 1959; AMNH 51728, Valle de Polo, Dominican Republic, W. G. Hassler coll., September 14, 1932; ASFS V 2608, 5 km NE Los Arroyos, 5800 feet (*ca.* 1750 meters) elevation, Pedernales, Dominican Republic, D. C. Leber coll., June 27, 1964; ASFS V 2985, 30 km N of Pedernales, 2680 feet (*ca.* 810 meters), Pedernales, Dominican Republic, hatched from an egg collected under a limestone rock in Cajetal, July 3, 1964, by R. Thomas; hatched July 16, 1964.

Diagnosis: An anole most closely allied to *A. aliniger* Mertens but differing in the absence of a scaleless, highly pigmented axillary area. Like *A. aliniger*, the new species differs from *A. chlorocyanus* and *A. coelestinus* in the greater enlargement of scales around the interparietal (Fig. 4), and in reduction of the dewlap in males.

Description: Head scales rather large, 6-8 scales across snout between second canthals. Frontal depression feeble, scales within it not smaller than those surrounding it. Five to seven scales border rostral posteriorly. Anterior nasal scale in contact with rostral. Three to four scales between supranasals.

Supraorbital semicircles separated by 1-2 scales, separated by one row of scales from supraocular disk. Seven to eleven smooth scales in the poorly defined supraocular disk which is separated from supraciliary by 2-3 rows of granular or subgranular scales. One rather short supraciliary, flanked medially

by smaller scales and continued posteriorly by granules. Six to eight canthals, second and third largest, decreasing thence forward, anteriormost under rostral. Three to five loreal rows.

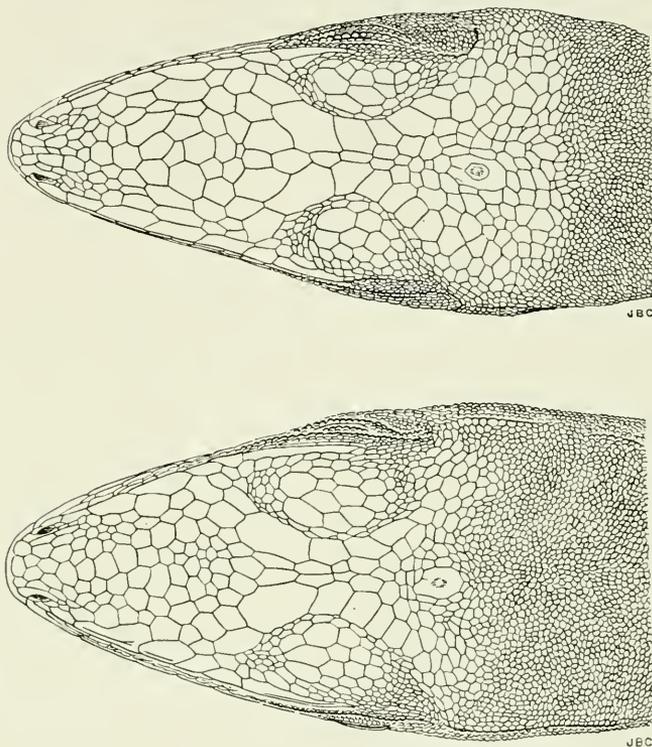


FIG. 4. Head squamation. Above: *A. singularis* Holotype, MCZ 72043; below: *A. coelestinus*, MCZ 74708. Both specimens from Pourcine, Massif de la Hotte, Haiti.

Temporal scales subgranular, smallest in center. A poorly defined intertemporal line. Supratemporals larger than temporals, increasing in size toward interparietal. Interparietal larger or slightly smaller than ear, separated from semicircles by 2-3 scales. Scales surrounding interparietal largest laterally but a very distinct zone of 5-6 rows of enlarged scales posterior to interparietal.

Suboculars broadly in contact with supralabials, anteriorly separated from canthal ridge by two scales, posteriorly merging into temporals. Seven to eight supralabials to center of eye.

Mentals broader than long, in contact posteriorly with 6-7 scales between infralabials (2 sublabials and 4-5 smaller scales); 5-7 sublabials in contact with infralabials. Central throat scales small, swollen, smooth.

Dewlap: Hardly differentiated, only indicated as a longitudinal fold; scales larger than throat scales, smaller than ventrals.

Trunk: Middorsals hardly enlarged, grading very gradually into flank granules. Axilla with normal granular scales. Ventrals larger, smooth, quadrate, juxtaposed, transverse. Postanals enlarged in male. Scales posterior to vent smooth.

Limbs: Largest forelimb scales smaller, largest hindlimb scales larger or smaller than ventrals, both weakly unicarinate. Supradigital scales smooth; 21-23 lamellae (27 in one hatchling) under phalanges ii and iii of fourth toe.

Tail: Verticils with four scales above, three below. Scales subequal.

Color in life: YPM 3194, Forêt des Pins, Haiti: Emerald green labials and limbs. Yellow eyelids, olive head and back, yellow green venter, last quarter of tail black with yellow tip.

YPM 3229, Nan Cafe, La Gonave Island, Haiti: Head silvery grey mottled with turquoise and brown, the latter extending to the shoulder. A brown spot just behind shoulder. Back silver gray mottled with turquoise. Tail and limbs very pale buff, tail banded with sky blue. Underparts pale turquoise becoming lemon on femora and at vent.

ASFS V 2608. 5 km NE Los Arroyos, Dominican Republic: Dorsal ground color gray to brown, a pattern of dark chevron-shaped middorsal blotches and smaller, roughly triangular lateral blotches. Light lateral stripes. Venter faint rust, speckled with greenish.

ASFS V 2985 (hatchling). 30 km N Pedernales, Dominican Republic: Dorsal ground color green with longitudinal darker stripes, especially middorsally.

Species status. On present evidence, *A. aliniger* and *A. singularis* are wholly allopatric. The question of species or subspecies status does therefore arise. My decision to describe *singularis* as a species is based upon two considerations: (1) a high valuation placed upon the axillary differences in pigmentation and squamation, which I assume to imply behavioral differences; (2) the presence of typical *aliniger* at Furey appears to imply a capacity

to invade the territory of an allied taxon — a feature more probable for a species than a subspecies. Both these points require further elaboration.

(1) It is frequent in *Anolis* for the most conspicuous and taxonomically useful differences between very closely allied species to be in structures such as the dewlap that are involved in species recognition and intraspecific agonistic behavior. Thus, in subgroup 1 of the present paper, the southern island form *A. coelestinus* has a dewlap with pale skin and small scales while the northern island species *A. chlorocyanus* has a dewlap with pigmented skin and greatly enlarged scales. *A. semilineatus* and *A. olssoni* differ in an exactly similar way, *A. semilineatus* having the dewlap skin pale, the dewlap scales small, *A. olssoni* having pigmented dewlap skin and greatly enlarged dewlap scales. (In the latter case there are other strong differences.)

Dewlap color, however, does vary intraspecifically in *Anolis* (e.g. in *A. distichus*, *A. brevirostris*, *A. cybotes*) and sometimes individually, as, of course, body pattern may do also. To what extent such color variation disturbs species recognition is quite unknown, and equally unknown are any differences in display behavior between allied full species such as *A. coelestinus* and *A. chlorocyanus* or *A. semilineatus* and *A. olssoni*.

In the present case, I have chosen to infer that the orange axillary spot of *aliniger*, attended as it is by loss of normal squamation in that area and contrasted with the unmodified axilla of *singularis*, is comparable to the species recognition marks that distinguish species pairs and not to the simpler color variations that may occur intraspecifically.

(2) The species pair *A. coelestinus*-*A. chlorocyanus* may be the only instance in which the geographic boundary between species is exactly that area of the island which at one time, as an open seaway, divided Hispaniola into northern and southern parts. It is certain that this seaway has been profoundly important for origin of many widely distributed Hispaniolan species; Mertens (1939) early recognized its importance. (See also Williams, 1961.) But it is in fact very unusual for allied species which have originated north and south of this important zoogeographic boundary to be precisely limited by it now that the seaway has become dry land. The situation which I described in the species pair *A. semilineatus*-*A. olssoni* is commoner: one or the other or perhaps both members of the species pair interpenetrate the range of the other to a greater or lesser extent. Usually, it would appear, there is,

as in *A. semilineatus*-*A. olssoni*, sufficient ecological difference between the members of a species pair to permit this, but in the case of *A. coelestinus*-*A. chlorocyanus* the ecologies are too similar to permit anything but a stand-off, with a very narrow, perhaps fluctuating zone of sympatry.

The case of *A. aliniger*-*A. singularis*, which is surely another example of a northern island-southern island pair, differs from that of *A. coelestinus*-*A. chlorocyanus* in that these are inhabitants of cooler upland areas and should now be quite separated by the whole extent of the hot Cul de Sac Plain and by much of the mesic woodlands on either side. That any *A. aliniger* occurs on the south side of the Cul de Sac Plain indicates, as I have suggested above, the former existence of a zone of passage right across the Cul de Sac for species now characteristic of cool upland climates. At such a period *A. aliniger* invaded the southern island and may well have met *A. singularis*. If contact occurred, certainly no merging of populations resulted. The Furey *aliniger* are quite unmodified, as typical as any from Valle Constanza. Perhaps there was a slight ecological difference with *A. singularis* living at higher elevations than *A. aliniger*. (The known true south island records of *A. singularis* would fit this pattern but the Gonave records would not.) Or perhaps *A. aliniger* displaced *A. singularis* in part of the latter's range.

Too little is known about either taxon to permit any but the most provisional hypothesis. It does, however, seem plausible to regard the invasion of the southern island by *aliniger*, without any indication of compromise of its characters, as evidence that it and *singularis* have indeed achieved species status and to infer that *A. aliniger* and *A. singularis* are, like *A. coelestinus*-*A. chlorocyanus*, too similar ecologically to occur together.

ACKNOWLEDGMENTS

I am indebted to Dr. Albert Schwartz (Albert Schwartz Field Series, ASFS), Mr. C. M. Bogert, American Museum of Natural History (AMNH), and Dr. Charles Reed, Yale Peabody Museum (YPM) for the privilege of examining specimens under their care. This paper, as part of a general study of West Indian anoles, has been supported by National Science Foundation grants NSF-G16066 and NSF-GB-2444. The illustrations were prepared by Mr. Joshua Clark. I have had the advantage of utilizing counts and tabulations made by Dr. A. S. Rand.



FIG. 5. Distribution of the Hispaniolan green anoles.

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(Received 10 May, 1965.)

TABLE 1.
Scale characters of the Hispaniolan green anoles

	<i>coelestinus</i>	<i>chlorocyanus</i>	<i>aliniger</i>	<i>singularis</i>
scales across snout	6-10	4-7	6-9	6-8
loreal rows	4-7	3-5	3-4	3-5
scales between supraorbital semicircles	1-3	0-2	0-1	1-2
scales between interparietal and semicircles	2-6	1-5	2-4	2-3
lamellae	23-32	27-34	21-24	21-23 ¹

¹ 27 in one hatchling, ASFS V 2985

TABLE 2.
Scale characters differentiating the Hispaniolan green anoles

<i>coelestinus</i>	<i>chlorocyanus</i>	<i>aliniger</i>	<i>singularis</i>
scales behind interparietal grading rather gradually into dorsal scales	as in <i>coelestinus</i>	Scales behind interparietal <i>not</i> grading into dorsals but several rows abruptly larger	as in <i>aliniger</i>
size of scales of dewlap ca. = ventrals	size of scales of dewlap > > ventrals	dewlap vestigial, size of scales of dewlap area < ventrals	as in <i>aliniger</i>
supradigital scales multicarinate	as in <i>coelestinus</i>	supradigital scales smooth	as in <i>aliniger</i>
axillary area with normal granular squamation	as in <i>coelestinus</i>	axillary area <i>without</i> granular scales	as in <i>coelestinus</i>

TABLE 3.

Color characters differentiating the Hispaniolan green anoles

<i>coelestinus</i>	<i>chlorocyanus</i>	<i>aliniger</i>	<i>singularis</i>
a white line on supralabials produced posteriorly to above the shoulders (absent in Ile Vache population)	never any white markings on side of head or neck	as in <i>chlorocyanus</i>	as in <i>chlorocyanus</i>
axillary area with vertical black and light bars or unpatterned	as in <i>coelestinus</i>	axillary area with a light spot (orange in life) followed by an ink-black blotch of larger or smaller extent — both concealed by normal position of arm	as in <i>coelestinus</i>
dewlap scales blue, skin olive-gray	dewlap scales white to blue, skin with black or (<i>cyanostrictus</i>) cadmium yellow basal spot	dewlap skin and scales greenish	as in <i>aliniger</i>

B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS.

SEPTEMBER 15, 1965

NUMBER 228

RELATIONSHIPS AMONG INDO-AUSTRALIAN ZOSTEROPIDAE (AVES)

BY

ERNST MAYR

During preparation of the manuscript of the Zosteropidae for Peters' Checklist of Birds of the World, I reviewed once more the relationships of the Indo-Australian white-eyes. The first attempt to arrange these species in natural groups was made by Stresemann in a pioneering work in 1931. The revisionary studies of the ensuing 25 years were summarized by G. F. Mees in a very thorough systematic review of the Indo-Australian Zosteropidae (1957, 1961). Mees' work is based not only on an exhaustive analysis of the literature, but also on an examination of most of the available museum material. His fundamental monograph will remain for many decades the basis of all taxonomic research in Indo-Australian white-eyes. In a few cases my own interpretation of relationship differs from his, resulting in a somewhat different sequence of species. This paper may serve to explain the reason why, in these few instances, I have adopted a sequence different from that chosen by Mees in his systematic review. I am deeply indebted to Dr. Mees for much valuable information on Zosteropidae.

Absolute criteria of relationship in the Zosteropidae do not exist at the present time, and neither Mees nor I can prove that the sequence adopted by one of us is "more correct" than the sequence adopted by the other. White-eyes have characteristic songs and call notes, and perhaps analysis of these and other behavioral characters may lead to a better understanding of relationships. I know of no other group of birds in which close relatives, for example the subspecies of *Zosterops atrifrons* or the semispecies of the superspecies *griscotineta*, may differ more from each other than do distantly related species. Indeed some

Oriental species are almost indistinguishable from African forms, from which they must have been isolated since remote times.

ZOSTEROPS CEYLONENSIS Holdsworth

This species is often considered closely related to *Z. palpebrosa*, and Mees (1957, p. 22) lists it immediately preceding *palpebrosa*. Yet, he states correctly, "morphologically *Z. ceylonensis* is undoubtedly rather closer to several other species than to *palpebrosa*" (*ibid.*, p. 26). For this reason I have placed it after *palpebrosa* and closer to some of the Indonesian species from which it might possibly have been derived.

ZOSTEROPS ERYTHROPLEURA Swinhoe

This species, with its rufous flanks, does not resemble any of the species (*palpebrosa* and *japonica*) with which it is usually placed. Being also the only white-eye restricted to the Palearctic region, I prefer to indicate its distinctness by placing it first in the sequence, as had been previously done by Stresemann (1931, p. 206).

ZOSTEROPS CONSPICILLATA Kittlitz

Mees (1957) lists this Micronesian bird as the last species of the genus. To me this species does not seem nearly as aberrant as *Z. cinerea*. Indeed, in spite of its paleness, a frequent character in island birds, *conspicillata* resembles in some ways the *japonica-palpebrosa* assemblage. Since several Micronesian birds were derived from the west (e.g. *Acrocephalus*), relationship of *conspicillata* with *japonica* is a distinct possibility. It is hoped that placing the species earlier in the sequence will bring it closer to its real relatives.

ZOSTEROPS WALLACEI Finsch

As Mees has stated rightly, this is an old and peculiar endemic. It seems distantly related to the western group of species (*atricapilla*, *everetti*, *nigrorum*, and others) and I have therefore placed it earlier in the sequence.

ZOSTEROPS FLAVA-CHLORIS-LUTEA group

I have adopted Mees' sequence for the sake of uniformity. I still feel, however, that these species are more closely related

to each other than believed by Mees. To separate *lutea* from *chloris* by 14 other species does not seem to be the best possible arrangement.

ZOSTEROPS CONSOBRINORUM Meyer

This species is so similar to *Z. chloris citrinella* that in any other genus one would consider them conspecific. Even though I have retained *Z. consobrinorum* as a full species, I have placed it next to *chloris*, while I now treat the very distinct peripheral forms *grayi* and *uropygialis* as full species (see also Mees, 1953, 1961).

ZOSTEROPS ATRIFRONS group

I agree, on the whole, with Mees' (1961) arrangement. However, *Z. atriceps* is best listed before the *atrifrons-minor-delicatula* series, because the latter is close to the forms on the islands east and northeast of New Guinea (*meecki*, *hypoxantha*) and should not be separated from them by *atriceps*.

In this group of species close relatives may appear rather different (belly, yellow or white; forehead, black or olive; eye-ring, absent or broad; throat, orange, yellow or whitish). The delimitation of the species is therefore a difficult task. Two of the most distinct forms, *minor* and *delicatula* of New Guinea are connected by the intermediate forms *chrysolacma* and *rothschildi*. Mees (1961) quite rightly combines *atrifrons* and *minor* in a single species, but if one goes that far one must also include *meecki* (close to *delicatula*) and *hypoxantha*.

I have maintained *Z. mysorensis* as a separate species, because in its combination of characters (no yellow on throat, heavy gray wash on breast and flanks, olive forehead, absence of eye-ring, blackish loreal region, and pale yellow under tail coverts) it resembles some other species (e.g. *ugiensis*) more closely than *atrifrons*.

ZOSTEROPS NATALIS Lister

Mees (1957) notwithstanding, there is much to indicate that this species is closer to one of the east Indonesian or Australian species (*chloris*, *lutea*, etc.) than to any of the Malaysian species. I agree in this with Stresemann and Chasen. Mees (1957) makes the peculiar comment that my (Mayr, 1944)

association of this species with *lutca*, instead of with *citrinella*, is an "unfortunate choice," overlooking that I include *citrinella* in *lutca* in the cited paper.

ZOSTEROPS RENDOVAE Tristram

The description of *rendovae* was based on a Rendova Island specimen misidentified as *Tephras olivaceus* Ramsay, but newly named *rendovae* since the name *olivaceus* Ramsay (nec *Certhia olivacea* Linnaeus 1766) was considered unavailable. That the original author, Tristram, considered *rendovae* a name for the Rendova bird far more than a replacement name for *olivaceus* is evident from his subsequent statement (1894, p. 30): "I give a figure (Pl. III, fig. 2) of *Zosterops rendovae* of Rendova Island . . . which I described in the Ibis for 1882, p. 135." Galbraith (1957) has well stated the reasons for retaining the name *rendovae* for the Rendova White-Eye to which it had been applied universally from 1882-1955, including general books in ornithology and evolutionary biology.

ZOSTEROPS LATERALIS Latham

The arrangement of the Australian races is largely based on unpublished research kindly made available to me by Drs. A. Keast and G. F. Mees.

The resulting sequence of species of Indo-Australian *Zosterops* is as follows:

<i>erythropleura</i>	<i>uropygialis</i>
<i>japonica</i>	<i>anomala</i>
<i>palpebrosa</i>	<i>atricaps</i>
<i>ceylonensis</i>	<i>atrifrons</i>
<i>conspicillata</i>	<i>mysorensis</i>
<i>salvadorii</i>	<i>fuscicapilla</i>
<i>atricapilla</i>	<i>buruensis</i>
<i>everetti</i>	<i>kuehni</i>
<i>nigrorum</i>	<i>novaequinea</i>
<i>montana</i>	<i>mctcalfi</i>
<i>wallacci</i>	<i>natalis</i>
<i>flava</i>	<i>lutca</i>
<i>chloris</i>	<i>griscotincta</i>
<i>consobrinorum</i>	<i>rennelliana</i>
<i>grayi</i>	<i>vellalavella</i>

<i>luteirostris</i>	<i>minuta</i>
<i>rendovae</i>	<i>xanthochroa</i>
<i>murphyi</i>	<i>lateralis</i>
<i>ugiensis</i>	<i>strenua</i>
<i>strescmanni</i>	<i>tenuirostris</i>
<i>sanctacrucis</i>	<i>albugularis</i>
<i>samoensis</i>	<i>inornata</i>
<i>explorator</i>	<i>cinerca</i>
<i>flavifrons</i>	

THE ABERRANT GENERA OF INDO-AUSTRALIA

Some white-eyes differ from the normal structure or coloration of the genus *Zosterops*, as represented by a species like *palpebroso* or *lateralis*, to such an extent that they have been separated generically. If all the larger white-eyes, with somewhat aberrant coloration and a longer or heavier bill, could be placed in a single genus, no one would mind. The fact of the matter is, however, that 13 genera have been proposed to accommodate 18 species. Excluding *Lophozosterops* (with 6 species), there are 11 generic names for 13 species. Some further simplification is possible by combining *Sanfordia* with *Woodfordia*, as well as the Micronesian *Kubaryum*, *Megazosterops*, and *Cinnyrorhyncha* with *Rukia*. In the "Oreosterops group" of authors, Mees (1953, pp. 57-66) recognizes six genera, reduced in 1957 to five by combining *Apoia* with *Lophozosterops*. Of these five genera, three (*Madanga*, *Tephrozosterops*, and *Oculocincta*) are monotypic, while *Heleia* has two species in one superspecies. The five genera seem to form a natural group and a renewed analysis may result in further lumping, perhaps of all five genera into *Heleia*.

The sequence chosen by Mees (1953) does not seem quite natural. By starting with the species that is most like *Zosterops* and also keeping the pattern of geographic distribution in mind, we arrive at the following sequence: *Tephrozosterops (stalkerii)*, *Madanga (ruficollis)*, *Lophozosterops (pinaiac, goodfellowi, squamicaps, javanica, superciliaris, dohertyi)*, *Oculocincta (squamifrons)*, and *Heleia (muelleri, crassirostris)*.

I entirely agree with Mees (*in litt.*) that *Hypocryptadius* Hartert does not appear to be a white-eye. Fresh material is needed to determine whether it should go to the Monarchini, Sylviinae, Timaliinae, or some other group.

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(Received 5 June, 1965.)

B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS.

SEPTEMBER 15, 1965

NUMBER 229

THE GENUS *DARLINGTONIA* (SERPENTES)
IN HISPANIOLA,
INCLUDING A NEW SUBSPECIES FROM THE
DOMINICAN REPUBLIC

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The West Indian island of Hispaniola is outstanding for the relatively large number of endemic snake genera which inhabit it. These include *Ialtris* Cope (with two species), *Uromacer* Duméril and Bibron (with apparently two or three species), *Hypsirhynchus* Günther, and *Darlingtonia* Cochran. The latter is a small snake (snout-vent length to about 300 mm) which was described (Cochran, 1935) on the basis of a single Haitian individual collected by P. J. Darlington from Roche Croix, about 5000 feet (1515 meters) altitude, near Pic Macaya in the Massif de la Hotte. Since the genus was first described, the snake has been found to be not uncommon in Haiti in the vicinity of Furey and Kenscoff on the Montagne Noire. Additional specimens from the Massif de la Hotte remain rare, and we have seen only one other snake (in addition to the type) from Camp Perrin in that region. Considering that there is a distinct faunal resemblance between the Massif de la Hotte, Massif de la Selle, and Sierra de Baoruco, all serially arranged from west to east along the south island of Hispaniola, we expected that ultimately *Darlingtonia* might be taken in the last named range. Such indeed was the case when in the summer of 1964 the junior author and David C. Leber succeeded in taking two females at a sawmill in the Baoruco. It was later learned that a single *Darlingtonia* had been collected in the República Dominicana by W. G. Hassler in 1935.

In an attempt to compare these eastern specimens with the more western populations, we have borrowed *Darlingtonia* from the following collections: American Museum of Natural History

(AMNH); Museum of Comparative Zoology, Harvard University (MCZ); United States National Museum (USNM); Museum of Zoology, University of Michigan (UMMZ). We wish to thank Charles M. Bogert, Grace M. Tilger, Ernest E. Williams, Doris M. Cochran, James A. Peters, Charles F. Walker, and George R. Zug for the loan of these small serpents; Mr. Leber and Ronald F. Klinikowski aided us in assembling material in the field (designated as ASFS), and Mr. Klinikowski has likewise made some of the illustrations for the present paper. We have examined 30 specimens in all, including the holotype (MCZ 38252) of the species, with all but five of these originating in the Furcy area. We are thus hampered in comparing these Furcy snakes with topotypical material from the east in the La Hotte, but for the moment there is no choice but to accept the agreement of the Montagne Noire material with that from the La Hotte (admittedly an unlikely possibility, *vide infra*). The snakes from the Sierra de Baoruco, which are distinct from the more western populations, may be named:

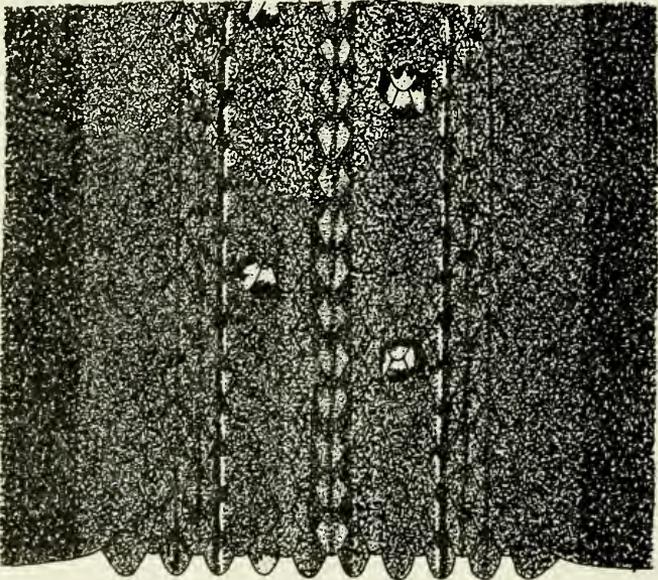


FIG. 1. *Darlingtonia haetiana haetiana*, pattern at midbody, ASFS X2080, Peneau, Bassin Bleu, 5000 feet, Dépt. de l'Ouest, Haiti.

DARLINGTONIA HAETIANA PERFECTOR¹ new subspecies

Holotype: MCZ 77217, a female, from 24 km SW Barahona, 3700 feet (1221 meters), Barahona Province, República Dominicana, taken by David C. Leber on 6 July 1964. Original number ASFS V 2897.

Paratypes: ASFS V 2898, same data as type, but collected by Richard Thomas; AMNH 49738, near Polo, 3000 feet (910 meters), Barahona Province, República Dominicana, W. G. Hassler, 19 August 1935.

Distribution: Known only from the Sierra de Baoruco in the República Dominicana, and probably occurring throughout moderate to higher elevations in that range.

Diagnosis: A subspecies of *Darlingtonia haetiana* distinguished from the nominate race by a combination of a wide buffy nuchal collar (Fig. 3), a bolder and more contrasting longitudinally lined and dotted dorsal pattern (Fig. 2), and by less ventral and subcaudal scales, giving a total underbody scale count from 174 to 178 in contrast to 181 to 193 (both sexes) in *D. h. haetiana*.

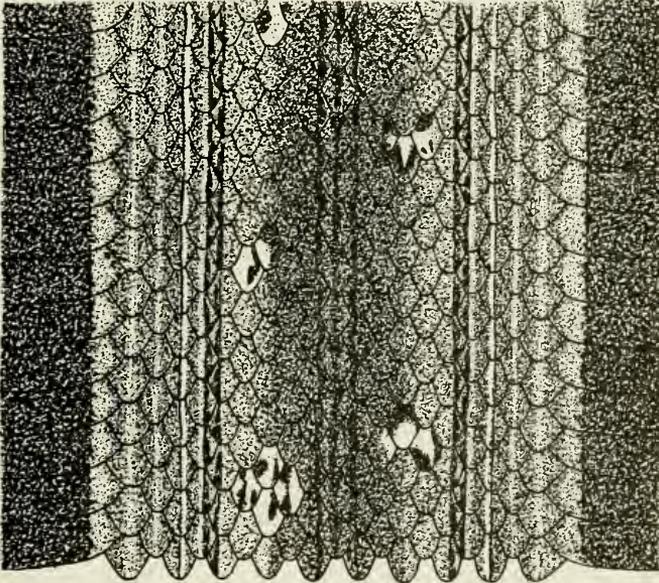


FIG. 2. *Darlingtonia haetiana perfector*, pattern at midbody, MCZ 77217, holotype, 24 km SW Barahona, 3700 feet, Barahona Province, República Dominicana.

¹From the Latin for "completer, finisher" in allusion to the fact that with the specimens from Barahona the genus is known from the entire south island, whereas previously it had been known only from Morne La Selle and Massif de la Hotte.

Description of holotype: A female with the following measurements and scale counts: snout-vent length, 190 mm, tail, 47 mm; ventral scales 133 (counted as suggested by Dowling, 1951), subcaudal scales in 41 pairs; anal single; supralabials 7/7; infralabials 8/8; loreal absent; preoculars 1/1; postoculars 2/2; temporals 1 + 1 on right side, 1 + 2 on left side; dorsal scale rows 19-19-17. Coloration and pattern in life: dorsolateral area light brown with a middorsal dark reddish brown zone including a black middorsal stripe; a narrow dark brown conspicuous lateral stripe on scale rows 4 and 5 on each side; midventral region with a wide band almost covering all of ventral scales including within it darker black blotches, the entire band with a blue iridescence; lowermost scale row on each side, and central part of second scale row and sometimes third scale row and lateralmost ends of ventrals brick red; 20 and 22 lateral dots on sixth to eighth scale rows on each side, each individual dot involving one, two, or three scales on adjacent rows, and yellowish orange with black margins in life. Tail brown above, black below. Head without a definitive pattern, but generally blackish to reddish brown or orange on parietals, the brighter and paler color delimiting a vague, dark, T-shaped figure with its bar across the supraoculars and frontal, and the stem along the parietal suture, joining on the neck the middorsal black longitudinal band; a pale bar across the anterior half of the frontal, the prefrontals and supranasals variously marbled with brown and paler. A buffy collar, edged posteriorly with black, and two scales in width, goes from the angle of the jaws on either side, and is interrupted middorsally by the median black band.

Variation: The female paratype (ASFS V2898) has a snout-vent length of 180 mm and a tail length of 44 mm; there are 136 ventral scales and 40 pairs of subcaudal scales. The supra- and infralabials, pre- and postoculars are as in the type. The temporals are 0 + 2 on both sides, the single anterior temporal being fused with the parietal. The scale rows are 19-19-17, and the loreal is absent. In color and pattern the paratype is very like the type, except that, due to a smaller amount of pale color on the anterior half of the frontal, the transverse dark bar of the T-shaped cephalic figure is wider and more conspicuous. The buffy collar is present and readily visible.

The male paratype (AMNH 49738) has a snout-vent length of 216 mm and a tail length of 63 mm; there are 132 ventral scales and 46 pairs of subcaudal scales. The supralabials, pre- and postoculars, and temporals are like those of the type, except that there are 1 + 2 temporals on each side. The infralabials are 7 on each side. The scale rows are 19-19-17, and the loreal is absent.

Although the male paratype is darker (possibly due to length of preservation) than the two smaller female *perfector*, the longitudinal zonation is still visible. The nuchal collar is bold and prominent. The head pattern is like that described for the type, except that the amount of pale coloration across the anterior portion of the frontal is less, thus making the transverse dark bar of the T-shaped figure broader. The ventral scales are entirely dark, with the lateralmost tips irregularly stippled light and dark.

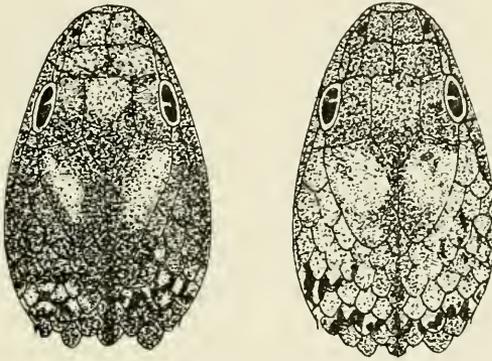


FIG. 3. Dorsal view of heads of *Darlingtonia haetiana*; left, *D. h. haetiana*, ASFS N2080; right, *D. h. perfector*, MCZ 77217.

Comparisons and discussion of variation: Since there are more specimens available from the Furey area than elsewhere, it is most profitable to first discuss the variation in snakes from this region, and then compare them both with the two western and three eastern serpents. At Furey, the scalation shows the following variation: ventrals in males (13 specimens) range from 137 to 144 (mean 139.7), ventrals in females (12 specimens) having the same range (mean 139.9). Subcaudals are 46 to 51 (mean 48.3) in males, and 41 to 50 (mean 45.3) in females. Ventrals + subcaudals are 185 to 193 (mean 188.0) in males, and 183 to 191 (mean 185.4) in females. Females have slightly less total underbody scales than do males. The largest male has a snout-vent length of 281 mm with a tail of 82 mm, whereas the largest female measures 305 in snout-vent length with a tail length of 83 mm. All specimens lack a loreal, and have 1/1 preoculars and 2/2 postoculars. The labials are normally 7/7 above and 8/8 below, although one snake has 7/8 supralabials, three snakes have 7/7 infralabials, and four have 7/8 infralabials. The temporals are either 1 + 2 or 1 + 1; four

snakes have 1 + 1 on each side, four have 1 + 1 and 1 + 2, and the balance have 1 + 2 on each side. The number of lateral dots varies from 0 (a single snake has no lateral dotting visible) and 4 (one dot on one side and three on the other), to a maximum of 54 (27 dots on each side); usually the number of dots on the two sides is not identical. The scale row formula is 19-19-17 with four exceptions; three of these are 20-19-17, and the other 21-19-17.

The Furey material shows an interesting ontogenetic pattern change. A series of six young snakes ranging in snout-vent lengths from 104 mm to 166 mm shows the development of the ventral dark band. In the smallest of these snakes (which still has evidence of the umbilicus at ventrals 115 to 117) the entire venter has a pale ground color with scattered dark brown or black blotches. The two snakes next in size (108 and 118 mm snout-vent) show the same condition, although the larger of these two shows the beginning of deposition of dark pigment ventrally. The next largest snake with a snout-vent length of 153 mm shows the obliterative effect of additional dark pigment so that the individual dark ventral blotches have become somewhat obscured. Finally, in two snakes with snout-vent lengths of 165 and 166 mm, the adult condition of a black or dark venter, with the original juvenal dark blotches barely discernible, is attained. In these young snakes the collar is pale and conspicuous; with increasing age the collar becomes fainter and less obvious so that in large adults it is much reduced and may be seen only as a small restricted pale nuchal area with some dark pigment deposited about it. Only two snakes from Furey are as pale as are the two *perfector*, and these two individuals have the lateral lines and dots as conspicuous as do the Baoruco snakes. In general, the Furey snakes are dark brown: description in life of a series of *D. h. haetiana* from Bassin Bleu, Peneau, Dépt. de l'Ouest, Haiti, noted the coloration as dark brown with a middorsal dark brown longitudinal band on a slightly lighter brown color (Fig. 1). The ventral ground color was dark brown with occasional whitish edges to the ventra's. The lateral margins of ventrals and first scale row on each side were brick red to orange-red, the extent of this color greatest anteriorly. The dorsal blotches were buffy-tan, outlined in brown. The collar (Fig. 3) was very much reduced or absent in this series which ranged in size from 159 to 245 mm in snout-vent length. Note also the lack of mention of the lateral stripe which was not obvious because of the dark lateral coloration.

From the above details in both scalation and coloration, it is apparent that *D. h. perfector* differs not only in having fewer

underbody scales than does *D. h. haetiana*, but also in having a prominent nuchal collar and prominent lateral lines.

There are two specimens of *Darlingtonia* from the Massif de la Hotte, the type and another from Camp Perrin. These two individuals are both females, the type having a snout-vent length of 294 mm and the second specimen a snout-vent length of 247 mm. The tail of the type (88 mm) is unusually long, longer than any specimen of either sex, regardless of snout-vent length, from the Furey area. The ventrals in these two snakes are 136 and 137, and the subcaudals 49 and 51, with total underbody scales 185 and 188. There are no other scale differences, although the Camp Perrin specimen has 1/2 preoculars and the type has 2 + 1 and 2 + 2 temporals. Both are pallid snakes with conspicuous lateral lines and without collars; the amount of ventral darkening is variable, involving almost the entire width of the ventrals in the type, and with a clear reddish area on the lateral ends of the ventrals in the second specimen. Using ventrals minus subcaudals as an index, the two western snakes both (with 86) lie just outside the range of the series of females from Furey (with a range of 87 to 102). Whether this hints at a basic difference between these two populations can be determined only by the acquisition of more material from the Massif de la Hotte. The extremely long tail of the type and, in the two La Hotte females, the relatively high number of subcaudals (49 and 51 versus 41 to 50 in Furey females), and the tail/snout-vent ratio of 29.9 and 31.2 (versus 23.7 to 27.2 in Furey females) are all likewise suggestive of differentiation.

Altitudinally, *Darlingtonia haetiana* ranges from 1000 feet (303 meters) at Camp Perrin to a known maximum of 5000 feet (1515 meters) at Roche Croix. Specimens from the Furey area, from localities which can be mapped, show an altitudinal range of from 5000 feet (1515 meters) at Kenseoff and Pencau to 5600 feet (1697 meters) at Furey. The narrow altitudinal range is doubtless an artifact of collection, since the wider altitudinal limits to the west indicate that the snake may occur much lower. Once again, the extreme deforestation of the accessible mountains near Port-au-Prince may have been a crucial factor in limiting this snake to more favored higher elevations. The elevations for *D. h. perfector* (3000 and 3700 feet = 910 and 1221 meters) are intermediate and within the known limits of the Massif de la Hotte distribution of *Darlingtonia*.

The series of five specimens from Peneau was collected in a montane ravine with dense growth of bamboo; the specimen from Kenscoff was secured under a pile of drying vetiver. The Camp Perrin snake was received from a native and there are no habitat data available for it. Of the two recent specimens of *D. h. perfector*, the type was taken under a rock in a small weedy clearing surrounded by broad-leaf forest and *cafetales*, and the paratype was taken within a mat of cut vines in the same clearing.

The absence of records of *Darlingtonia* from the area between Furey and the eastern end of the Sierra de Baoruco is puzzling. If *Darlingtonia* has the altitudinal limits indicated by the La Hotte specimens, it is strange that it has not been taken at such localities as Forêt des Pins in extreme eastern Haiti or along the Dominico-Haitian border. It may be significant, however, that the junior author and Mr. Leber visited the type locality of *D. h. perfector* in the summer of 1963, and although they secured a long series of *Wetmorena*, no *Darlingtonia* were taken. The two specimens were secured at the same locality a year later. One would expect that *Darlingtonia* occurs throughout much of the south island montane massifs, but, on the other hand, it is possible that the populations are in reality disjunct. Only further collecting may prove which is the case.

HEMIPENIS

The everted hemipenis of *Darlingtonia haetiana* is relatively small (extending to the level of the 6th or 8th subcaudal), and bilobed; the sulcus spermaticus is deeply forked; and the sulcate side (we depart from the usage of Dowling and Savage, 1960, and use sulcate and non-sulcate instead of medial and lateral for the surfaces of the everted organ) is strongly differentiated from the non-sulcate side in being covered with papillae from the region of the sulcus spermaticus to the apices. The sulcus spermaticus proceeds through the papillate region to the apices. This papillate zone is sharply set off from the non-sulcate side which is uniformly adorned with very small spines. The organ has the appearance of having an elongate cordate shield (papillate zone) affixed to the sulcate side (Fig. 4). A row of enlarged but progressively smaller spines begins on each edge of the non-sulcate side about midway the length of the organ (level of third subcaudal) and proceeds basally and diagonally, becoming lost in the profusion of smaller spines on the basal sulcate side. Papillate calyces cover the papillate sides of each lobe; the papillae become

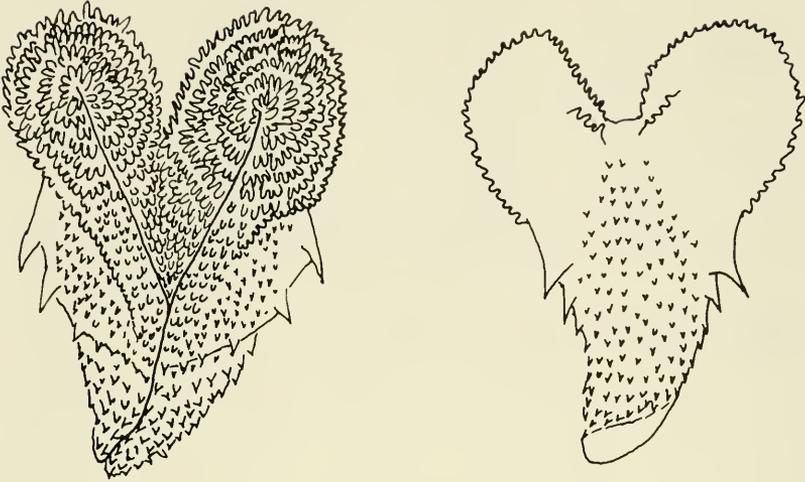


FIG. 4. Hemipenis of *Darlingtonia haetiana*; left, sulcate surface; right, non-sulcate surface; MCZ 65100, near Palmiste, Furey, Dépt. de l'Ouest, Haiti.

smaller and more sparse on the more basal portions of the hemipenis. Several larger, isolated papillae are present on the non-sulcate surfaces of the lobes or in the crotch between them. One specimen, ASFS X2078, appears abnormal in having more sparse and less prominent calyces, and accessory sulci partially dividing the papillate zone, making the organ almost capitate.

SPECIMENS EXAMINED

Darlingtonia haetiana haetiana: Haiti, Dépt. du Sud, Roche Croix, northeastern foothills, Massif de la Hotte (= Pic Macaya), about 5000 feet (1515 meters) altitude, MCZ 38252 (type); Camp Perrin, 1000 feet (303 meters), ASFS X3058; Dépt. de l'Ouest, Pencau, Bassin Bleu, 5000 feet (1515 meters), ASFS X2077-81; Furey, MCZ 60060-61, MCZ 66996-98, UMMZ 123097 (4 specimens), USNM 123803; Vendôme near Furey, MCZ 65104-07; near Palmiste, Furey, MCZ 65098-101; Morne Bourette, USNM 117286; Kensecoff, 5000 feet (1515 meters), ASFS X2254.

Darlingtonia haetiana perfector: República Dominicana, Barahona Prov., 24 km SW Barahona, 3700 feet (1221 meters), MCZ 77217, ASFS V2898 (type and paratype); AMNH 49738, near Polo, 3000 feet (910 meters) (paratype).

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(Received 2 June, 1965.)

B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS.

SEPTEMBER 15, 1965

NUMBER 230

NOTES ON SOME NON-PASSERINE BIRDS FROM EASTERN ECUADOR

By

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A new collection of birds from eastern Ecuador contains a number of significant specimens. The Ecuadorian segment of the upper Amazon basin has been generally neglected by ornithologists since Chapman's study of 1926, while the adjacent areas of Colombia and Peru have been more recently investigated. The latter studies have raised questions about the continuity of populations along the eastern base of the Andes and this new collection answers some of these questions by documenting the presence of certain forms in eastern Ecuador.

In 1963 and 1964, during the months June-September, I made collecting trips to eastern Ecuador, working at altitudes between 300 and 1,500 meters. In 1963, I spent a month and a half at Limoncocha, and a month on Mount Sumaco. Accompanied by Richard D. Chandler in 1964, I returned to collect on the slopes of Sumaco for two months. A collection of 1,900 specimens from these two expeditions is deposited in the Museum of Comparative Zoology. The present paper contains the most noteworthy records from among the 145 forms of non-passerines represented in this collection.

COLLECTING LOCALITIES

COTAPINO (often labeled on maps as "Concepción"): 0°45'S, 77°25'W; alt. 700 m¹; 25 June-12 July 1964; 250 specimens.

At the junction of Río Pueuno and Río Cotapino, this hacienda serves as a departure point for Sumaco trips. Besides an airstrip

¹ Altitudes are based on readings taken with a pocket altimeter at each locality.

and some 60 acres of cultivated land, Cotapino offers shelter and a small number of Quechuan Indian laborers. Most of the specimens were collected here with mist nets.

CUYUJA: $0^{\circ}25'S$, $78^{\circ}03'W$; alt. 2,400 m; 19 June 1964; 9 specimens.

Chandler and I visited this town 10 km east of Papallacta, hoping to find conditions comparable to those on the slopes of Sumaco. Collecting here was incidental, but promising, because the deforestation characterizing Papallacta has not yet reached Cuyuja.

EUGENIO: $0^{\circ}46'S$, $77^{\circ}24'W$; alt. 700 m; 16-22 July 1964; 111 specimens.

A day's foot travel northwest toward Sumaco from Cotapino, the locality takes its name from the lone Quechuan inhabitant of this last settlement on the way to Sumaco.

LIMONCOCHA: $0^{\circ}25'S$, $76^{\circ}38'W$; alt. 300 m; 25 June-2 August 1963; 300 specimens.

Limoncocha is the site of a large missionary base camp, including an airstrip, housing for United States missionary families, and a Quechuan village, all of which has been established since 1955 on the shores of a lake in the midst of tropical forest. The large lake whose lemonade-colored water inspired the name, Limoncocha, lies two kilometers inland from the mouth of Río Jivíno on the Río Napo. There are few such lakes in eastern Ecuador, and none as unspoiled as Limoncocha. Consequently, the lake and its outlet have yielded some unique specimens, several forms new to Ecuador, and at least one new race.

LOWER RÍO PUCUNO: $0^{\circ}46'S$, $77^{\circ}28'W$; alt. 500 m; 19-31 August 1963; 135 specimens.

Halfway between Cotapino and Eugenio, a traveller must ford the Río Pucuno afoot. In 1963, high water made the river impassable for a few days, during which delay I collected along the banks above and below the ford.

MONTALVO: $02^{\circ}05'S$, $76^{\circ}57'W$; alt. 250 m; 5 specimens.

I purchased several specimens of apparent interest from this locality from R. Olalla, who worked here as an independent collector in 1964.

RÍO NEGRO: $01^{\circ}25'S$, $78^{\circ}03'W$; alt. 1,200 m; 12-14 September 1964; 35 specimens.

Along the road near this village, a few specimens were collected for comparison with those from similar altitudes on Sumaco.

MOUNT SUMACO: Mount Sumaco, an isolated massif rising to about 4,000 m, lies about 40 km southeast of Baeza, and about 100 km southeast of Quito. Four collecting camps were established on the southeast slopes. I have arbitrarily prefixed the name Sumaco to all localities above Eugenio, the highest point settled by Quechuan Indians.

SUMACO, GUATICOCHA: $0^{\circ}45'S$, $77^{\circ}24'W$; alt. 750 m; 16-24 August 1964; 123 specimens.

Only a few hours due west of Eugenio lies this tiny, perfectly round, and very deep lake, where Chandler and I established a camp.

SUMACO, HEAD OF RÍO GUATARACO: $0^{\circ}40'S$, $77^{\circ}35'W$; alt. 1,350 m; 24 July-5 August 1964; 350 specimens.

The junction of several brooks in a series of waterfalls a few hundred meters below this camp, marks the beginning of the Río Guataraco.

SUMACO, PALM PEAK (translated from local Quechuan hunters' designation, *Ramus-Urcu*): $0^{\circ}39'S$, $77^{\circ}36'W$; alt. 1,500 m; 6-14 August 1964; 209 specimens.

Palm Peak is the rim of the altiplano which slopes gradually upward for two days' travel to the final steep slope of the mountain peak. Most of the collecting was done on the altiplano.

SUMACO, UPPER RÍO PUCUNO: $0^{\circ}36'S$, $77^{\circ}35'W$; alt. 1,200 m; 11-16 August 1963; 135 specimens.

The highest camp in 1963 was on the narrow ridge separating the two principal rivers of this face of Sumaco, the Pucuno and the Guataraco.

SYSTEMATIC NOTES

NYCTICORAX PILEATUS (Boddaert)

Limoncocha, 1 ♂.

This wide-ranging form has not been recorded before from Ecuador, where its occurrence was to be expected. This individual was shot in the cow pasture at Limoncocha, a habitat somewhat unusual in eastern Ecuador, as cattle in the country are confined mostly to the highlands.

IXOBRYCHUS EXILIS LIMONCOCHAE subsp. nov.

Type: Adult male, No. 285,860, Museum of Comparative Zoology, collected at Limoncocha, alt. 300 m, Río Napo, eastern Ecuador, by D. W. Norton, on 6 July 1963.

Diagnosis: Similar to nominate *exilis*, but cheeks and auriculars shading to chestnut, ventrum less streaked. Similar to *erythromelas* in color of cheeks, but wing and bill somewhat longer, ventrum less richly colored, throat less streaked; dorsum of female grayish brown, not reddish brown as in *erythromelas*. Distinguished from *bogotensis* by chestnut rather than ochraceous cheeks, by lighter ventrum, with less streaking on throat, and by a somewhat shorter bill. Generally smaller than *peruvianus*, with ventrum, head, and wing coverts tawny rather than ochraceous.

Range: Known only from the type locality.

MEASUREMENTS

		Wing	Culmen (exposed)
<i>limoncochae</i>	(1 ♂ — type)	120 mm	45 mm
	(1 ♀)	120	46
<i>exilis</i>	(4 ♂)	112-121 (117.8 ± 1.7)	44-49 (46.3 ± .09)
	(1 ♀)	112	43
<i>erythromelas</i>	(3 ♂)	106-113 (109.3 ± 1.7)	42-44 (42.7 ± 0.5)
	(2 ♀)	109-113 (111.0 ± 1.4)	40.0
<i>bogotensis</i>	(2 ♂)	116-122 (119.0 ± 2.1)	40.0
	(5 ♀)	113-125 (120.8 ± 2.1)	37-40 (39.0 ± 0.6)
<i>peruvianus</i>	(1 ♂)	125	53

Remarks: The two specimens of *limoncochae* were collected with a single shot and, therefore, are presumed to have been mated, although their gonads were not enlarged.

While examining comparative material, I found that a female (AMNH No. 151,639) from Antioquia, Colombia, is referable to *bogotensis*, which extends the known range of that race considerably to the northwest.

I tentatively identified as *peruvianus* a mounted specimen in adult male plumage at the Colegio San Bolívar in Ambato, Ecuador. The wing measures 127 mm and the culmen 50 mm. Although there were no data, the curator of the collection, who is the widow of the collector, claimed that her husband shot all his specimens in Ecuador. Corroboration of this doubtful record would extend the known range of *peruvianus* north from coastal Peru (Dept. Libertad) to western Ecuador.

The origins of the races in northern South America are deserving of speculation. Significantly, I believe, the southern limits of migration of the two North American races are just to the north (eastern Panama). *Ixobrychus exilis* may originally have been a temperate and entirely migratory species. In this case,

the South American races have arisen at the southern limits of the wintering populations, and may represent descendants of a few birds which gave up the migratory habit to breed near the equator. The South American forms must then be more recent developments than the splitting of the migratory population into eastern and western subspecies, because the four southern forms are neatly divisible morphologically into eastern and western types. The easternmost form, *erythromelas*, seemingly shows the extreme in characteristics of nominate *exilis* of eastern United States, in its small size and generally reddish brown coloring. The westernmost, *peruvianus*, is similarly related to *hesperis* of the western United States, as it shows the extreme of large size and grayish brown coloring. In between, *limoncochae* is a less extreme eastern type, and *bogotensis* a less extreme western type.

Specimens examined: limoncochae: Ecuador, Limoncocha, 1 ♂, 1 ♀; *erythromelas:* Surinam, Paramaibo, 3 ♂, 1 ♀; *bogotensis:* Colombia, Savana de Bogotá, 2 ♂, 4 ♀; Antioquía, 1 ♀; *peruvianus:* Peru, Dept. Lima, Vegueta, 1 ♂, 1 imm.; "Ecuador", 1 [♂].

ARAMIDES CALOPTERUS Selater and Salvin

Sumaeo, Guaticoecha, 1 ♂; Montalvo, 1 ♂.

A specimen from Montalvo, collected by R. Olalla in April 1964, is significantly lighter than any in a series from Río Suno and Sumaeo. However, I believe Olalla dries skins in direct sunlight, which would cause fading, and explain this disparity.

PORPHYRULA MARTINICA (Linnaeus)

Limoncocha, 1 ♂, 1 ♀.

Although it is recorded from western Ecuador, I find no previous record of this wide-ranging species in eastern Ecuador, where its occurrence was to be expected.

PORPHYRULA FLAVIROSTRIS (Boddaert)

Limoncocha, 1 ♂.

The species, new to Ecuador, is apparently uncommon in upper Amazonia, for de Schauensee (1949: 432) includes it in the faunal list of Colombia, also on the basis of a single specimen (Florencia). Individuals occur regularly at Limoncocha, but I have not seen any elsewhere in eastern Ecuador.

JACANA SPINOSA INTERMEDIA (Selater)

Limoncocha, 2 ♀.

Specimens from Limoncocha are clearly referable to *intermedia*. This first record of the species from eastern Ecuador extends the known range of *intermedia* south from eastern Colombia to at least the Río Napo in Ecuador. Hellmayr and Conover (1948:9) questioned the validity of *peruviana*, of north-eastern Peru but comparison of 14 specimens from northeastern Peru with a series of *intermedia* from Venezuela, Colombia, and Ecuador, shows Peruvian specimens to be much the largest and darkest in the group, and easily separable from the reasonably uniform *intermedia* specimens.

VANELLUS RESPLENDENS (Tschudi)

Limoncocha, 2 ♂ ; Mt. Cotopaxi, Laguna de Limpio, 2 ♀.

The Andean lapwing seems never to have been recorded from below 2,000 m anywhere in its range (Ecuador to northern Chile). The Limoncocha specimens were observed daily (personal communication) on the grassy airfield of the mission station (alt. 300 m) from February to June 1963, before I collected them there in July. This unusual pair, frequenting an artificial habitat cleared only recently of tropical forest, proved to be two males coming into adult plumage and having small gonads. These birds were much tamer than individuals observed and collected on Mt. Cotopaxi. The unique record probably represents young strays lost during the seasonal altitudinal migrations of this species in the Andes. Aside from the airstrip, the only other sizable unforested areas near Limoncocha are the gravel bars of the nearby Río Napo. This pair was indeed traced twice to the gravel bars during the daylight hours. Significantly, the Quechuan Indians of Limoncocha could give no local name for this bird, whereas all regularly occurring species on the Napo receive specific and descriptive Quechuan names.

GENUS EUTOXERES

Eutoxeres condamini condamini (Bourcier): Cotapino, 3 ♂, 5 ♀.

Eutoxeres aquila aquila (Bourcier): Eugenio, 2 ♂ ; Sumaco, head of Río Guataraco, 1 ♂ ; Sumaco, Guaticochoa, 1 ♀.

The ranges of these sibling species overlap in eastern Ecuador and adjacent areas of Colombia and Peru. Since Chandler and I

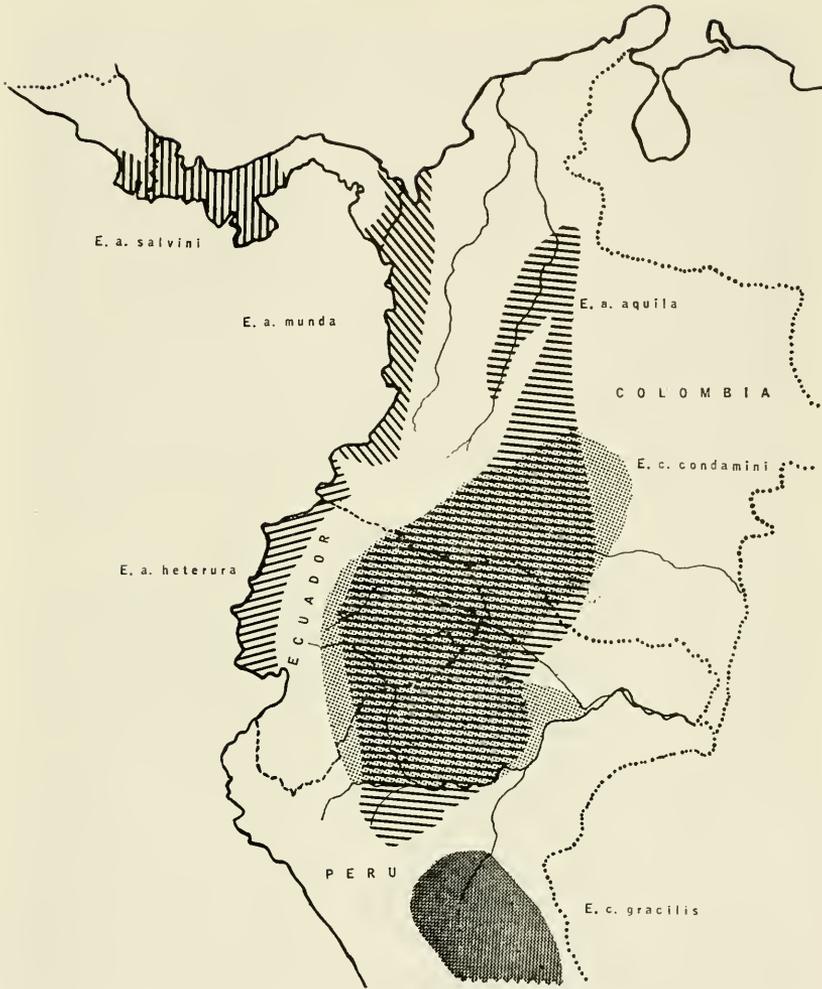


FIG. 1. Distribution of *Eutoxeres aquila* and *Eutoxeres condamini*.

never found both species in the same locality, it is possible that there is a difference in the habitat preferences of the two species. It seems that *E. condamini* occurs in open cultivated areas, at low elevations, whereas *E. aquila* occurs in dense forest at any altitude up to at least 1,500 m.

The distribution of the forms of *Eutoxeres* may be related to the distribution of a principal food source. Greenewalt (1960: legend, Pl. 34) observed *E. aquila* feeding on "platanillos," or plantains of the genus *Heliconia*, using its highly specialized, downcurved bill to draw nectar from the deep, upright bracts of the flowers. Chandler and I had best results netting both species of *Eutoxeres* when the nets were placed close to *Heliconia* plants, which further suggests the dependence of *Eutoxeres* upon the plantains. The genus *Eutoxeres* occurs in northwestern South America, roughly where the greatest concentrations of the 35-odd species of *Heliconia* also occur. The flowering periods of the various species of *Heliconia* doubtless span the year, probably providing a steady supply of food for the hummingbirds.

Observations made in eastern Ecuador suggest that the critical factor in determining local distribution of the sibling species is the abundance of *Heliconia* plants. When land in eastern Ecuador is cleared, and particularly when bananas are planted, many "platanillos" invade the clearing. Apparently, *E. c. condamini* establishes itself in the midst of this abundance, while *E. a. aquila* retreats to the forest. Although both forms have been recorded sympatrically at La Morelia, Colombia (de Schauensee, 1949: 541), and at the mouth of Río Curaray (Zimmer, 1950: 1), I suspect that *condamini* is found in the settlements while *aquila* is found farther afield. These records reflect either inexactness in recording the locality, or possibly the passage of time between collectors' visits, during which a locality supporting *aquila* was cultivated, thereby attracting *condamini*.

The origin of these sibling species merits some speculations. The simplest explanation of the present distribution of the species of *Eutoxeres* is that an original South American population was split by the Andean uplift, giving rise to *condamini* to the east and *aquila* to the west of the cordillera. Subsequently, *aquila* has colonized the isthmus of Panama, and has spilled eastward over the Andes to invade the range of *condamini*.

GENUS TOPAZA

Topaza pyra (Gould): Cotapino, 1 ♂; Sumaco, Guaticochoa, 1 ♀.

These specimens are the first definitely to extend the known range of *pyra* so far up the Río Napo, contradicting Oberholser's (1902: 322) assertion that the species does not occur above Coea on the upper Napo. Of greater interest is the proof that *T. pyra*

occurs west of *T. pella pamprepta*, an endemic form known only from Boca Suno on the Napo in eastern Ecuador. The population of *T. p. pamprepta* seems to be surrounded by the morphologically similar *T. pyra*, isolated in Boca Suno, 2,000 km from the other races of *pella*, which occur in the Guianas and in Pará, Brazil. The validity of *pamprepta*, and the present range extension of *pyra* make it impossible to accept Peters' (1945: 92) suggestion that *pella* and *pyra* might be conspecific. I have examined the type of *pamprepta*, finding Oberholser's (1902: 322) description and the data given by the collectors, both accurate. The type is similar in pattern to nominate *pella*, but it is distinguished by a much longer tail and somewhat shorter bill. One can conclude that the curiously spotty distributions of the taxa of *Topaza* are artifacts due to the rarity of these equatorial hummingbirds. Future records of *pella* may come from northern Brazil, between Ecuador and the Guianas.

TROGON RUFUS SULPHUREUS Spix

Sumaco, Guaticocha, 1 ♂ ; Sumaco, Guaticocha, 1 ♀ (preserved as a skeleton).

Although this subspecies was to be expected in eastern Ecuador, Peters (1945: 157) omits both eastern Ecuador and eastern Colombia from its range. Apparently, the only previous records were specimens labeled with doubtful accuracy as being from Coca, Río Napo, and "Equateur" (Zimmer, 1948: 29). The present record shows *sulphureus* to occur almost to the foot of the Andes and up to nearly 800 m in this part of its range.

CAPITO NIGER PUNCTATUS (Lesson)

Limoneocha, 3 ♂ , 4 ♀ ; Lower Río Pueuno, 1 ♂ ; Cotapino, 1 ♂ , 1 ♀ .

The subspecific status of this species in upper Amazonia is in confusion. Several authors have disputed Brodkorb's (1939) two races, *macintyreii* of eastern Ecuador and *conjunctus* of northeastern Peru. Examining a large series from Colombia, Ecuador, and Peru, I fail to find any of the consistent geographic variations mentioned by Brodkorb. Furthermore, the 12 birds from Limoneocha show all extremes in pileum color and streaking of the ventrum. Bond (1954: 49) synonymized *conjunctus* with *macintyreii*, but distinguished *macintyreii* from *punctatus* on the basis of the amount of ventral streaking in one female from Villavicencio, Colombia. Two of four Limoneocha

females have the ventrum as lightly streaked as this female from Villavicencio. I therefore agree with Peters (1948: 25) and ascribe to *punctatus* birds of upper Amazonia from Colombia to northeastern Peru.

PICUMNUS RUFIVENTRIS RUFIVENTRIS (Bonaparte)

Limoncocha, 1 ♂ ; Cotapino, 1 ♂ ; Eugenio, 1 ♂ ; Sumaco, Palm Peak, 1 ♂ , 1 ♀ .

Chandler and I found these birds quite common up to at least 1,500 m on Mt. Sumaco, although the species is usually considered an inhabitant of the Tropical Zone (de Schauensee, 1949: 641). At Palm Peak, specimens were taken simultaneously with such typically subtropical forms as *Cyanocorax yncas*.

ACKNOWLEDGMENTS

I thank Dean Amadon of the American Museum of Natural History, James Bond of the Philadelphia Academy of Natural Sciences, and George E. Watson of the U.S. National Museum, all of whom lent comparative material for this study. Richard D. Chandler was a valuable companion and collector on the trip in 1964. I am especially grateful to Raymond A. Paynter, Jr. for his guidance during the preparation of this paper.

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(Received 15 June 1965.)

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