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ANOLIS ALUMINA, NEW SPECIES OF GRASS ANOLE FROM THE BARAHONA PENINSULA OF HISPANIOLA

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ABSTRACT. A new species, *Anolis alumina*, from the Barahona Peninsula of Hispaniola is described on the basis of two scale characters and dewlap color in males. Electrophoretic and morphological analyses show that *alumina* is more closely related to *A. semilineatus* than to *A. olssoni*. Limited distributional data suggest that the new species is more eurytopic than either of the other two species of Hispaniolan grass anoles, occurring in habitats ranging from lowland desert scrub to high elevation pine savannah.

During 1973 and the winter of 1974, I initiated an electrophoretic study of the grass anoles of Hispaniola, using material that had been collected by various researchers in the Harvard *Anolis* group; the results, though incomplete, suggested that animals found south of the Massif de la Selle — Sierra de Baoruco mountain chain are taxonomically differentiated from the white-dewlapped *A. semilineatus* Cope of the northern part of Hispaniola.

While collecting in the Dominican Republic during the summer of 1974, Raymond B. Huey and I journeyed to the south slopes of the Sierra de Baoruco to look for grass anoles. We were fortunate to enjoy the hospitality of the Alcoa Exploration Company at their bauxite mining operation at Cabo Rojo, Pedernales Province, while we explored the mine area and surrounding countryside.

As we drove up to the mine one morning, Huey spotted a small animal dart across the road in front of our vehicle. After

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perhaps ten minutes of frantic searching and chasing the elusive lizard in the pine savannah into which it fled, I succeeded in grabbing the animal which promptly exhibited his displeasure by erecting his pale greenish-yellow gular fan. I suspected at once that we had captured a previously undescribed species of *Anolis* which, in honor of our hosts, I name

Anolis alumina, new species

Holotype. 31.5 km north of Cabo Rojo, Pedernales Province, Dominican Republic (elevation 1150 m), MCZ 143824, P. E. Hertz and R. B. Huey collectors, 8 July 1974.

Paratypes. Dominican Republic: Pedernales Province: Pedernales: ASFS V2816, R. Thomas collector, 3 July 1964; 5 km north of Pedernales: ASFS V2544–V2545, R. Thomas collector, 25 June 1964; 9 km north of Pedernales: ASFS V21496, R. Thomas collector, 27 July 1969; 6 miles north of Pedernales: ASFS V30118–V30127, D. C. Fowler and A. Schwartz collectors, 23 August 1971; 21 km north of Cabo Rojo: ASFS V30058, D. C. Fowler collector, 21 August 1970; 23.5 km north of Cabo Rojo: MCZ 143849–143851, P. E. Hertz and R. B. Huey collectors, 8 July 1974; 28 km north of Cabo Rojo: MCZ 143822–143823, P. E. Hertz and R. B. Huey collectors, 7 July 1974; 30 km north of Cabo Rojo: MCZ 146632–146633, W. E. Haas collector, 20 July 1975; 31.5 km north of Cabo Rojo: MCZ 143825–143827, P. E. Hertz and R. B. Huey collectors, 8 July 1974; MCZ 146627–146631, W. E. Haas and E. E. Williams collectors, 19 July 1975; 7 km north, 17.6 km southeast of Cabo Rojo: ASFS V30079–V30083, D. C. Fowler and A. Schwartz collectors, 22 August 1971; 5 miles northeast of Oviedo: ASFS V289, R. Thomas collector, 7 August 1963; 13.1 miles southwest of Enriquillo: ASFS X9966, A. Schwartz collector, 30 July 1963. *Barahona Province:* southern outskirts of Barahona: ASFS V30980, B. R. Sheplan collector, 12 September 1971; MCZ 106995, E. E. Williams, A. S. Rand, and E. Marcano collectors, 28 July 1968; 5 km south of Barahona: ASFS V20552, R. Thomas collector, 22 June 1969; 7 km southwest of Barahona: ASFS V23423, A. Schwartz collector, 4 January 1971; 4.1 miles southwest of Barahona: ASFS V30407–V30415, D. C. Fowler, A. Schwartz, and B. R. Sheplan collectors, 9 December 1971; 4 km northwest of Naranjal:

ASFS V20954; R. Thomas collector, 4 July 1969; 1 km south
of Cabral: MCZ 140011–140012, T. P. Webster collector,
4 November 1973; 4.9 miles northwest, 0.3 miles west of
Cabral: ASFS V30815, D. C. Fowler collector, 8 September
1971; Polo: AMNH 50320, W. G. Hassler collector, no col-
lecting date. *Haiti:* Département de l'Ouest: Belle-Anse: MCZ
140104–140111, T. P. Webster collector, September 1973.

Diagnosis. An *Anolis* closely related to *A. semilineatus* and
A. olssoni Schmidt, distinguished from both by smooth scales in
the frontal depression (Fig. 1), enlarged middorsal scales grad-
ing into the granular scales of the flank (rather than abruptly
distinct) (Fig. 2), and a pale greenish-yellow gular fan in males
(rather than white or orange).
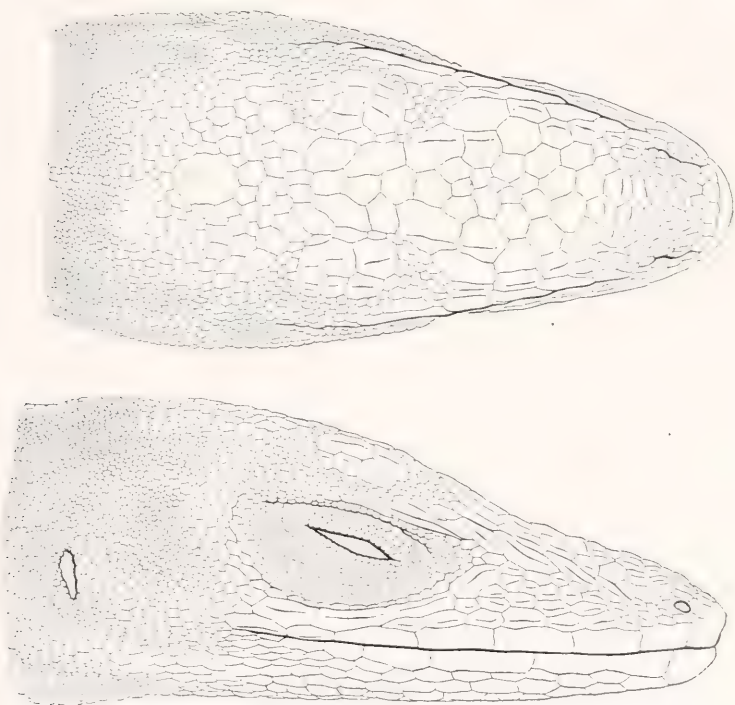
Figure 1. Dorsal and lateral views of the head of holotype of *Anolis
alumina* (MCZ 143824).
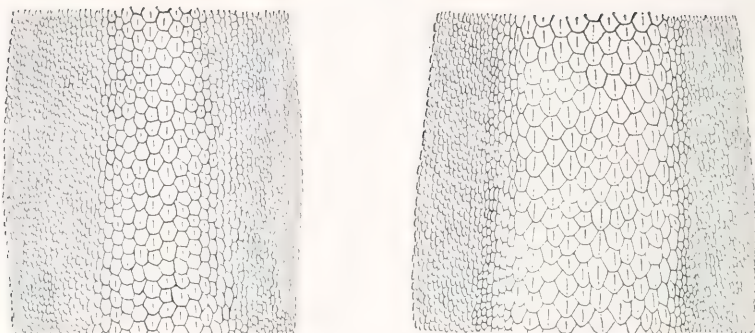
Figure 2. Enlarged middorsal scales of (left) *Anolis alumina* (MCZ 143824) and (right) *A. semilineatus* (ASFS V8093).

Head. Most head scales keeled. Six to eight scales across head between second and third canthals. Frontal depression extremely shallow (except in one specimen), its scales smooth and varying in size but never larger than the anterior supraorbital.

Supraorbital semicircles usually separated by one scale row (separated by two scales in one specimen, in contact in two specimens) and separated from supraocular disc by one row of small scales or in contact with supraocular disc (two specimens). Supraocular disc consists of two to five large keeled scales and zero to three smaller keeled scales, usually surrounded by granular scales. Supraocular disc separated from elongate supraciliary by one to three rows of granular scales and/or a small elongate scale at anterior side of contact.

Canthus distinct, canthal scales four to five, second largest, diminishing in size anteriorly. Naris anterior to canthal ridge. Anterior nasal scale small, in contact with rostral scale. Four to five vertical loreal rows.

Temporal scales subgranular. Two to four rows of granular supratemporals (larger than temporals), grading into subgranular scales which grade dorsally into the larger scales surrounding the interparietal. Interparietal about as large as the ear, separated from supraorbital semicircles by two to three scales (four in one specimen). Suboculars keeled (sometimes markedly so) and in contact with supralabials. Four to six supralabials from rostral to center of the eye. Rostral scale markedly rounded on dorsal surface.

Mentals wider than long, two small elongate scales inserted between posterior tips. One to five (usually three) sublabials on each side contact infralabials. Central throat scales keeled, elongate. Gular fan large in males, absent in females. Scales of gular fan singly keeled, elongate or oval, about the same size as ventrals, not clearly arranged in rows.

Trunk. Unicarinate middorsal scales, arranged in longitudinal rows, about-as broad as long, grading laterally into small keeled or granular flank scales. Seventeen to 24 middorsals in standard distance (tip of snout to center of eye) in males, 15 to 19 in females. Ventrals in longitudinal rows, unicarinate, imbricate, and in some specimens slightly mucronate. Fifteen to 24 ventrals in standard distance in males, 11 to 18 in females. Enlarged postanal scales present in males.

Limbs and digits. Hand and foot scales multicarinate. Largest arm and leg scales unicarinate, about as large as enlarged middorsals. Fifteen to 18 lamellae under phalanges two and three of fourth toe.

Tail. Oval to circular in cross section two and one-half to three times snout–vent length.

Size. Largest male 40 mm snout–vent length. Largest female 37 mm snout–vent length.

Color in life. Dorsal surface of head tan to chestnut. Flanks chestnut. Middorsal stripe (or series of elongate blotches which meet medially) a peppered off-white, bordered on either side by a narrow tan stripe. Venter and mandible of both sexes and throat of females white with moderate brown peppering. Conspicuous white lateral stripe on maxilla from tip of snout along flank to hind leg, extending in some specimens to base of tail. Scales of gular fan (in males only) white with brown peppering. Skin of gular fan pale greenish-yellow. Iris blue.

Distribution. Anolis alumina appears to be widely distributed on the Barahona Peninsula and on the south slopes of the Sierra de Baoruco-Massif de la Selle mountain range (Fig. 3). Most specimens from this area which had been previously assigned to *semilineatus* are now designated as paratypes of *alumina* on the basis of the two diagnostic scale characters.

Preliminary observations suggest that the habitat preferences of *Anolis alumina* are similar to those of other Hispaniolan grass anoles. The type series was collected in the undergrowth of a pine savannah at middle elevations; the animals were

spotted while perching below two feet in the vegetation, and usually fled by dropping to the ground and scurrying into dense clumps of grass or between rocks. Other collectors have reported the animals sleeping on living and dead desert shrubs, on dead *Acacia* in and along the margins of cleared fields, and on dead grass and twigs in or near meadows. Albert Schwartz (personal communication) has collected three specimens at night from under rocks in hammock woods, a sleeping habit previously unreported for members of the *semilineatus* group. D. C. Fowler collected a single specimen asleep at a height of four feet on the leaf of a tree.

COMPARISONS WITH OTHER SOUTHERN ISLAND POPULATIONS IN THE *SEMILINEATUS* COMPLEX

Comparison of *alumina* with neighboring populations of grass anoles on the south island of Hispaniola supports the distinction of *alumina* as a full species. *A. alumina* and *semilineatus* are easily distinguished from *olssoni* on the basis of the size of the throat scales in females and the gular fan scales in males: in the latter species, throat scales are greatly enlarged and are much larger than the ventrals. We can then refer to *alumina* and *semilineatus* as members of the more primitive *semilineatus* complex within the *semilineatus* species group, and consider the enlarged throat scales of *olssoni* a derived character (Williams, 1961). *A. olssoni* can then be ignored (as unambiguously distinct) in morphological comparisons of southern island grass anoles because the only confusion of *alumina* and *olssoni* appears to have arisen from the fact that both species have pigmented (as opposed to "white," as in *semilineatus*) dewlaps.

Cope (1864) lists the type locality of *semilineatus* as "Hayti." The type specimen (BMNH 1946.8.5.85) resembles the Petionville *semilineatus* series in its keeled head scales and its dorsal standard distance counts. Since the Port-au-Prince area was, and still is, the most travelled part of Haiti, one is tempted to suggest that the type locality of *semilineatus* may plausibly be restricted to Petionville.

A series of *semilineatus* (ASFS V16698–V16707) geographically close to *alumina* was collected at the top of the road to the Alcoa mine near Cabo Rojo at an elevation of 4400 feet, approximately eight road kilometers above the type locality of *alumina*. The two diagnostic scale characters indicate that the

ASFS series is unquestionably *semilineatus*. In addition, their maxillary-lateral stripes are considerably darker than those on the nearest *alumina*, though this may be the result of different preservation techniques. These animals are smaller than their geographically closest Haitian conspecifics, but several males are larger than any of the specimens of *alumina* that we have at hand. It is possible that *semilineatus* replaces *alumina* at high elevations in the Sierra de Baoruco and Massif de la Selle, but much more material is needed to establish this point.

Because of inadequate collecting, our knowledge of the fauna on the dry north slopes of the Sierra de Baoruco is scant. *Semilineatus* is unknown in the Valle de Neiba and Plaine du Cul-de-Sac except at its westernmost edge near Port-au-Prince. *A. olssoni* is somewhat better represented in the valley itself, but there are few records of its presence on the north slopes of the Sierra de Baoruco. Based upon our limited knowledge of this area, it appears that *alumina* is restricted to the lowlands in the southeastern corner of the Valle de Neiba near Barahona and Cabral.

To the west of the range of *alumina*, in the central section of the southern island, there are a series of populations here regarded as *semilineatus*, characterized by large body sizes (snout–vent length of largest adult male is 46 mm), very distinct mid-dorsal stripes, markedly keeled head scales (including those of the frontal depression), and distinctly enlarged middorsal scales which do not grade into the granular flank scales. The following are the south island specimens so characterized:

HAITI: 5 km south of Dufort, MCZ 63046–63047; Ça-Ira, MCZ 64841, 64844–64846, 64850, 64852, 64857, 64858; 4 miles southwest of Gressier, ASFS V8335; 10 miles north of Jacmel, ASFS V37867; 4 miles northwest of Jacmel, ASFS V9804; 3 miles east of Jacmel, ASFS V9759–V9760; Bascap Rouge, MCZ 65024; 3 miles east of Cayes Jacmel, ASFS V9723–V9725; 2 miles west of Marigot, ASFS V9770; 9.7 miles southwest of Seguin, ASFS V38159–V38160; 3.8 miles southwest of Seguin, ASFS V38187; 10 miles north-northeast of Marigot, ASFS V9732–V9735; mountains south of Gasseleine River at Marbial, AMNH 69036; Peneau, ASFS X1354, X1550; Obléon, MCZ 60015–60016; Basin Bleu, MCZ 60017–60020; Furcy, MCZ 58011, 59553, 60025–60027, 63417–63426, ASFS X1596, X1905, V8357–V8366; 4.8 km south of Pétionville, ASFS V8083–V8116; Boutilliers Road, MCZ

60021–60024, 60028–60029, 63038–63039, 112099–112100,
ASFS V36199, V36231–V36232, V36551; 6 miles west of
Pétionville, ASFS V8347; Pétionville, ASFS X3340–X3345.

In addition, we have a single specimen of *semilineatus* (MCZ
131150), which had been mistakenly included in a series of
olssoni, from Savanne Zombi, a high elevation (1500 meters)
locality in eastern Haiti. Since *olssoni* is otherwise known to
occur only in relatively xeric lowlands (and along some middle
elevation roadsides on the north island), I consider the locality
data for these specimens doubtful and have omitted them from
the range maps (Fig. 3) for these species.

Figure 3. Locality records for (top) *Anolis alumina* (solid circles),
A. semilineatus (open circles), and (bottom) *A. olssoni*. Locality records
from collections in American Museum of Natural History, Museum of
Comparative Zoology, United States National Museum of Natural History,
and Albert Schwartz Field Series. Dotted lines indicate the Massif de la
Selle and Sierra de Baoruco.

A. semilineatus specimens from localities at the western end of the Tiburon Peninsula (near Duchity, Carrefour Zaboka, Jérémie, and Les Platons) are similar to, though smaller than, those just described. The most variable characters in these lizards are dorsal scale size and body size which, as in populations on the north island, appear to vary clinally with elevation (Hertz, in preparation). It seems reasonable to regard these as *semilineatus*, at least *provisionally*.

ELECTROPHORETIC STUDIES

As a check on the taxonomic status of *alumina*, I have analyzed eleven samples of grass anoles using starch gel electrophoresis; sample sizes varied between six and 42 animals (Fig. 4). Five of these populations are white-dewlapped animals from the north island of Hispaniola. Constanza (population A) is the type locality of *A. cochranae*, which Williams and Rand (1961) described as distinct from *semilineatus*, but which I consider an altitudinal variant of *semilineatus*. In addition, I have grouped the Pétionville sample with those from the north island because the animals there are morphologically and electrophoretically indistinguishable from north island *semilineatus*. [Williams (1965) has reported that *Anolis aliniger*, a north island green anole, has been found near Pétionville, and Schwartz (1974) noted that several other northern island lizard species are known from southern island localities in the area. Thus, the western side of the Cul-de-Sac Plain appears to be an area of "faunal leakage" from the north island to the south island, and Pétionville may, at least for my purposes in this description, be considered a north island locality.]

I used material from two *alumina* populations in the electrophoretic analysis: animals from the type locality (28–31.5 km north of Cabo Rojo) and those from Belle-Anse, Haiti. The latter population exists on the south coast of Haiti at the western boundary of the Barahona Peninsula, cut off on the north from the rest of the island by the Massif de la Selle, the Haitian analogue of the Sierra de Baoruco.

Three populations from the north island were available to represent *olssoni*. Since both *olssoni* and *semilineatus* are without question good species, electrophoretic comparison of them provides a means of assessing the significance of various degrees of genic differentiation within the species group.
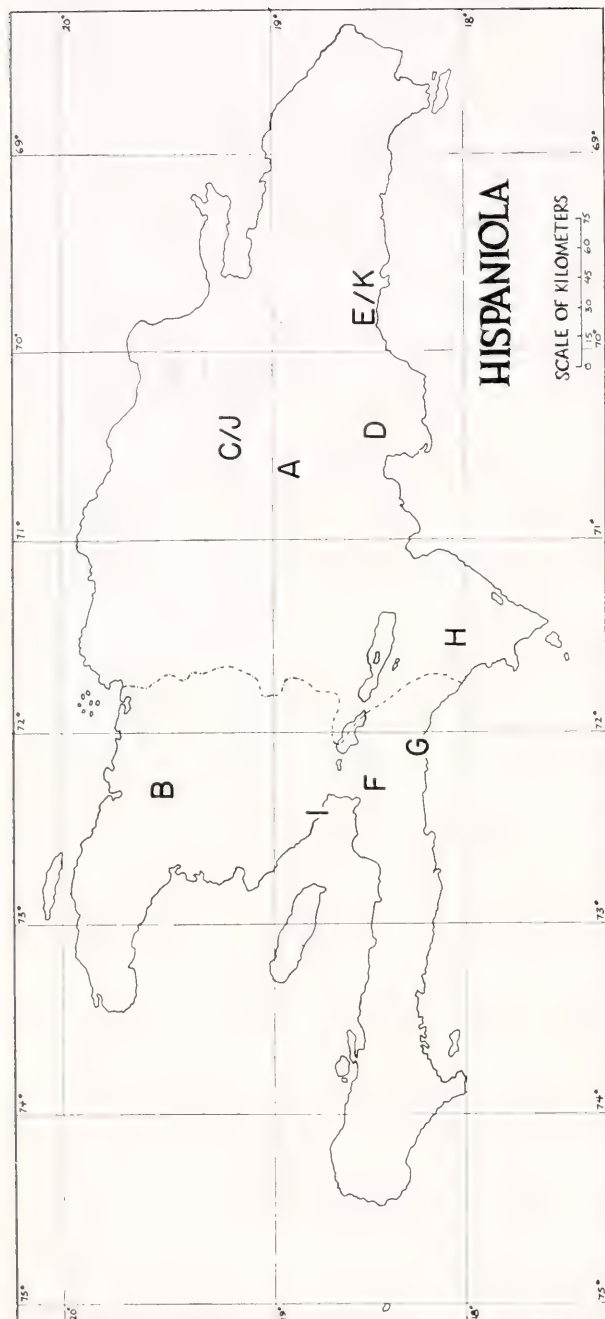
Figure 4. Animals from the following localities were used in the electrophoretic analysis:

A. semilineatus

A: Constanza, La Vega, D. R. (N = 26)
B: Marmelade, Artibonite, Haiti (N = 6)
C: Hotel Montaña, La Vega, D. R. (N = 12)
D: San José de Ocoa, Peravia, D. R. (N = 42)
E: Riviera del Caribe, Dist. Nac., D. R. (N = 10)
F: Pétionville, l'Ouest, Haiti (N = 7)

A. alumina

G: Belle-Anse, l'Ouest, Haiti (N = 18)
H: 28 km N Cabo Rojo, Pedernales, D. R. (N = 20)

A. olssoni

I: Source Matelas, l'Ouest, Haiti (N = 10)
J: Hotel Montaña, La Vega, D. R. (N = 12)
K: Riviera del Caribe, Dist. Nac., D. R. (N = 12)

The methods of sample preparation and horizontal starch gel electrophoresis are adapted from techniques described by Selander et al. (1971). All proteins were extracted from tissue and water homogenates prepared from material which was frozen in the field. (The less-than-ideal freezing conditions in the field resulted in some protein denaturation; two proteins, Indophenol oxidase and an Isocitrate dehydrogenase, were eliminated from consideration because of their lability.) Buffer systems and assays used in this study are similar to those used in previous *Anolis* studies (e.g., Webster 1975); details of the technique and assay formulas are available from the author upon request.

TABLE 1

Proteins assayed in the electrophoretic survey

Albumin	Alcohol dehydrogenase
Protein A	α–Glycerophosphate
Protein B	dehydrogenase
Protein C	Glutamic oxaloacetic
Leucine aminopeptidase	transaminase
Phosphoglucose isomerase	6–Phosphogluconate
Lactate dehydrogenase–	dehydrogenase
1 and 2	Phosphoglucomutase–1 and 2
Isocitrate dehydrogenase–2	Peptidase
Malate dehydrogenase–1 and 2	Fumarase

Nineteen proteins produced consistently scorable bands in all individuals (Table 1); allele frequencies for these proteins are used for the calculation of indices of electrophoretic similarity of pairs of populations. Webster (1975) has argued that Nei's (1972) normalized identity of genes, I, is the preferred index of genetic similarity of two populations. When $I = 0$, the populations share no alleles; when $I = 1$, all gene frequencies in the two populations are identical. I use Nei's I as an index of genetic similarity here and assume in the calculation of I values that each polypeptide is the product of one gene.

I present I values for paired localities in Table 2. It is readily apparent that the populations fall into three distinct groups which correspond to the three species recognized on the basis of scale characters. The average similarity value for paired comparisons of six *semilineatus* populations from the north island

TABLE 2

Electrophoretic similarity of eleven populations of grass anoles as measured by Nei's (1972) I. Populations indexed as in Figure 4.

	A	B	C	D	E	F	G	H	I	J	K
A	—	.99	.96	.93	.98	.99	.81	.80	.85	.83	.86
B		—	.95	.98	.97	.99	.75	.79	.84	.82	.85
C			—	.94	.94	.90	.85	.78	.85	.81	.87
D				—	.97	.98	.82	.81	.85	.82	.85
E					—	.98	.80	.78	.85	.83	.86
F						—	.81	.75	.86	.83	.87
G							—	.99	.71	.66	.73
H								—	.72	.64	.71
I									—	.95	.97
J										—	.97

is 0.96 (range 0.90–0.99), for the three *olssoni* populations
$\bar{I} = 0.96$ (range 0.95–0.97), and for two *alumina* populations
$I = 0.99$.

Average similarity values between paired populations of the
different species are much lower: *semilineatus* to *alumina*, $\bar{I} =$
0.80 (range 0.75–0.85); *semilineatus* to *olssoni*, $\bar{I} = 0.84$ (range
0.81–0.87); and *alumina* to *olssoni*, $\bar{I} = 0.70$ (range 0.64–
0.73).

Only one of the 19 proteins assayed is completely differen-
tiated in animals from the topotypic sample of *Anolis alumina*,
a fast variant (i.e., one that migrates further from the origin)
of albumin which is also the dominant albumin variant in the
animals from Belle-Anse. However, the topotypic *alumina* pop-
ulation is fixed for an allele of Isocitrate dehydrogenase–2 which
appears in only two other populations: 94 per cent at Belle-
Anse (also *alumina*) and 7 per cent at Pétionville (*semilinea-
tus*). Similarly, a slow variant of 6–Phosphogluconate dehydro-
genase is the only 6–PGD allele in topotypic *alumina* and the
predominant (89 per cent) 6–PGD allele at Belle-Anse, but
only occurs at a maximum frequency of 20 per cent in other
populations. Finally, the topotypic sample of *alumina* had a
low frequency (5 per cent) of a slow allele of Malate dehydro-
genase–1, a protein that was monomorphic for a faster allele in
all other populations surveyed.

The electrophoretic data provide support for the species status
attributed to *alumina* on the basis of external morphological
characters. Mayr (1970) and Selander and Johnson (1973)
have noted the dangers in attempting to differentiate species on
the basis of the number of protein differences between them:
we have no independent method for assessing just how much
genetic differentiation is involved in speciation even within a
rather narrowly-defined taxon. It is, however, permissible to
use Nei's index of genetic similarity to compare the distinctive-
ness of populations of *alumina, olssoni* and *semilineatus*. Paired
comparisons of *alumina* and *semilineatus* populations (Table 2)
show that, on average, populations of these species are less simi-
lar electrophoretically than are *olssoni* and *semilineatus;* on the
other hand, *alumina* and *olssoni* are much less similar to each
other than either is to *semilineatus*.

The fact that only one of the nineteen proteins assayed can be called diagnostic of *alumina* is not an argument against the designation of *alumina* as a full species (see Lewontin, 1974: 180–182, for a discussion of electrophoretic evidence of introgression in closely related species). Ayala and Powell (1972) and Prakash (1969) have demonstrated that closely related species of *Drosophila* share many alleles, but that each species carries a particular allele at a different frequency. We find a similar situation with respect to three other proteins in *alumina* and *semilineatus:* IDH–2, 6–PGD, and MDH–1.

RELATIONSHIPS WITHIN THE SPECIES GROUP

Williams (1961) has proposed a model for speciation within the *semilineatus* species group which is based upon the Pleistocene division of Hispaniola into northern and southern islands. He suggested that *semilineatus* is the autochthonous grass anole of the south island and that *olssoni* is the autochthon of the northern component. Williams then suggested, on the basis of somewhat limited distributional data, that *semilineatus* invaded the north, while *olssoni*, probably restricted by the absence of suitable habitat, did not successfully extend its range throughout the south.

Our current knowledge about the distributions of the Hispaniolan grass anoles, summarized in Figure 3, shows *olssoni* with a rather limited south island distribution. In fact, *olssoni* appears to be restricted on the south island to lowland areas within the currently known range of *alumina* on the Barahona Peninsula. The occurrence of *olssoni* on the Barahona Peninsula, however, does not invalidate Williams' scheme for differentiation within the group and subsequent invasion of the north by *semilineatus*. *A. olssoni* probably originated on the north island and then invaded the south, after the recession of a Pleistocene seaway, through the relatively dry lowland corridor at the eastern edge of the Valle de Neiba near what is now the city of Barahona. Movement southward along the relatively mesic coast and westward across the deserts of the Barahona Peninsula and foothills of the Sierra de Baoruco probably followed its initial invasion of the southern island from the northeast.

The differentiation of *semilineatus* from *alumina* can be attributed to a classical allopatric speciation phenomenon that requires only minor modification of Williams' (1961) scheme.

The range of *alumina* is separated from the western portion of the southern island by the Sierra de Baoruco-Massif de la Selle mountain range which comes close to the sea west of Belle-Anse, Haiti. The north slopes of these mountains appear to be sufficiently dry to limit the contact of the two species today; if the climate was similar during the Pleistocene, the arid areas may have limited genetic exchange between the animals on either side of the mountains and established a sufficient reproductive barrier to allow speciation. The presence of *alumina* at two localities near Cabral on the north side of the Sierra de Baoruco can be attributed to a very limited northward invasion through the same corridor through which *olssoni* moved south into the Barahona Peninsula.

The Barahona Peninsula and particularly the south slopes of the Sierra de Baoruco are becoming well known as a center of differentiation of the Hispaniolan saurofauna. Williams (1962, 1963) recognized the biogeographic importance of the region with reference to *Anolis barahonae* and *A. hendersoni*. Schwartz (1964, 1967a, b, 1974), and Schwartz and Klinikowski (1966) have further documented differentiation there for the *Anolis ricordi* complex and the lizard genera *Leiocephalus*, *Ameiva*, and *Diploglossus*.

On the electrophoretic evidence, *alumina* is genetically less similar to *semilineatus* than is *olssoni*. If the degree of electrophoretic dissimilarity of two species can be taken as an index of either their time of divergence or the magnitude of environmental difference between their ranges, one can suppose that *alumina* and a "proto"-*semilineatus* diverged before Pleistocene seaways isolated the ancestors of *semilineatus* and *olssoni* or that the selective regimes of the Barahona Peninsula at the time of differentiation of *alumina* and *semilineatus* were perhaps more different from those on the rest of the southern island than were conditions on the northern island. Both suggestions are plausible and not incompatible.

The less enlarged middorsal scales suggest that *alumina* is the most primitive of the three species in the *semilineatus* species group. A plausible and conservative model of evolution within the group would suggest that *olssoni* evolved from a "proto"-*semilineatus* stock which had already diverged from an ancestral *alumina*-like grass anole (lacking distinctly enlarged middorsal scales). The subsequent enlargement of dewlap scales in *olssoni*

may have accompanied the dramatic change in dewlap color as a reproductive isolating mechanism to limit its hybridization with *semilineatus*. The repeated changes in Pleistocene sea level would probably have allowed such sequential derivations to occur.

Perhaps *alumina* and *olssoni*, species which may be evolutionarily one step removed from each other, were different enough to allow ecological segregation and sympatry as *olssoni* invaded the eastern section of the south island. In contrast, an invasion by *olssoni* across the western end of the Cul-de-Sac Plain may have been inhibited by either unsuitable habitat or by competitive interactions with resident populations of *semilineatus*. Although *semilineatus* and *olssoni* are syntopic at a number of localities on the northern island (Hertz, in preparation), there is no reason to suggest that reciprocal invasions in either direction should have equal probabilities of success. *A. semilineatus* may have undergone an ecological shift as it invaded the northern island, thereby allowing sympatry with *olssoni*. But individuals of *olssoni* invading in the other direction may have been swamped by competition from the resident *semilineatus*. Clearly, we must know the ecology of both species in much greater detail before we can draw any firm conclusions about competitive patterns that may have shaped their current distributions.

The description of a third species of Hispaniolan grass anole does not provide us with a necessarily complete analysis of the systematics of the *semilineatus* species group. There are several issues about which I must withhold final judgment pending the collection of additional data. Although I feel that I can with some confidence align the holotype of *semilineatus* with series of specimens from the Pétionville area, I cannot confidently comment upon the systematic status of the grass anoles from the western portion of the southern island. The electrophoretic evidence tells us that populations of *semilineatus* near Pétionville probably have had recent gene exchange with or are derived from populations on the north island; data from other studies (Williams, 1963; Schwartz, 1974) suggest that faunal leakage in this part of the Cul-de-Sac Plain may, in fact, be a common phenomenon. In fact, the animals found near Pétionville may be directly derived from north island *semilineatus* and may not be conspecific with some other south island populations for which we have no electrophoretic data.

We cannot yet fully assess the possibility that north and south island populations of *semilineatus* differentiated after the *semilineatus* invasion of the north through the western end of the Cul-de-Sac. Pleistocene sea level rose and fell a number of times, reseparating and rejoining the two component islands of Hispaniola with each creation and recession of the seaway. If *semilineatus* invaded the north during an early oceanic recession, subsequent inundation of the low elevation plain may have split the range of *semilineatus* into two portions, allowing differentiation. North island animals may then have reinvaded the south near Pétionville and Furcy, and may be distinct from animals at the distal end of the Tiburon Peninsula. Electrophoretic data from *semilineatus* on the western end of the Tiburon Peninsula should clarify this point.

ACKNOWLEDGMENTS

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B R E V I O R A

Museum of Comparative Zoology

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CROCODILIANS FROM THE LATE TERTIARY OF NORTHWESTERN VENEZUELA: *MELANOSUCHUS FISHERI* SP. NOV.

CARMEN JULIA MEDINA[1]

ABSTRACT: *Melanosuchus fisheri* n. sp., the first fossil record of this alliga-torid genus, is based on two skulls from the Urumaco Formation of Huay-querian (Pliocene) age in the northern part of the State of Falcón, Venezuela. Relationships between *M. fisheri* and the living *M. niger* are uncertain. *M. fisheri* occurs together with five other crocodilian taxa of gigantic size. This assemblage and the numerous associated chelonians suggest that the Urumaco area in Huayquerian times may have borne some resemblance to the present Amazon basin.

RESUMEN: Se describe *Melanosuchus fisheri*, una nueva especie de un género aligatórido hasta ahora sin un registro fósil, basada sobre dos ejemplares coleccionados en la Formación Urumaco, de Edad Huayqueriense, en la parte norte del Estado Falcón, Venezuela.

During the summer of 1972, a paleontological expedition from the Museum of Comparative Zoology, in collaboration with the Escuela de Geología of the Universidad Central de Venezuela and the Ministerio de Minas e Hidrocarburos, worked in the vicinity of Urumaco, Distrito Democracia, Estado Fal-cón, northwestern Venezuela. A rather large number of verte-brate fossils, most of them reptiles, were collected in the Uru-maco Formation, of Huayquerian age (Pascual and Diaz de Gamero, 1969; for a definition of Huayquerian, see Pascual and Odreman, 1973). Among the crocodilian materials are two skulls, representing two growth stages of a species of caiman, that have strikingly large orbits, extending as far forward as maxillary tooth 10, and a palatal exposure of the vomer. These features (and others) occur, among living crocodilians (Wer-

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[1]Museo de Ciencias Naturales de Caracas

muth, 1953), only in the black caiman, *Melanosuchus niger* (Spix). The two specimens are beyond doubt referable to the genus, of which they constitute the first fossil record, and are specifically distinct from the living form.

Melanosuchus fisheri[1] sp. nov.

Type: Museo de Ciencias Naturales de Caracas No. 243, a skull lacking the pterygoids, parts of the ectopterygoids, palatines, jugals and premaxillaries, and parts of the left postfrontal and quadrate.

Hypodigm: The type and MCZ No. 4336, a skull — lacking the pterygoids, the left quadrate and quadratojugal, and parts of the basioccipital and left squamosal — and the posterior two-thirds of both rami of the mandible. Both specimens have suffered some distortion, and, as in much of the Urumaco material, the bone surfaces are poorly preserved.

Horizon: Upper part of the upper member of the Urumaco Formation in the "capa de huesos" or "tortugas" of the field geologists.

Localities: The type was found approximately $\frac{1}{2}$ km northwest of Campo El Mamón, east of the El Jebe fault; MCZ No. 4336 about 4 km northeast of El Mamón, some 20 m west of the Chiguaje fault. Campo El Mamón is 2.5 km north of Urumaco.

Diagnosis: Differing from *M. niger* as follows: skull more robust; snout deeper, heavier; posterior portion of maxilla wider; interorbital bar more arched anteroposteriorly, not concave above, thicker dorsoventrally; preorbital ridges on snout faint rather than strong; central portion of posterior border of cranial table transverse, not curved; palatine fenestrae shorter; 12 maxillary teeth, not 13–14, posterior ones larger; mandible heavier, thicker; external mandibular foramen not as deep. (For measurements see Table 1.)

Discussion: I have examined six skulls of *M. niger*, five in the American Museum of Natural History and one in the Museum of Comparative Zoology. The skull of this species has been well described by Mook, (1921), Kälin (1933), and Medem (1963). The last two authors figure and discuss growth stages, Kälin on the basis of 22 specimens ranging in occiput-snout

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[1]Named for Dr. Daniel C. Fisher, finder of both specimens. By an odd coincidence, the type was the first and MCZ 4336 the last specimen to be collected from the Urumaco Formation by the expedition.

length from 158.5 to 508 mm, Medem on 9 ranging from 99
to 466 mm. Kälin's series came from Isla Marajo, north-
eastern Brazil, Medem's from southern Colombia, thus nearly
from opposite extremes of the species range.

It can be stated with confidence that the diagnostic char-
acters of *M. fisheri* do not fall within the limits of individual
or geographic variation or of ontogenetic change in *M. niger*.
The degree of arching of the interorobital bar in the type
(MCZ 4336 is crushed down in this region) is not approached
even in the youngest specimen in Medem's series, and the depth
of the bar evidently does not increase, relatively, with age in the
living species. The concavity in the dorsal surface of this bar in
M. niger tends to become shallow, although not to the point of
disappearance, in large individuals, but in those comparable in
size to the two specimens of *M. fisheri* it is very well defined.
All specimens of the living species have very prominent ridges
on the snout (even the youngest shows some traces of them),
a conspicuous difference from the extinct form in which they
are very feebly expressed. The two last differences are asso-
ciated; the ridges on the snout of *M. niger* that run postero-
medially from the vicinity of maxillary tooth 4 merge with the
sides of the interorbital bar and contribute to its concavity. The
posterior border of the cranial table is quite or nearly transverse
in the youngest specimens of *M. niger* figured by Kälin and by
Medem, but it rapidly becomes curved anteriorly with advanc-
ing age, clearly differing from that of *M. fisheri*. In both speci-
mens of the extinct species the number of maxillary teeth can
be seen to be 12 in number, one or two less than in the living
form, with the posterior ones being larger. The skull of *M.
fisheri* is more robust than that of its relative, as is shown by the
more massive snout and posterior portion of the maxilla, the
heavier mandible, and the more solidly constructed interorbital
and ectopterygoid bars. The external mandibular foramen is as
long as that of *M. niger* but is decidedly shallower, with the
surangular in consequence being deeper. This feature and the
smaller size of the palatine fenestra are probably also associated
with the greater robustness of the skull of *M. fisheri*. For the
rest, the skulls of the two species are similar, the suture patterns,
to the extent that these can be determined in the fossils, being
essentially identical. The palatal portions of the vomers are
clearly visible in MCZ No. 4336 as small, irregularly rhomboidal
figures. The largest skull of *M. niger* recorded by Kalin is
508 mm in length. Whether or not *M. fisheri* attained to com-
parable size, or exceeded it, is of course uncertain.

Relationships between the two species must remain speculative for the present. As indicated above, nearly every character in which they differ is associated with the more robust skull of *M. fisheri*. If evolution within *Melanosuchus* proceeded in the direction of a lightening of the skull (in which case the more prominent ridges on the snout of *M. niger* could be interpreted as remnants of a previously more robust structure remaining along lines of stress) then an ancestor-descendant relationship would be likely. If not, the ancestor of the living species has yet to be found.

Melanosuchus fisheri occurs together with five other crocodilian species in the Urumaco Formation: *Dinosuchus terror* Gervais, *Mourasuchus amazonensis* Price, *Gryposuchus jessei* Gürich, *Ikanogavialis gameroi* Sill, and *Balanerodus?* sp. (Bryan Patterson, personal communication). *Ikanogavialis* is so far known only from the Urumaco. Of the others, none of which has hitherto been found in Venezuela, *Balanerodus* is known from the Miocene (Friasian) of Colombia (Langston, 1965) and the rest from the late Tertiary (Huayquerian?) of western Brazil. All are of very large to gigantic size. Compared to any of them *Melanosuchus fisheri*, even if it reached the dimensions of *M. niger*, was a pygmy. This crocodilian assemblage and the numerous chelonians associated with it suggest that the Urumaco area may at the time have had some resemblance to the Amazon basin, and bring some support to Wood and de Gamero's views (1971) concerning late Cenozoic geomorphologic changes in northwestern Venezuela.

Notes on the measurements (Table 1): Kälin's system of measuring (1931, fig. 1A) has been followed, but additional measurements, those of Medem and those that illustrate certain diagnostic features, are also given. Wherever possible Kälin's indices (1931: 536–8, 663–679) have been calculated. With one exception, these fall within or very close to his ranges for *M. niger* based on specimens 200 mm and over in skull length, the size at which adult proportions appear to be attained. The exception is snout length × 100/skull length (Kälin's No. 3), which is 51.21 in the type and 52.34 in MCZ 4336, well below the range, 57.20[1] to 68.80 (n 13) for the Brazilian sample of

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[1]Kälin lists an index of 47.70 for a skull 356.5 mm in length. Either this specimen is decidedly anomalous (with a snout relatively shorter than Medem's 99.0 mm long skull) or a printer's error has occurred; I suspect the latter.

M. niger. This is too great a difference to be attributable to the distortion of the fossils; the snout is shorter relative to skull length in *M. fisheri.* However, calculations of the index from Medem's measurements of specimens 200 mm and over show the Colombian sample (n 6) to range from 51.35 to 58.5 — thus on the whole shorter-snouted than the Brazilian — with the two fossils falling either just below or just within this.

I also give measurements of MCZ 4043, the skull of *M. niger* described by Mook, a specimen that has the advantage, from a comparative standpoint, of being close to MCZ 4336 in size. It was obtained by Louis Agassiz from "the Rio Madeira" (perhaps not far from its junction with the Amazon).

Figure 1. *Melanosuchus fisheri* sp. nov. MCZ 4336, ventral view of skull showing the vomers. × ½.

Figure 2. *Melanosuchus fisheri* sp. nov. MCZ 4336, ventral view of skull.
× ½. The apparently small size of the premaxillary foramen may be due
in part to some overlap of the two sides of the specimen in this area.
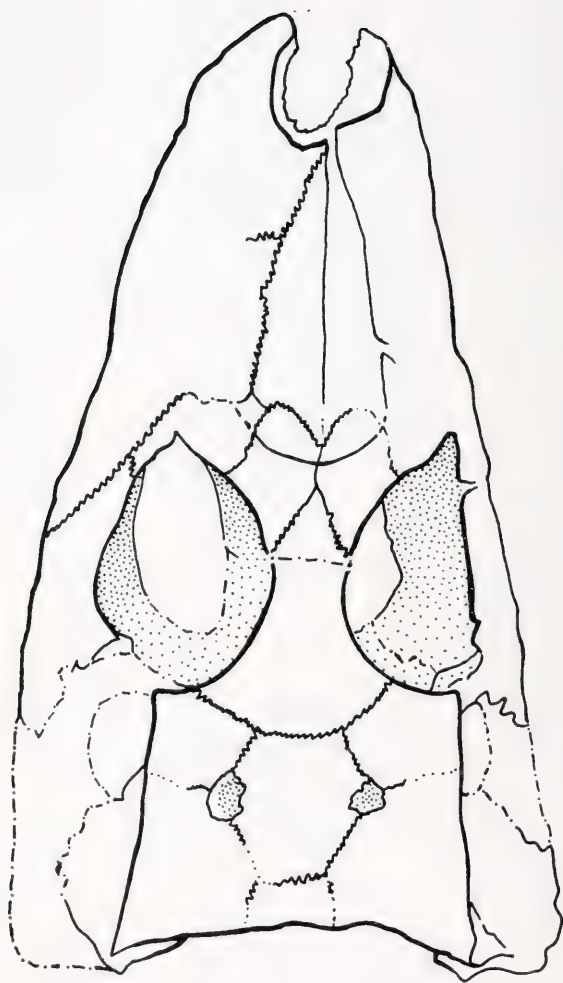
Figure 3. *Melanosuchus fisheri* sp. nov. Type, MCNC 243, dorsal view. × ½.

Figure 4. *Melanosuchus fisheri* sp. nov. Type, MCNC 243, dorsal view. $\times$ ½.

Figure 5. *Melanosuchus fisheri* sp. nov. Type, MCNC 243, left lateral view. × ½.
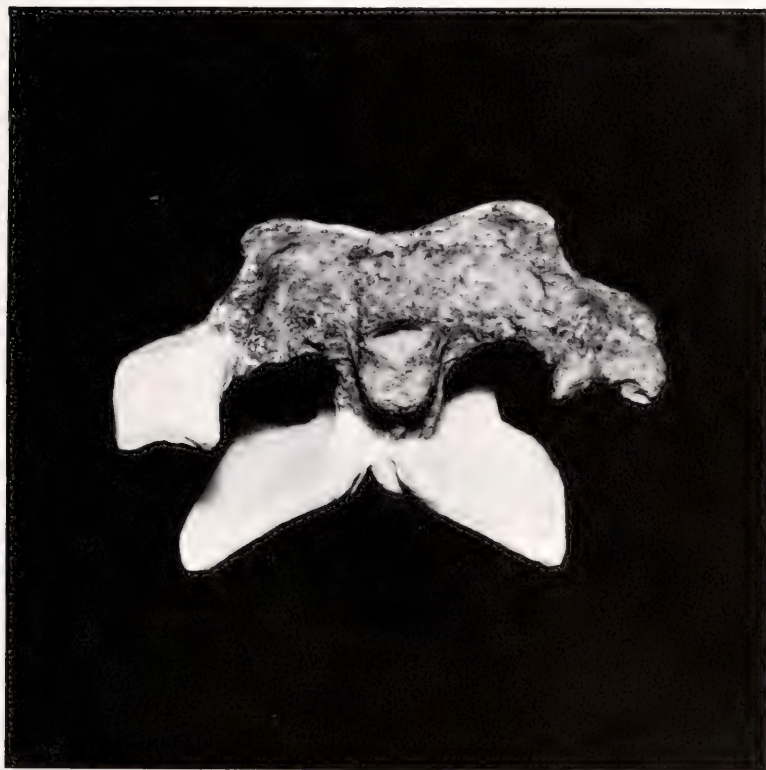
Figure 6. *Melanosuchus fisheri* sp. nov. Type, MCNC 243, occipital view.
× ½.

TABLE 1
Measurements in mm.

| | *M. fisheri* | | *M. niger* |
	MCNC 243	MCZ 4336	MCZ 4043
Skull.			
Length from condyle to tip of pmx.	240.0ca	—	347.0
Length from post. margin of cranial table to tip of pmx.	243.0ca	306.0	348.0
Length of ant. margin of orbit to tip of pmx.	127.0ca	157.0ca	194.0
Length of orbit	67.3	91.3	93.4
Length of palatine fenestra	—	56.5ca	81.3
Length of anterior narial aperture	—	37.0ca	35.9
Length of cranial table	48.3	54.9	55.0
Width of cranial table ant.	72.2	85.0	91.9
Width of cranial table post.	85.0	99.0ca	100.5
Width across quadratojugals	135.0ca	198.0ca	185.0
Width at level of postorbital bars	129.0ca	—	160.0
Width at level of ant. margins of orbits	—	—	153.0
Width at level of mx 4	95.0ca	131.0ca	129.3
Width at level of pmx 4	66.3	94.0ca	81.9
Width of palatine bar at center	—	31.0	27.1
Width of maxilla at palatal fenestra	26.2	35.1	24.9
Width of ectopterygoid bar	—	15.2	11.0
Length of ectopterygoid bar	—	24.5	21.1
Depth of snout between pmx. 3 and 4	—	37.0	30.2
Depth of snout between mx. 3 and 4	—	48.7	34.0

Table 1 (cont.)

Depth of interorbital bar	19.8	25.0	17.4
Width of interorbital bar	19.2	27.4	20.8
Width of condyle	21.4	—	24.8
Depth of condyle	14.4	—	18.0
Length of pmx. 4	7.6	12.0	11.1
Length of mx. 4	8.2	—	12.6
Length of mx. 9	7.8	12.0	11.0
Length of mx. 10	9.4	—	9.6
Length of mx. 11	9.0	15.0	8.3
Length of mx. 12	7.1	10.0	7.7
Mandible			
Width at ant. end of ext. mandibular foramen	—	31.0	22.4
Width of surangular above foramen	—	17.1	11.9
Depth of surangular above foramen	—	27.9	18.0
Width of angular below foramen	—	30.0	20.8
Length of external mandibular foramen	—	61.0ca	66.6
Depth of external mandibular foramen	—	28.6	33.3

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B R E V I O R A

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ON A NEW SPECIMEN OF THE LOWER CRETACEOUS THEROPOD DINOSAUR *DEINONYCHUS ANTIRRHOPUS*

JOHN H. OSTROM

ABSTRACT. A new specimen of *Deinonychus antirrhopus*, described here, provides morphological and dimensional data on skeletal elements missing in previously known specimens. Included are the femora, pubes, complete ilia and the sacrum. The pubis is normal in its morphology, but unusual in its length (more than twice that of the ischium) and orientation (apparently ventrad). The femur is shorter than the tibia and features an unusual "posterior trochanter" that may have been the attachment site of muscles that powered the offensive leg kick and use of the pedal talon.

INTRODUCTION

My original reports on the unusual theropod dinosaur *Deinonychus antirrhopus* (Ostrom, 1969a, 1969b) necessarily were incomplete because some skeletal elements were not then represented in collections. Specifically, much of the postorbital region of the skull was not known, nor were the femur, pubis or sacrum. These deficiencies now have been partially resolved thanks to the discovery in July, 1974 by a Harvard University expedition to Montana, of another specimen of *Deinonychus antirrhopus*. The purpose of this paper is to provide descriptions of the previously unknown elements that are provided by the new specimen, and to correct certain inaccuracies that were presented in my earlier studies of this remarkable species.

Abbreviations of institutional names cited herein are as follows:

   AMNH — American Museum of Natural History, New York City.

MCZ — Museum of Comparative Zoology, Harvard University.

YPM — Peabody Museum of Natural History, Yale University.

Materials: A partial skeleton (MCZ 4371, Field No. 74M #7) including fragments of the snout and mandibles with teeth, a nearly complete but poorly preserved vertebral series including the entire tail, the right forelimb and manus, fragments of the left manus, a complete pelvis and sacrum, both hind limbs and feet, and various rib and gastralia fragments; discovered by Steven Orzack and collected by F. A. Jenkins and party, July 1974.

Geologic and Locality Data: Upper part of Unit V (see Ostrom, 1970), otherwise known (in part) as the Little Sheep Mudstone Member of the Cloverly Formation (Moberly, 1960), Lower Cretaceous. The quarry site is situated 1 km south of
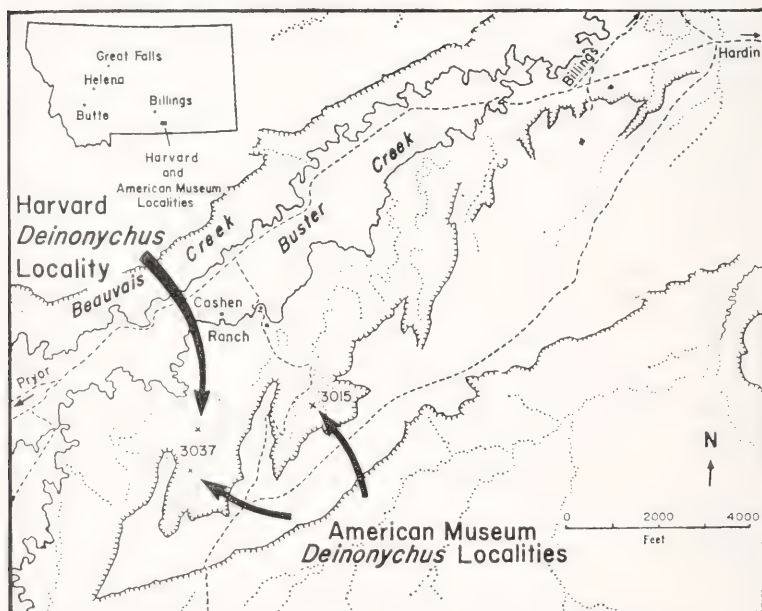
Fig. 1. Locality map showing the Harvard *Deinonychus* site, together with the previously known American Museum sites in southern Montana.
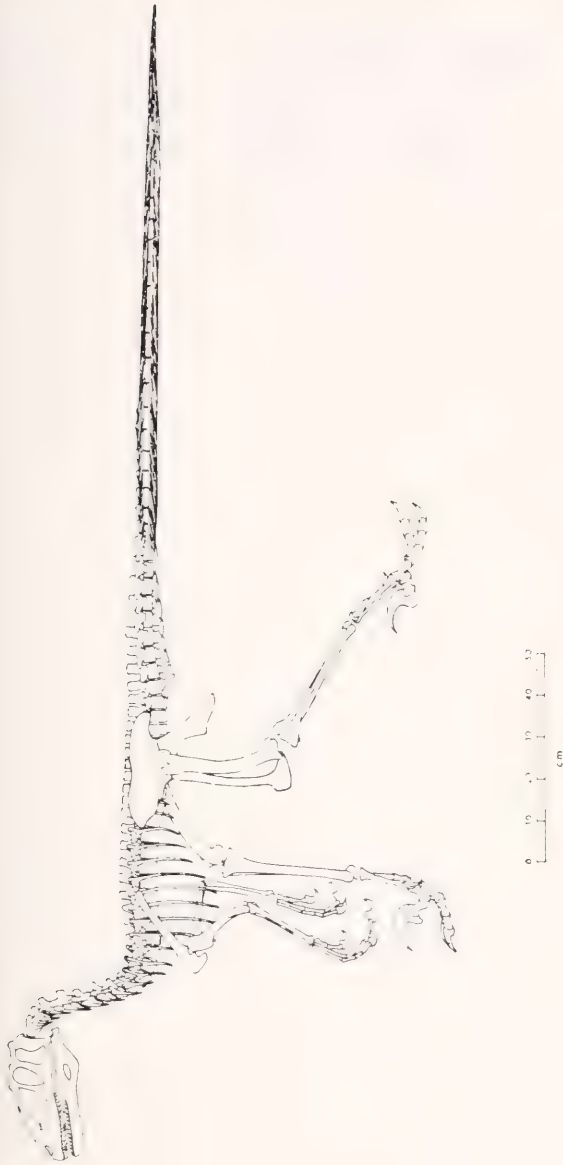
Fig. 2. Revised skeletal reconstruction of *Deinonychus antirrhopus.*

the Cashen Ranch house, NE ¼ Sec. 32, T. 4 S., R. 29 E., Big
Horn County, Montana. This site is within a few hundred
meters of the two American Museum *Deinonychus* sites (see
Fig. 1) reported previously (Ostrom, 1969b), and appears to
be at approximately the same stratigraphic level as that of
AMNH 3037. If my previous correlations (1969b, 1970) are
correct, this level is well below that of the Yale *Deinonychus*
Quarry near Bridger, Montana, which occurs in the lower part
of Unit VII (equals part of the Himes Member of the Cloverly
Formation as interpreted by Moberly, 1960).

DESCRIPTION

Excluding many isolated teeth of *Deinonychus* reported from
numerous Cloverly sites (Ostrom, 1970), the present specimen
brings the total minimum number of *Deinonychus* specimens to
six individuals. The collections from the Yale Bridger Quarry,
however, consist almost entirely of disarticulated remains that
may well include more than the three individuals represented by
the three articulated caudal series recovered there. As Table 1
shows, the new specimen is the largest of all presently known
specimens, and together with AMNH 3015 provides the first
evidence of growth patterns and allometry in this taxon. The
following descriptive material deals primarily with those skeletal
elements that were not known at the time of the earlier studies.
These include the femur, pubis and sacrum, and certain aspects
of the ilium, pes and metatarsus.

Femur: Contrary to my earlier guess, the femur of *Deinony-
chus* is shorter than the tibia by about 10 per cent. This is not
an unusual difference, nor is it unusual for the tibia to exceed
the femur length in theropods. But this new fact does require a
reassessment of my earlier interpretation about the cursorial
capacity of *Deinonychus* — a reassessment that will be discussed
briefly later.

The femur of *Deinonychus* is moderately robust, with a slight
antero-posterior curvature and of hollow construction (Fig. 3).
The head is sharply offset medially from the shaft by means of
a stout but distinct neck. The axis of the neck projects trans-
versely (parallel to the plane formed by the distal condyles) at
about 100 degrees to the femoral shaft. The head is roughly
ovoid and broadly convex, but with a slightly flattened area
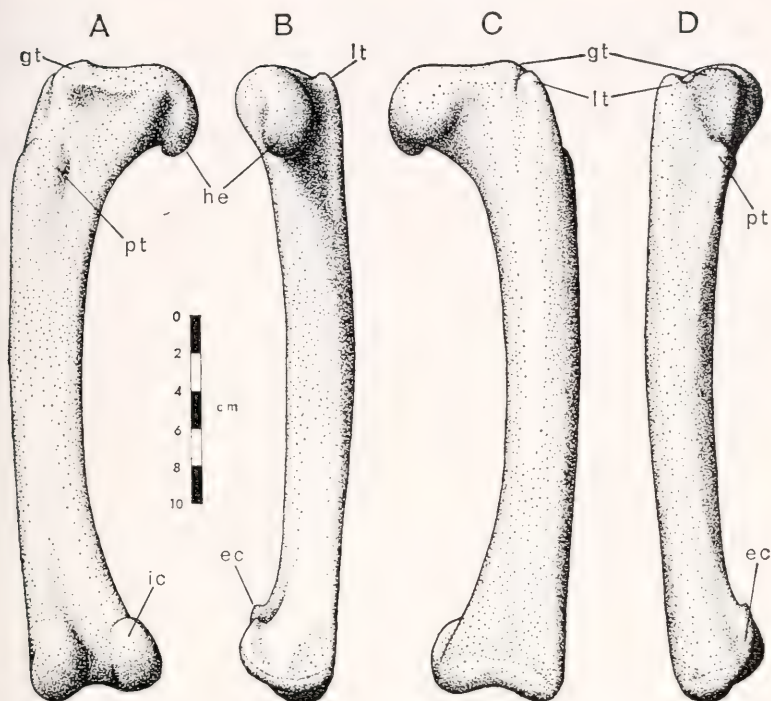
Fig. 3. Left femur (restored) of *Deinonychus antirrhopus* (MCZ 4371) in posterior (A), medial (B), anterior (C), and lateral (D) views. Abbreviations: ec — external condyle; gt — greater trochanter; he — head; ic — internal condyle; lt — lesser trochanter; pt — posterior trochanter.

anterodorsally and with a distinct proximal posterorinferior lip or overhang that sets the head off from the inferior region of the neck. Externally, the neck expands dorsally into a large "greater trochanter," which presumably marks the attachment site of the M. iliotrochantericus. External and slightly anterior to this feature is a robust, but not large, "lesser trochanter" (anterior trochanter of some authors). Unlike some theropods (i.e., *Allosaurus*), this last structure is separated from the "greater trochanter" by only a narrow shallow groove rather than by a deep cleft. The "lesser trochanter" of theropods is generally considered as the insertion site of the M. ilio femoralis.

Distal to these "trochanters" and posterior to the "lesser tro-chanter," is a distinct prominence or boss which projects latero-posteriorly. Similar, but much less prominent features occur on many other theropod femora, but it has received little or no attention and has not been given a formal designation. In this paper, for lack of a better term, it is referred to as the "posterior trochanter." Its significance is not known, but it is situated in the general region where we might expect the M. ischiotro-chantericus (= M. ischiofemoralis of birds?) to insert. More will be said of this later.

The uncrushed portions (near midlength) of the shaft are nearly circular in section with a minimum transverse diameter of approximately 38 mm and an anteroposterior diameter of about 32 mm. Dimensions increase slightly toward both ends. Surprisingly, no recognizable fourth trochanter is preserved in either femur, nor is there any discernible scar indicating the insertion site of the M. caudifemoralis. Distally, the condyles are well developed and sharply separated in posterior (ventral) aspect by a deep intercondylar groove. The external condyle is nearly twice as large (both proximodistally and in anteropos-terior dimension) as the internal condyle. Femoral and other dimensions are given in Table I.

Pubis: Perhaps the most important aspect of the new speci-men is the presence of both pubes. In my original study of *Deinonychus* (Ostrom, 1969b), I tentatively but incorrectly identified an isolated bone of curious shape as a right pubis, chiefly because it was found in the quarry immediately adjacent to a right ischium of about the same length. Subsequently I became convinced that it could not possibly be a pubis and after further study concluded that it was a right coracoid of unusually large size (Ostrom, 1974).

The pubes of *Deinonychus* are of normal theropod design (Fig. 4), but of surprising length relative to the short length of the ischium. In fact, the pubis is more than double the length of the ischium, a condition that is unique among thero-pods. Although crushed in some regions, the major features are all discernible. The proximal end is moderately stout, but the actual articular surfaces for contact with the robust pubic pe-duncle of the ilium and the thinner peduncle of the ischium are not recognizable. There appears to have been a shallow obtu-rator notch immediately adjacent to the ischial suture, as shown
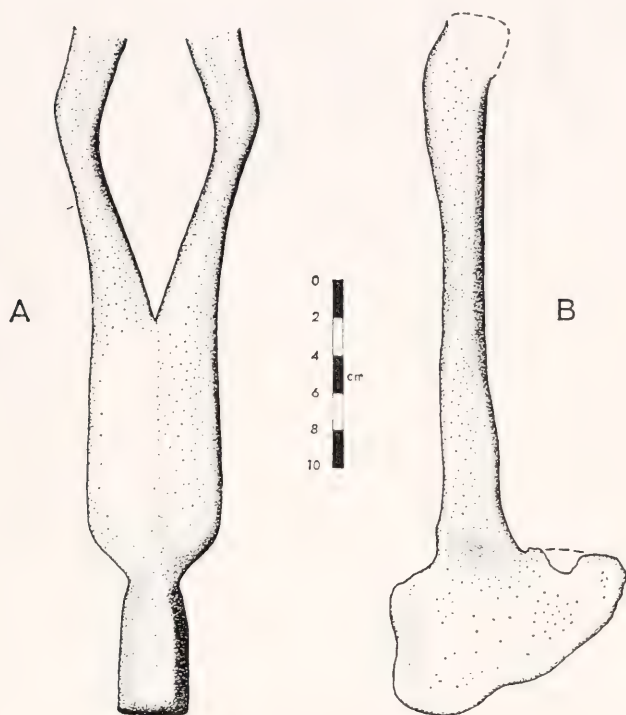
Fig. 4. Pubes (restored) of *Deinonychus antirrhopus* (MCZ 4371) in anterior (A) and left lateral (B) views.

by remnants on the left side. The pubic shafts are oval in section, with the greatest diameter in the transverse direction. Just short of mid-length, the shafts expand medially and the two pubes join in a massive symphysis that measures 210 mm, or more than half the total pubic length. Over most of the symphysial length, the pubes are quite broad, forming a transverse apron of 60 to 67 mm width. The distal extremity contrarily is narrow transversely, but expanded longitudinally into the typical theropod "footlike" structure. This pubic "foot" is approximately 135 mm long (anteroposteriorly), but only 35 mm in its maximum preserved width.

There is no doubt any longer about the form of the pubis, but doubts still exist about the *in vivo* position of the pubes (and

perhaps of the ischia as well) because of the manner in which the new specimen is preserved. The animal was buried lying on its ventrum, with the pubes pushed up and backward, tightly pressed against the ischia and the underside of the tail, and oriented parallel to the proximal caudals and the axis of the sacrum. The fact that *both* the pubes and the ischia are preserved tightly pressed together and directed *backward* suggests that in life these two bones may not have been arranged as divergently as in most other theropods. It further suggests that the pubes may have been oriented nearly perpendicular to the sacral axis, or perhaps even slightly posterior to that perpendicular. In the revised skeletal reconstruction (Fig. 2), I have so oriented the pubes at right angles to the long axis of the ilium and the sacrum.

Ilium: Prior to the discovery of the Harvard specimen, only one incompletely preserved ilium (AMNH 3015) was known of *Deinonychus.* Fortunately, both ilia are preserved in MCZ 4371, and a more accurate description is now possible. Unexpectedly, the ilium turns out to be much longer than I concluded from the American Museum specimen, with both extremities tapered or triangular, rather than rectangular in outline. In lateral aspect, the iliac blade is long, quite low, and with nearly uniform height throughout, except at the extremities. The anterior process is longer than the posterior process, as measured from the center of the acetabulum. Except for the tapered extremities, the long low profile and the off-
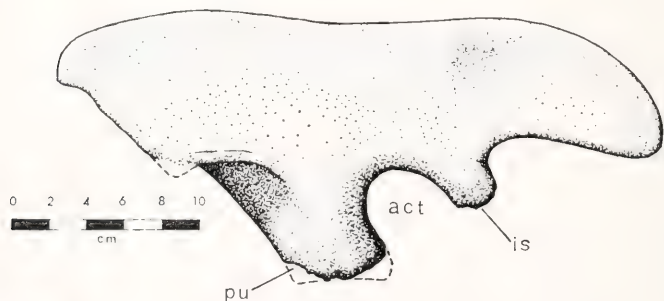
Fig. 5. Left ilium (restored) of *Deinonychus antirrhopus* (MCZ 4371) in lateral view. Abbreviations: act — acetabulum; is — ischiac peduncle; pu — pubic peduncle.

center position of the acetabulum resemble the conditions of coelurosaurs in general, and those of ornithomimids in particular.

As was noted in my earlier description of the American Museum ilium, the pubic peduncle is much more massive and longer than the ischiac peduncle, and, perhaps more important, it is directed downward and *backward,* rather than down and forward. The significance of this unusual orientation was not recognized then, but now in the light of the preserved position of the pubes in MCZ 4371, it seems reasonable to equate this with a possible ventrad or ventroposterior orientation of the pubes. Figure 6 shows my best estimate of the pelvic arrangement in *Deinonychus,* compared with *Struthiomimus* and *Tyrannosaurus.*

Ischium: Although both ischia are present in MCZ 4371, they add little to our knowledge of ischial morphology beyond that which was provided by previous specimens. However, the
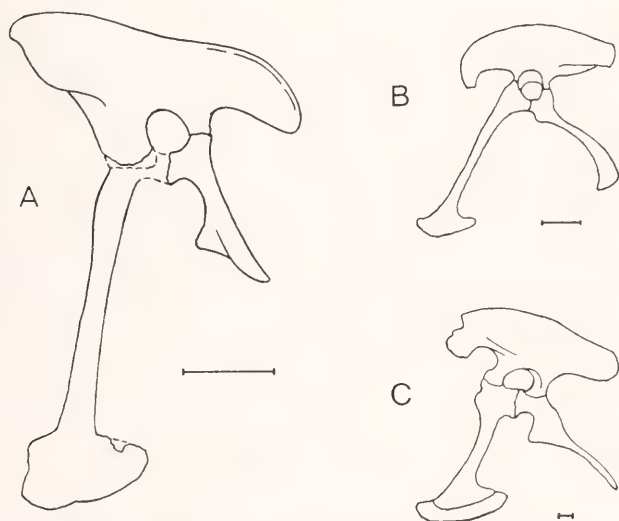
Fig. 6. Comparison of the pelves (lateral views) of *Deinonychus,* MCZ 4371, (A); *Struthiomimus,* AMNH 5339, (B); and *Tyrannosaurus,* AMNH 5027, (C); to show the unusually disproportionate lengths of the pubis and ischium in *Deinonychus.* The scale lines equal 10 cm.

new specimen does establish that the ischia were united at their distal extremities by a well-developed symphysis. Whether the symphysis extended proximally to the level of the obturator flange, as I suggested previously (Ostrom, 1969b) on the basis of the surface texture of that process, cannot be established here. The anterior ischial surfaces are concealed by the broad pubic apron, which has been crushed against the ischia, and the posterior surfaces likewise are covered by the proximal caudal vertebrae that were pressed down against them.

Sacrum: The sacral series, absent in previously known specimens, is difficult to decipher because the anterior portion is incomplete and the full dorsal vertebral count is not known in MCZ 4371. On the basis of the degree of co-ossification and the form of the sacral ribs, I conclude that the sacrum consisted of five segments in which the centra and neural spines were fused together. A sixth centrum, presumably representing the last dorsal, seems to be fused to the first sacral. This segment, and the one behind it, has relatively weakly developed sacral ribs or transverse processes as compared with those of the following segments, but these anterior segments seem to have had firm articulation with the anterior processes of the ilia. On that basis, both might be considered as dorsal, rather than sacral vertebrae.

Pes: Both feet and metatarsi are well preserved and apparently complete in the new specimen, offering verification of most of my original interpretations, but also providing a few new details. The new specimen suggests that the first metatarsal probably consisted of a distal portion only, rather than separated distal and proximal moieties. There is no evidence in either foot (both of which are otherwise complete) of a proximal portion of metatarsal I, as I suggested earlier (1969b, fig. 72). Since both feet and metatarsi in this specimen were preserved fully articulated, it seems unlikely that this particular element should be accidentally missing in both.

Also, as preserved in MCZ 4371, the first digit may not have been reverted to the rear as far as I originally restored it (1969b, Fig. 74). However, since the first metatarsal was not fused to the second, and appears to have been ligamentously joined to the metatarsus, its preserved position (in the absence of any clear appositional scar) may or may not approximate the natural position in life.
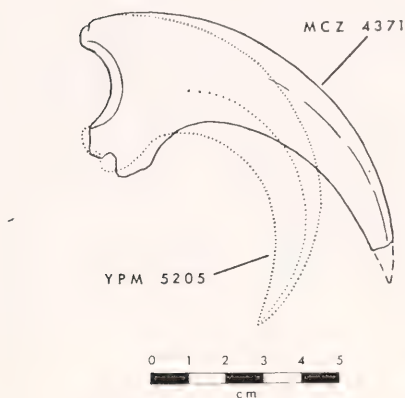
Fig. 7. Contrasting morphology of the second pedal ungual in the type specimen of *Deinonychus* (YPM 5205) and the new Harvard specimen.

One final observation that pertains to the distinctive *"Deinonychus"* character preserved in the new specimen: that is the very different geometry of the foot talon. As Figure 7 shows, the claw in the type specimen (YPM 5205) is much more strongly curved than is that of MCZ 4371. Preservation of the type ungual is virtually perfect with no distortion or crushing and only a few small fragments missing. That is not true of the new specimen, but what distortion is apparent here does not seem to account for the conspicuous difference in shape. Barring preservational distortion, the difference could be due to individual, ontogenetic, or sexual variation. At this point, I have no opinion on the correct explanation, but simply report the difference.

DISCUSSION

In my original study (1969b) of *Deinonychus*, I assumed equal lengths for the femur and tibia, in the absence of any knowledge about the femur. The new specimen shows that the femur is shorter (approximately 90 per cent of tibia length) than I had thought and thus is similar to *Struthiomimus*. This might indicate higher running speeds than I suggested in that

study ("moderately, but not unusually fast"). However, more important than femur/tibia ratio as an index of cursorial velocity, is the length of the metatarsus relative to the tibia. In the American Museum specimen (3015) of *Deinonychus*, this ratio is a surprisingly low .48. In MCZ 4371, it is .45. These values are well below those of any other theropod now known, and when compared with those of such well-known fast-running birds as *Struthio* (.95), *Dromaius* (.96) and *Casuarius* (.85) (where the femur is only about half as long as the tibia) and the presumed fleet-footed *Struthiomimus* (.68), the only reasonable conclusion is that *Deinonychus* was not the most fleet-footed of theropods.

This conclusion is reinforced by other data revealed by the new specimen. MCZ 4371 is a larger individual than AMNH 3015, but not uniformly so. The forelimb is 20 per cent longer in MCZ 4371 and the tibia 18 per cent longer, but the metatarsus is only 12 per cent longer than in AMNH 3015. If the above similar tibia and forelimb values represent an overall average difference in size between these two individuals, then metatarsal growth did not keep pace during ontogeny with the growth of other long bones. The metatarsal fraction of total hind limb length diminished with age, suggesting a corresponding decline in cursorial ability. At the time of my earlier study, I was puzzled by the relative brevity of the metatarsus, but suggested that its unusually short length may have been correlated with the specialized offensive claw of the second toe. I am still of that opinion, especially in view of the apparent ontogenetic decline in relative metatarsal length revealed by the Harvard and American Museum specimens.

The design and orientation of the sicklelike claw on digit II show that the offensive or damaging stroke of this weapon was flexion — a strong backward thrust of the claw and toe. This probably was coordinated with a powerful backward kick of the entire hind leg. This means that the combined power of all the hind limb retractor muscles (those that are usually involved in the locomotory power stroke) may have contributed to the action of this unusual and presumably lethal device. Considering the size and shape of the pedal talon, it is very likely that the toe and the metatarsus were subjected to considerable extensional and shear stresses when this weapon was employed — possibly much higher stresses than usual during normal loco-

motory action of the foot and leg[1]. If so, what were the principal muscles available to counteract such stresses in these regions? Presumably, they were the equivalents of the M. gastrocnemius and the digital flexors (particularly the M. flexor perferans et perforatus digiti II and M. flexor perforatus digiti II) of modern birds. As the primary flexor of the ankle, the gastrocnemius is the chief muscle available to oppose extensional stresses applied to the metatarsus and the foot. But as the chief ankle flexor, the mechanical requirements of the gastrocnemius dictate a proximal insertion on the posterior surfaces of the metatarsus. This arrangement, with its extremely short lever arm, provides little or no added strength to the metatarsal shafts against hyperextension or fracture. However, a shortened metatarsus would reduce the length of the resistant (hyperextensional) lever arm and thus can be considered as an adaptation to minimize the possibility of metatarsal hyperextension or fracture. This explanation is further supported by the fact that there is no positive evidence of an enlarged or particularly powerful "gastrocnemius." There are no tubercles evident on the femur distal extremity that might be the origin sites of such a muscle, and there is no hypotarsus-like structure, or any other evidence of muscle scars, on the proximal posterior surfaces of the metatarsals.

Speculative though the above interpretations may be, they are further supported by a comparison of hind limb proportions in *Deinonychus* with those of both cursorial (*Struthiomimus*) and graviportal (*Tyrannosaurus*) theropods (see Fig. 8). The propodial — epipodial proportions of *Deinonychus* resemble those of *Struthiomimus*, but the metapodial — pes proportions resemble those of *Tyrannosaurus* (although not as massive). In the latter, the short metatarsus can be viewed as related to the great weight-bearing (and shear stress) problems in *Tyrannosaurus* (estimated live weight, 7,000 kg). In *Deinonychus*, however, any excessive shear stresses across the metatarsus must have

[1]It is interesting that the Yale *Deinonychus* collection includes a damaged second phalanx of digit II which was fractured and healed during the animal's lifetime. The broken extremities were displaced transversely and mended in this position, but perfectly aligned longitudinally. The longitudinal alignment apparently allowed the claw to function normally after healing, with only a sideways displacement of the arc of claw flexion. This specimen clearly indicates that the talon-bearing toe of *Deinonychus* was subject to intense stress.
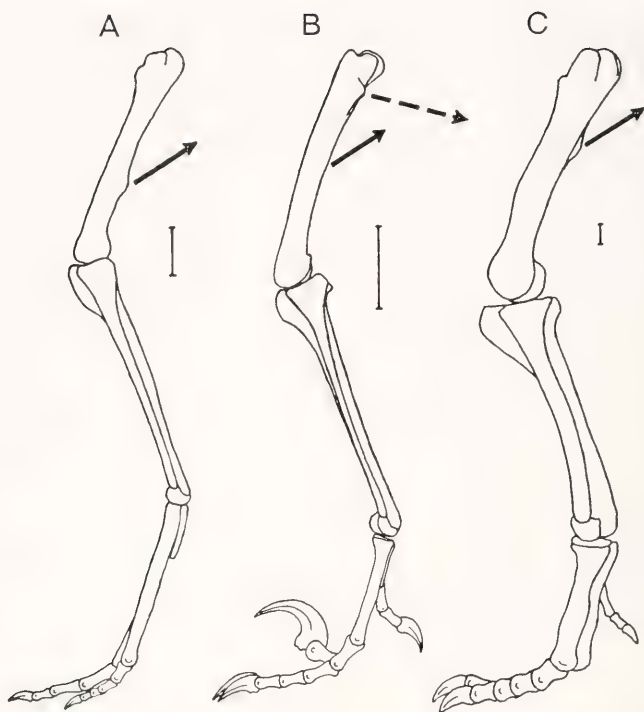
Fig. 8. Comparison of hind limb proportions in *Struthio-mimus*, AMNH 5339, (A); *Deinonychus*, MCZ 4371, (B); and *Tyrannosaurus*, AMNH 5027, (C). Notice that the prox-imal elements of *Deinonychus* resemble those of cursorial *Struthiomimus*, but the distal proportions are more like those of graviportal *Tyrannosaurus*. The solid arrows indicate the loca-tion and approximate orientation of the chief locomotory mus-cle, the M. caudi-femoralis. The dashed arrow (B) indicates the possible position of the M. ischio-trochantericus, a second-ary femoral retractor which may have powered the offensive leg stroke. Scale lines equal 10 cm.

been derived from sources other than weight (which is estimated at less than 75 kg). Use of the foot talon against a larger prey animal might well have resulted in high stresses across the metatarsus, thereby favoring a shortened metapodial component. That could account for the peculiar distal proportions combined with the otherwise "cursorial" design of the tibia and femur.

The above observations lead to one further speculation about the hind limb of *Deinonychus* and its probable actions. As noted in the descriptive section, there is a well-developed prominence (referred to here as the posterior trochanter) on the outer posterior proximal surface of the femur just distal to the "greater trochanter." This feature is present in many other theropods, where it is far less prominent, but as far as I am aware, it has not received any particular attention or interpretation. Even though any analogy here with modern birds may be questionable, it is interesting to note that a bony prominence also occurs in this same region in many modern birds. This avian feature is the site of insertion of the M. ischio-femoralis (= the M. ischio-trochantericus of reptiles), one of the major retractors of the hind leg. Traditionally, the M. caudi-femoralis is considered the principal femoral retractor in modern reptiles (and especially in the extinct bipedal theropods and ornithopods), providing most of the stride power. The M. caudi-femoralis inserts on the fourth trochanter, or on a conspicuous scar near midshaft of the femur. This insertion site is well developed in virtually all reptiles, and particularly so in all theropods. The absence of a fourth trochanter in *Deinonychus*, or of any recognizable scar that can be equated with the caudi-femoralis, is a curious anomaly that I am unable to explain.

I am not suggesting that the M. caudi-femoralis was absent, or even reduced, or that the M. ischio-trochantericus (with its lesser leverage) had assumed part or all of the locomotory function of that muscle. Rather, I wonder if the unusual prominence of the "posterior trochanter" here may not be related to the special predatory foot adaptations in *Deinonychus* which obviously were designed for application in a backward "killing" stroke — a motion quite separate and (perhaps necessarily) independent of limb movements concerned with locomotion. Turning our attention to another unusual feature of *Deinonychus*, recall the extraordinary brevity of the ischium and the proximal placement of the obturator flange — a possible origin site of the M. ischio-trochantericus. I cannot help wondering

about the possible connection between these three unusual features of *Deinonychus:* the offensive foot talon; the abbreviated ischium with a proximally situated obturator flange; and the prominent posterior trochanter of the femur. The last two features could well have been the origin and insertion sites of the ischio-trochantericus, which could have powered the *offensive* backward stroke of the hind leg, as opposed to the backward *locomotory* power stroke of the leg. The locomotory power stroke almost certainly was produced by contraction of the caudi-femoralis, despite the apparent absence of an insertion scar or a fourth trochanter.

Why should the offensive backward stroke of the femur be powered by a different set of muscles from the more usual locomotory stroke? Perhaps the answer lies in the fact that the most important locomotory muscle of the reptilian hind leg is the M. caudi-femoralis, which originates on the proximal caudal vertebrae — an origin site which is *not* immovably fixed, and which also is the power base of the tail. The tail obviously is the critical balancing appendage, especially in bipedal reptiles (both obligate and facultative). Bipedal progression and dynamic balance must be coordinated, so it is not surprising that it is the locomotory musculature (M. caudi-femoralis) that is involved with both the propulsive leg stroke and the balancing actions of the tail. On the other hand, the same kind of linkage between the mobile balancing appendage and an *offensive* stroke of the hind leg might be counterproductive. Precise equilibration during any offensive leg stroke would be absolutely essential for an accurate and effective killing stroke, but if the same muscles contributed both to movements of the balancing tail and the offensive leg kick during an aggressive encounter, then the two actions could not be produced independently. Precision of both movements would be seriously impaired. If muscle contractions powering the offensive leg stroke also produced deflection of the balancing tail, or vice versa, one could well be detrimental to the other. Thus it seems logical to conclude that the musculature that powered one action must have been freed as much as possible from producing or contributing to the other action. The M. caudi-femoralis, as it is organized in modern reptiles, cannot meet this requirement. A femoral retractor that does satisfy this constraint, though, is the M. ischio-trochantericus with its *immobile* origin on the ischium, rather than the tail.

SUMMARY

There are no absolute explanations of fossil evidence. The preceding discussion has been offered only as possible reasons for the combination of unusual osteological characters that are peculiar to *Deinonychus* and other dromaeosaurid theropods (*Dromaeosaurus, Velociraptor, Saurornithoides, Stenonychosaurus*). These features are: 1) the sicklelike claw of the second toe; 2) the short metatarsus; 3) a prominent posterior trochanter; 4) a long pubis and an unusually short ischium with a proximally placed obturator flange; and 5) an unusual caudal series with extensive ossified tendons. The foot clearly functioned both for locomotion and as a predatory weapon. In that light, the hind limb proportions seem best explained as a compromise between high cursorial requirements (femur/tibia ratio) of a predator and the need for a strong metatarsal foundation for the foot weapon. The short ischium and prominent posterior trochanter are interpreted as the probable attachment sites of the offensive leg musculature (M. ischio-trochantericus), and the unusual caudal tendons (absent in non-dromaeosaurid theropods) reflect the extreme equilibration requirements of *Deinonychus* and its allies.

ACKNOWLEDGEMENTS

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Table I

Comparative Measurements of *Deinonychus* Specimens

	MCZ 4371	AMNH 3015	YPM 5235
Ilium			
Length	325 mm	245* mm	
Length anterior to acetabulum	165 mm	100* mm	
Length posterior to acetabulum	110 mm	80* mm	
Height above acetabulum	80 mm	72 mm	
Ischium			
Length	175 mm	161* mm	161 mm
Pubis			
Length	380 + mm	—	
Maximum transverse width of apron	67 mm	—	
Symphysis length	210 mm	—	
Length of distal "foot"	134 mm	—	
Width of distal "foot"	35 mm	—	
Femur			
Length	336 mm	—	
Distal width	70 mm	—	
Proximal width	85 + mm	—	
Least shaft diameter	31.6 mm	—	

	MCZ 4371	AMNH 3015	YPM 5240	YPM 5205
Tibia				
Length	368 mm	312 mm		
Length with astragalus	382 mm	324 mm		
Distal width	72.7 mm	63.3 mm		
Proximal width	59 mm	44.8 mm		
Least shaft diameter	28.5 mm	18 mm		
Maximum proximal dimension	83.5 mm	74 mm		
Metatarsal I length	45.6 mm	—	45.5 mm	
Metatarsal II length	144.3 mm	129 mm	—	134 mm
Metatarsal III length	164.4 mm	151* mm	—	150* mm
Metatarsal IV length	150.4 mm	134 mm		141 mm
Metatarsal V length	78 mm	>34 mm		53.3? mm
Phalanges (Pes)				
I^1 Length	34.8 mm	—		32.9 mm
I^2 Length along outer curve	48 mm	—		>47 mm
II^1 Length	47 mm	37.7 mm		43.5 mm
II^2 Length	49.9 mm	42.2 mm		49.6 mm
II^3 Length along outer curve	>118 mm	>85 mm		>122 mm
III^1 Length	64.4 mm	52.5 mm		59.4 mm
III^2 Length	44 mm	33 mm		39.9 mm
III^3 Length	41.3 mm	28 mm		37.6 mm
III^4 Length along outer curve	>75 mm	>50 mm		>67 mm

Table I — *Continued*

	MCZ 4371	AMNH 3015	YPM 5240	YPM 5205
Phalanges (Pes) — *Continued*				
IV¹ Length	55.5 mm	44.7 mm	—	50 mm
IV² Length	41.8 mm	35.9 mm	—	36 mm
IV³ Length	35.2 mm	32.2 mm	—	30.6 mm
IV⁴ Length	32.6 mm	26.3 mm	—	28.7 mm
IV⁵ Length along outer curve	>60 mm	>42 mm	—	>55 mm
Humerus				
Length	254 mm	237* mm		
Distal transverse width	51 mm	42.1 mm		
Proximal transverse width	53.8 mm	41* mm		
Width across deltopectoral crest	—	43.5 mm		
Least diameter of shaft	21 mm	18.2 mm		

	MCZ 4371	AMNH 3015	YPM 5220	YPM 5206
Ulna				
Length	208 mm	186 mm	180 mm	
Distal transverse width	35.8 mm	32 mm	30 mm	
Proximal transverse width	34.4 mm	31.2 mm	29 mm	
Least diameter of shaft	13.7 mm	11.8 mm	10.9 mm	

Radius			
Length	192 mm	172* mm	172 mm
Distal transverse width	26.8 mm	23.8 mm	21.4 mm
Proximal transverse width	18.1 mm	20.6 mm	20.2 mm
Least diameter of shaft	10.3 mm	10 mm	9 mm
Metacarpal I length	—	35.5 mm	45.8 mm
Metacarpal II length	>90 mm	—	93.7 mm
Metacarpal III length	90* mm	73.4 mm	82 mm
Phalanges (Manus)			
I^1 Length	77.3 mm	—	74.1 mm
I^2 Length along outer curve	>100 mm	80* mm	>95 mm
II^1 Length	64.2 mm	62.2 mm	54 mm
II^2 Length	83.4 mm	70.7 mm	76.5 mm
II^3 Length along outer curve	>105 mm	—	>80 mm
III^1 Length	35 mm	21.7 mm	29.9 mm
III^2 Length	23.2 mm	15.5* mm	20.5 mm
III^3 Length	—	47.3 mm	—
III^4 Length along outer curve	—	—	>54 mm

* = approximate dimension

B R E V I O R A

Museum of Comparative Zoology

WEST INDIAN ANOLES: A TAXONOMIC
AND EVOLUTIONARY SUMMARY
1. INTRODUCTION AND A SPECIES LIST

ERNEST E. WILLIAMS[1]

ABSTRACT. Accumulation of morphological, karyological and ecological data on West Indian anoline lizards permits and requires a taxonomic analysis more elaborate than usual and employing both formal and informal taxonomic categories. The categories are defined in this, the first paper of a series, and a species list of West Indian anolines displays the new arrangement.

INTRODUCTION

Since the pioneer study by Etheridge (1960) there has been a remarkable growth both in our factual knowledge and in the sophistication of our knowledge of one group of lizards — the anolines. This has been especially true in the islands of the West Indies. The mainland members have at the same time received less attention and have proved more refractory. (Certainly the latter fact has influenced the first.)

There is, however, nowhere any gathering together of the new knowledge. Partly this results from the continuing activity. Not even species lists have remained constant. A statement that Cuba or Hispaniola has x species is outdated before it is published. In the same way ecological information, ideas and theory have expanded far past the published record. It is not easy to keep on top of the field.

Just because of this it is necessary that beginnings of a summary be made. Both for old hands and for newcomers an exposition of how far we've come, where we are, and where

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we might go will be a useful thing. I propose as a first step a taxonomic-evolutionary summary. The summary is inevitably provisional and, more than that, intended to promote research, provoke criticism and encourage the search for further evidence and the endeavor for greater understanding.

My objective has been to illuminate ecology and evolution. The taxonomic study I will here provide is one means to that end. The West Indian anoles are a group of enormous diversity, but the interest of this diversity is not in its bare existence but in its structure and origin — its balance, the interlocking of its parts and the historical paths by which this was achieved.

This is no simple radiation — not just the checkerboard subdivision of some original widespread unit. Here the severed units have doubled back upon one another and are completely layered, juxtaposed and interdigitated. The fitting together of so many species is the problem.

Such complexity involves several levels. One such level is generic. In the West Indies I recognize three very distinct genera, two genera autochthonous and old, species-poor and obviously relict, one genus species-rich beyond ordinary imagining, a colonizing and expanding group, a newer invader from the mainlands that adjoin the West Indies to the west and south. The latter is, of course, the group, as full of problems as of interest, that must receive the maximal attention it deserves.

In point of fact, there are few problems for the two old species-poor genera, but also little information.

One of these two genera, *Chamaeleolis*, is represented by two giant casque-headed arboreal species on Cuba which much resemble the tree-crown giants of the *Anolis equestris* group with which they share the island (Garrido and Schwartz, 1968). The species of *Chamaeleolis*, however, are more primitive osteologically, more chameleon-like in movement and appearance and apparently rarer than giant *Anolis*.

The other of the genera, *Chamaelinorops*, initially erroneously reported from the tiny mile-square island of Navassa, west of southwestern Hispaniola, is, in fact, from the south island of Hispaniola, dwarf, ground-dwelling and extremely peculiar osteologically. Richard Thomas (1966) recognizes only a single species.

Chamaeleolis and *Chamaelinorops*, except that they are true anoles sharing the characteristic adhesive pads of *Anolis* and the typical *Anolis* dewlap, are not close to each other nor to

Anolis. Their greatest interest lies in the possibility that they may represent an early (pre-Miocene ?) invasion of the Greater Antilles and may be relics of an earlier island radiation of which we otherwise know nothing.

The three species just mentioned apart, the remaining anolines of the West Indies are here regarded as belonging to the genus *Anolis.* Fortunately this overlarge taxon divides naturally, as Etheridge showed in 1960, into two sections called by Etheridge alpha and beta. Though this is a dichotomy based on an apparently trivial character, it makes excellent geographic sense. Savage (1973) has suggested that, instead of two sections, two genera be recognized — *Anolis* Daudin (type *Anolis carolinensis* Voigt) and *Norops* Wagler (type *Anolis auratus* Daudin). This would substitute formal designations for the currently informal ones but it would leave no formal (or informal) term for the two sections (or genera) taken together. Savage's action is well taken if alpha *Anolis* are closer to *Chamaeleolis* and *Phenacosaurus* than to beta *Anolis* or the betas are closer to *Chamaelinorops* than to the alphas. This is a point I regard as at least doubtful, preferring to leave it in decent obscurity until there is more and better evidence. My own suggested phylogeny for anolines would have the alpha anoles the more primitive (as they certainly are in many respects), and the beta type of caudal transverse process (which does not resemble those of other iguanids or of other lizard groups) arising secondarily, but only once, from the alpha condition in which the transverse process is absent. The transverse processes of *Chamaelinorops* have only a verbal similarity to those of beta anoles; I question the closeness of the relationship. Richard Etheridge would disagree with this scheme fundamentally. Very recent immunological data (Dessauer et al.) reported at the 1974 meetings of the American Society of Ichthyologists and Herpetologists question the fundamental distinction. I remain convinced of the reality of the two groups but, while so much remains controversial, I do not see the value of the formal designation; it is not even useful mnemonically.

MEANS TO ANALYSIS OF A RADIATION: THE GROUP TERMS UTILIZED

The two sections of *Anolis* have, according to my interpretation, provided three and only three invasions of the West

Indies — one by *betas* into Jamaica, one by *alphas* into His-
paniola, and a third by *alphas* into St. Lucia. (But see Yang,
Soulé and Gorman [1974] for the evidence for a landfall for
the third invasion in Grenada instead.) All the extraordinary
proliferation, diversity and complexity of *Anolis* in the West
Indies has arisen out of these three stocks by intra-island radia-
tion and inter-island interchange. There is therefore a formidable
problem in analysis.

Fortunately, part of the basic information is already available.
A just published checklist of West Indian Amphibians and Rep-
tiles by Schwartz and Thomas (1975) provides an informed and
very careful list of Antillean taxa (including *Anolis*) with original
citations and synonymies, as well as the distributions as known
to the date of publication. The species are, however, listed
alphabetically; no taxonomic arrangement or indication of rela-
tionship is attempted. The taxonomic ordering presented below,
in remedying this, endeavors to synthesize a great deal of bio-
logical information.

I have myself seen 72 species or members of superspecies of
West Indian anoles in the field, six additional alive in captivity,
and 33 more as preserved specimens. Only three species, all
very recently described from Cuba, are known to me only from
descriptions (*A. pygmaequestris, A. juangundlachi* and *A. fugi-
tivus*). I have collected and studied anoles on all four of the
Greater Antilles, on several of the Lesser Antilles and on one
island in the Bahamas. This field knowledge I regard as basic
to an undestanding of the group. I have also participated in,
encouraged or aided studies at many other levels — osteology,
karyotypes, electrophoresis, aut- and synecological studies. All
of this information is utilized in the classification below.

No classification can mirror perfectly the complexity of the
evolutionary events that have produced the more than 100
species of West Indian *Anolis*. Nor, indeed, are the minuter
details of relationship and evolutionary sequence so well under-
stood (or likely to be) that we should attempt so perfect a
system. Nonetheless the wealth of species to be allocated and the
amount and variety of detail known about these same species
seem to me to afford at once the possibility and the justification
for an arrangement elaborate much beyond the usual. I there-
fore utilize a number of informal terms, partly based on those
employed by Etheridge in 1960, but descending into greater
detail. I define these below.

FORMAL AND INFORMAL CATEGORIES USED

Section. The primary dichotomy, a group osteologically defined at the highest level below the genus. Proposed by Etheridge (1960) for his alpha-beta division with *Anolis* osteologically defined on presence or absence of transverse processes on posterior caudal vertebrae.

Subsection. A division setting off a major portion of a section, again osteologically defined. This term, not used by Etheridge, distinguishes *punctetus* and *carolinensis* subunits within the alpha section, basing them on the relationship of interclavicle and clavicle. In the shorthand terms used below, the relationship is described in terms of an arrow-shaped or T-shaped interclavicle.

Series. A phyletic unit under the subsection definable on multiple characters. Osteological, chromosomal and even scale characters are utilized. Ordinarily this includes more than one species group and displays substantial morphological and even chromosomal diversity, i.e., products of a complex radiation that inferentially included several intermediate or annectent forms now extinct.

I have found series to be the unit in terms of which evolution is most conveniently discussed. I shall, therefore, in succeeding papers mention more characters under this unit than under taxa at a higher or lower level. This permits higher comparability between series and puts on display also many of the features and conditions the evolution of which I will later trace.

This is not to say that the greater number of characters makes the definition of series sharper or more rigorous. On the contrary, precisely because series are the units within which evolution is most readily seen, recognition of series is a matter of some subtlety — as Tables 1–4 show. Morphological and karyological characters may broadly overlap (Table 1). Ecology and geography are major clues, but convergence in ecological adaptations is rampant (Table 2), and geography must be used with discretion.

A balancing of all the evidence — not all of which is on record in Tables 1–4 — is the basis for the recognition of series.

subseries: a category utilized when a series has several recognizable subunits, ordinarily including more than one species group.

species group: the products of a simple radiation but often including species now widely sympatric (they may exhibit chromosomal diversity). I have sometimes used species group for a single species when that species is very distinct and may well be the last remnant of a radiation.

species subgroup: employed when readily definable and sympatric subgroups can be determined.

superspecies: the products of a radiation, the representatives of which are still completely or mostly allopatric and usually chromosomally uniform. Species status often uncertain. (See below.)

species: the most recent evidence indicates that the recognition of valid species is much harder than was formally assumed. It cannot be routinely assumed that allopatry or parapatry imply subspecific status. As I indicate above, I have used the superspecies category for a number of equivocal or doubtful cases.

subspecies: intraspecies differentiation differs so much in different species that this unit is of very different value from one case to another. I do not report currently recognized subspecies in the species list below. I will do so in the detailed species group and species definitions to come, but I will do so without passing judgment on their validity. I imply only that the differentiation so indicated — in contrast with that implied by the use of superspecies — is clearly intraspecific.

THE ANOLINES OF THE WEST INDIES:[1]

Taxon	Island or Bank[2]
Genus *Chamaeleolis* COCTEAU	
species *chamaeleonides* DUMERIL AND BIBRON 1837	Cuba
porcus COPE 1864	Cuba
Genus *Chamaelinorops* SCHMIDT	
species *barbouri* SCHMIDT 1919	Hispaniola
Genus *Anolis* DAUDIN	
Alpha section	
punctatus subsection	
roquet series	
luciae species group	
luciae superspecies	
luciae Garman 1887	St. Lucia
blanquillanus Hummelinck 1940	Blanquilla
bonairensis Ruthven 1923	Bonaire
richardi superspecies	
richardi Dumeril and Bibron 1837	Grenada, Tobago
griseus Garman 1887	St. Vincent

[1] My definition of the West Indies is, like most definitions of the West Indies, idiosyncratic. I omit from this list the anoles of Providencia and San Andres (*pinchoti* and *concolor* respectively) although other reptiles on these islands have West Indian affinities, because the anoles themselves have no Caribbean relatives. I include the anoles of Bonaire and Blanquilla (*bonairensis* and *blanquillanus*) because they are obvious members of the *roquet* species group of the southern Lesser Antilles.

[2] Non-West Indian ranges are not cited here but will be given in the fuller discussion in succeeding papers in this series.

Taxon	Island or Bank
trinitatis REINHARDT AND LUTKEN[3]	St. Vincent, introduced on Trinidad
roquet species group	
roquet superspecies	
aeneus Gray	Grenada, introduced on Trinidad, Guyana
extremus Garman 1840	Barbados, introduced on Bermuda
roquet Lacepede 1788	Martinique
cuvieri series	
ricordii species group	
roosevelti GRANT 1931	Culebra
ricordii superspecies	
ricordii Dumeril and Bibron 1837	Hispaniola
barahonae Williams 1962	Hispaniola
baleatus Cope 1864	Hispaniola
cuvieri species group	
cuvieri MERREM 1820	Puerto Rico
bimaculatus series	

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[3]The device of using capitals for the names of species describers except in the case of the members of superspecies is entirely for the purpose of making the sharply distinct sympatric species contrast with those *closely related* allopatric or mostly allopatric species about which questions of species status have often arisen. The emphasis on this difference does *not* imply that many or most of the members of superspecies are not biological species. Many are known to be in contact without interbreeding or with only a small zone of infertile hybrids. It calls attention solely to the demonstrable fact that the differentiation of members of a superspecies has not achieved the grade of *ecological* differentiation that permits them to be widely sympatric.

stratulus subseries
  evermanni species group
    evermanni STEJNEGER 1904   Puerto Rico
  stratulus species group
    stratulus subgroup
      stratulus COPE 1861   Puerto Rico
    distichus subgroup
      distichus superspecies
        distichus Cope 1861   Bahamas, introduced in Florida
        dominicensis Reinhardt and Lütken 1862   Hispaniola, introduced in Florida
      brevirostris superspecies
        brevirostris Bocourt 1870   Hispaniola
        caudalis Cochran 1932   Gonave, Hispaniola
        Species A Webster and Burns[1]   Hispaniola
        altavelensis NOBLE AND HASSLER   Alto Velo
bimaculatus subseries
  acutus species group
    acutus HALLOWELL 1856   St. Croix
  bimaculatus species group
    bimaculatus subgroup
      gingivinus COPE 1864   Anguilla Bank
      sabanus GARMAN 1887   Saba
    bimaculatus superspecies
      bimaculatus Sparrmann 1784   Statia Bank

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[1]Webster and Burns (1974) demonstrated the distinctness of this taxon, but did not name it.

Taxon	Island or Bank
leachii Dumeril and Bibron 1837	Antigua Bank
marmoratus superspecies	
nubilus Garman 1887	Redonda
lividus Garman 1887	Montserrat
marmoratus Dumeril and Bibron 1837	Guadeloupe Bank
ferreus Cope 1864	Marie Galante
oculatus subgroup	
oculatus COPE 1880	Dominica
wattsi species group	
wattsi superspecies	
wattsi Boulenger 1894	Antigua
forresti Barbour 1923	Barbuda
schwartzi Lazell 1972	Statia Bank
pogus Lazell 1972	Anguilla Bank
cristatellus series	
cybotes subseries	
cybotes species group	
cybotes superspecies	
cybotes Cope 1862	Hispaniola
haetianus Garman 1887	Hispaniola
armouri Cochran 1934	Hispaniola
shrevei Cochran 1939	Hispaniola
longitibialis Noble 1923	Hispaniola
whitemani Williams 1963	Hispaniola

    marcanoi Williams 1975 — Hispaniola
  cristatellus subseries
    pulchellus species group
      gundlachi subgroup
        gundlachi PETERS 1876 — Puerto Rico
      pulchellus subgroup
        krugi PETERS 1876 — Puerto Rico
        pulchellus DUMERIL AND BIBRON 1837 — Puerto Rico
        poncensis STEJNEGER 1904 — Puerto Rico
    cristatellus species group
      cristatellus superspecies
        cristatellus Dumeril and Bibron 1837 — Puerto Rico
        scriptus Garman 1887 — Inagua, Caicos Bank, Mariguana
      monensis superspecies
        monensis Stejneger 1904 — Mona
        cooki Grant 1931 — Puerto Rico
carolinensis subsection
  occultus series
    sheplani subseries
      sheplani SCHWARTZ 1974 — Hispaniola
    occultus subseries
      occultus WILLIAMS AND RIVERO 1965 — Puerto Rico
  darlingtoni series
    darlingtoni species group
      darlingtoni COCHRAN 1935 — Hispaniola

Taxon	Island or Bank
insolitus WILLIAMS AND RAND 1969	Hispaniola
monticola series	
fowleri species group	
fowleri SCHWARTZ 1973	Hispaniola
christophei species group	
christophei WILLIAMS 1960	Hispaniola
monticola species group	
etheridgei subgroup	
etheridgei WILLIAMS 1962	Hispaniola
rimarum THOMAS AND SCHWARTZ 1967	Hispaniola
monticola subgroup	
monticola SHREVE 1936	Hispaniola
rupinae WILLIAMS AND WEBSTER 1974	Hispaniola
koopmani RAND 1961	Hispaniola
carolinensis series	
equestris species group	
equestris superspecies	
equestris Merrem 1820	Cuba
luteogularis Noble and Hassler 1935	Cuba
noblei Barbour and Shreve 1935	Cuba
smallwoodi Schwartz 1964	Cuba
baracoae Schwartz 1964	Cuba
pigmaequestris GARRIDO 1975	Cuba
chlorocyanus species group	

chlorocyanus superspecies[1]
   chlorocyanus Dumeril and Bibron 1837   Hispaniola
   coelestinus Cope 1862   Hispaniola
aliniger superspecies
   aliniger Mertens 1939   Hispaniola
   singularis Williams 1965[2]   Hispaniola
hendersoni species group
   hendersoni superspecies
   hendersoni Cochran 1923   Hispaniola
   bahorucoensis Noble and Hassler 1933   Hispaniola
   dolichocephalus Williams 1963   Hispaniola
carolinensis species group
   carolinensis subgroup
   carolinensis superspecies
   [*carolinensis* Voigt 1832][3]
   porcatus Gray 1840   Cuba
   smaragdinus Barbour and Shreve 1935   Great Bahama Bank
   fairchildi Barbour and Shreve 1935   Cay Sal
   maynardi Garman 1888   Little Cayman
   longiceps Schmidt 1919   Navassa

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[1]These may be only ecological equivalents, *not* closest relatives. Were this demonstrated, the superspecies grouping should be dropped.

[2]There is an undescribed blue-dewlapped form resembling *A. singularis* in the Sierra Martin Garcia of the Dominican Republic.

[3]Cited as the type species of the group only.

Taxon	Island or Bank
	Acklins
brunneus Cope 1894	Cuba, Bay Islands, Half Moon Cay
allisoni BARBOUR 1928	Cuba
isolepis COPE 1861	
angusticeps subgroup	
angusticeps superspecies	
angusticeps HALLOWELL 1856	
paternus Hardy 1966	
argillaceus species group	
argillaceus COPE 1862	Cuba
centralis PETERS 1970	Cuba
loysiana DUMÉRIL AND BIBRON 1837	Cuba
lucius series	
lucius species group	
lucius superspecies	
lucius Duméril and Bibron 1837	Cuba
argenteolus Cope 1861	Cuba
vermiculatus species group	
bartschi COCHRAN 1928	Cuba
vermiculatus DUMÉRIL AND BIBRON 1837	Cuba
alutaceus series	
alutaceus species group	
alutaceus superspecies	
clivicola Barbour and Shreve 1935	Cuba
alutaceus Cope 1861	Cuba

cyanopleurus COPE 1861   Cuba
cupeyalensis PETERS 1970   Cuba
fugitivus GARRIDO 1975   Cuba
juangundlachi GARRIDO 1975   Cuba
mimus SCHWARTZ AND THOMAS 1975   Cuba

spectrum superspecies
   spectrum Peters   Cuba
   vanidicus Garrido and Schwartz 1972   Cuba

semilineatus species group
   semilineatus COPE 1864   Hispaniola
   olssoni SCHMIDT 1919   Hispaniola
   new species[1]   Hispaniola

Beta section
   grahami series
     grahami species group
       garmani STEJNEGER 1899   Jamaica
       grahami superspecies
         grahami Gray 1845   Jamaica, introduced into Bermuda
         conspersus Garman 1887   Grand Cayman
         opalinus GOSSE 1850   Jamaica
         lineatopus GRAY 1840   Jamaica
         reconditus UNDERWOOD & WILLIAMS 1959   Jamaica

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[1] An undescribed species from the Barahona Peninsula (Hertz, in preparation). The third species previously recognized, *A. cochranae* Williams, has been demonstrated to merge clinally into *semilineatus*.

Taxon	Island or Bank
sagrei series	
valencienni species group	
valencienni DUMERIL AND BIBRON 1837	Jamaica
sagrei species group	
sagrei superspecies	
sagrei Dumeril and Bibron 1837	Cuba, Bahamas, Little Cayman, costal areas of Mexico, Belize, introduced into Florida
luteosignifer Garman 1888	Cayman Brac
bremeri Barbour 1914	Cuba
nelsoni Barbour 1914	Swan Island
homolechis superspecies	
homolechis Cope 1864	Cuba
quadriocellifer Barbour and Ramsden 1919	Cuba
jubar Schwartz 1968	Cuba
mestrei BARBOUR AND RAMSDEN 1916	Cuba
allogus superspecies	
ahli Barbour 1925	Cuba
allogus Barbour and Ramsden 1919	Cuba
rubribarbus BARBOUR AND RAMSDEN 1919	Cuba
imias RUIBAL AND WILLIAMS 1961	Cuba
ophiolepis COPE 1861	Cuba

TABLE 1¹

Selected characters of West Indian *Anolis* series

SERIES	Autotomy planes open	Splenial present	Inscriptional ribs²	Karyotype (2n)	Vertebral crest	Caudal crest	Dewlap	Pre-sacrals	Lumbars (mode)	Aseptate caudals
[α — arrow interclavicle = *punctatus* subsection]										
(*roquet*)³	+	+	4:0	36/34	—	—	♂	24	3/4	7/8
cuvieri	+	±	3:2/3:1	36	+	+	♂♀	24	3(2)	7/8
bimaculatus	+	±	3:1	26-33	—	±	♂	24	3/4	5/6
cristatellus	+	±	2:2	36/27-29	—	±	♂	24/23	3/4	2-7
[α — T — interclavicle = *carolinensis* subsection]										
occultus	±	?	6:0/5:1	36	(+)	—	♂♀	24	3	all/8
darlingtoni	—	?	4:0/3:1	?/44	(+)	—	♂♀	24	3	all
monticola	+	?	3:1	36/40-48	+	+	♂♀/♂	24	5	7/8
equestris	+	+	3:1	36	+	+	♂♀	24	3	9/10
carolinensis	+	(—)	3:1/2:2	36	—	—	♂	24	3/4	6-8
lucius	+	—	3:1	36/34	—	—	♂ or none	24	4	6
alutaceus	+	—	3:1	36	—	—	♂	24	5	7
β										
grahami	+	—	3:1	30/30-37	—	—	♂	24	3/4	7
sagrei	+	—	2:2	30/28	—	±	♂♀/♂	24	3/4	5

¹Osteological data are from the notes and tables for his thesis, which were generously provided by Richard Etheridge. Karyotype information is from George Gorman.

²Inscriptional ribs are calcified cartilage elements embedded in the myocommata in iguanid lizards (Etheridge, 1965). They are either attached to the corresponding dorsal ribs or float free in the myocommata (as in the present table). The number of fixed or floating inscriptional ribs is a taxonomic character reported by a numerical formula (as in the present table), which gives first the number of fixed ribs, second the number of free ribs.

³In my listing this is a sub-series, but as the only West Indian representative of mainland series that are poorly understood, they deserve a place here.

TABLE 2
ECOMORPHS[1]

SERIES	generalist	crown giant	twig giant	twig dwarf	trunk crown	trunk crown dwarf	trunk ground	grass bush	trunk	rock and other
α — arrow interclavicle										
(roquet)										
cuvieri	+									
bimaculatus	+									
cristatellus		+			+	+	+		+	
α — T interclavicle										
occultus				+						
darlingtoni			+	+						
monticola								+	+	+
equestris		+		+		+				
carolinensis					+				+	
lucius										+
alutaceus								+		
β										
grahami		+			+	+	+			
sagrei			+				+ +	+		+

[1] In the sense of Rand and Williams (1969) and Williams (1972) adaptive types distinctive in size, shape and color and in other aspects of their morphology and with characteristic stations in trees or on the ground, as suggested by their names. Different ecomorphs are often syntopic, but members of the same ecomorph are usually allotopic (climatically separated) or allopatric (geographically separated).

TABLE 3

Distribution of series

SERIES	Cuba	Jamaica	Hispaniola	Puerto Rico	Lesser Antilles
[α — arrow interclavicle = *latifrons* subsection]					
cuvieri (roquet)			+	+	+
bimaculatus			+	+	+
cristatellus			+	+	
[α — T — interclavicle = *carolinensis* subsection]					
occultus			+	+	
darlingtoni			+		
monticola			+		
equestris	+		+		
carolinensis	+				
lucius	+				
alutaceus	+		+		
β					
grahami		+			
sagrei	+	+			

TABLE 4

Taxonomic source (series) of ecomorphs by island

	genera-list	crown giant	twig giant	twig dwarf	trunk crown	trunk ground	grass bush	trunk	other
Cuba		*equestris*		*caro-linensis*	*caro-linensis*	*sagrei*	*alutaceus + sagrei*	*caro-linensis*	*lucius + sagrei*
Jamaica	*grahami*	*grahami*	*sagrei*	*(grahami)*	*grahami*	*grahami + sagrei*			
His-paniola		*cuvieri*	*darling-toni*	*occultus + dar-lingtoni*	*caro-linensis*	*cristatellus*	*alutaceus + monti-cola*	*bima-culatus + monti-cola*	*monticola*
Puerto Rico		*cuvieri*		*occultus + bima-culatus*	*bima-culatus*	*cristatellus*	*cristatellus*		
Northern Lesser Antilles	*bima-culatus*								
Southern Lesser Antilles	*roquet*								

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B R E V I O R A

Museum of Comparative Zoology

LIZARD KARYOTYPES FROM THE GALAPAGOS ISLANDS: CHROMOSOMES IN PHYLOGENY AND EVOLUTION

D. PAULL,[1] E. E. WILLIAMS[1] AND W. P. HALL[2]

ABSTRACT. The iguanid lizards, *Conolophus subscristatus, Tropidurus albemarlensis, T. delanonis,* and *T. duncanensis* have similar $2n = 36$ karyotypes. *C. subcristatus* has a 12 metacentric macrochromosome and 24 microchromosome karyotype that is here shown to be primitive for the Iguanidae and probably for all lizards, while the three Galapagos *Tropidurus* have identical patterns to *Tropidurus* species from eastern South America and differ from the primitive karyotype of *C. subcristatus* by non-Robertsonian modifications of three pairs of macrochromosomes.

All available karyotypic data for the Iguanidae are summarized and used to discuss how one may determine which karyotypes are "primitive" within radiations and what possible roles Robertsonian karyotypic variation may play in the process of evolution. Analysis of karyotypic and systematic information suggests a causal relationship between karyotypic differentiation and the rapid proliferation of new species, such that the need for geographic isolation seems to be minimized by the chromosomal differentiation.

INTRODUCTION

Among the karyotypically well-studied families of squamate reptiles, the iguanid lizards are known to show great chromosomal diversity, with most of the variation apparently resulting from Robertsonian mutations (centric fusions and/or fissions) (Gorman, 1973; Hall, 1973). To more fully understand the biological significance and evolution of this diversity, workers

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at the Museum of Comparative Zoology have been accumulating karyotypes for as many and diverse iguanid species as possible. As part of this program, during the winter of 1969-70 Paull was able to karyotype four iguanid species from the Galapagos Islands. Two of the four principal phyletic branches of the family, the "iguanines" and the "tropidurines" (Savage, 1958; Etheridge, 1964) are represented in these islands, and both were sampled in the study. All four species showed a $2n = 36$, 12 metacentric macrochromosome, 24 microchromosome pattern which is believed by some to be primitive for the Iguanidae or, indeed, for all lizards (Gorman et al., 1967, 1969; Webster et al., 1972; Gorman, 1973).

Addition of karyotypes for these four species to our data base provides the occasion to discuss the evidence of "primitiveness" for karyotypes within a radiation and the role Robertsonian karyotypic variation may play in the process of evolution. However, we must first describe the karyotypes of the Galapagos lizards sampled.

KARYOTYPES OF GALAPAGOS IGUANIDS

(D. Paull and W. P. Hall)

Specimens examined: Representatives of two distantly related branches of the Iguanidae have reached the Galapagos, presumably by overwater colonization. The iguanine species in the Galapagos belong to the endemic genera *Amblyrhynchus* (one species, the marine iguana) and *Conolophus* (two species of land iguanas). Of these, *Conolophus subcristatus* was karyotyped. The tropidurine radiation is represented in the archipelago by eight endemic species of *Tropidurus* (lava lizards). Additionally, *Tropidurus* has a South American continental radiation of 12 species (Etheridge *in* Peters and Donoso-Barros, 1970). Island species karyotyped were *Tropidurus albemarlensis, T. delanonis* and *T. duncanensis*. Table 1 lists the species karyotyped and their collection localities.

Methods: All chromosome preparations were made in the Galapagos Islands using laboratory facilities kindly supplied by the Charles Darwin Research Station on Santa Cruz Island. Cells were spread for karyotyping by air drying smears of methanol:acetic acid (3:1) fixed suspensions of testis, bone marrow or spleen tissues prepared directly from colchicine pretreated animals. The techniques used were similar to those of Evans et

Table 1
Galapagos specimens karyotyped

species	locality	individuals karyotyped
Conolophus subcristatus	South Plazas Id., Las Plazas	1
Tropidurus albemarlensis	South Plazas Id., Las Plazas	6
Tropidurus albemarlensis	Bartolome Id., Sullivan Bay	4
Tropidurus albemarlensis	Santa Cruz Id., between Galapagos Hotel and Darwin Station	6
Tropidurus delanonis	Hood Id., behind beach, Gardiner's Bay	5
Tropidurus duncanensis	Duncan Id., small cove on NE end	2

al. (1964), Bianchi and Contreras (1967) and Patton and Hsu (1969).

Results: All species had 36 chromosomes, with 12 biarmed macrochromosomes and 24 microchromosomes (Fig. 1). No cytologically distinct sex chromosomes or intrageneric variation of any kind was seen. However, conspicuous differences in arm ratios and relative sizes of the macrochromosomes were noted between the genera (Fig. 1).

In *Conolophus subcristatus* (Fig. 1, lower), taking the macrochromosomes in order of size, beginning with the largest, pair one is very slightly submetacentric; pair two is distinctly submetacentric, with the long arm slightly less than twice as long as the short; pairs three and four are almost exactly metacentric and, in many spreads, indistinguishable in size; pair five is nearly metacentric; and pair six is submetacentric, with the long arm about 1.5 to 2.0 times the length of the short arm. Pairs one and two are similar in length, three and four are slightly but distinguishably shorter than two, five is distinguishably shorter than four, and six is conspicuously shorter than five. Some of the microchromosomes seem to be metacentric or submetacentric, but our preparations do not resolve their structures well enough to allow them to be unequivocally paired.

Figure 1. Comparison of male karyotypes from *Tropidurus delanonis* (above) and *Conolophus subcristatus* (below). Both figures are printed to the same magnification.

Figure 2. Comparison of male *Tropidurus* karyotypes. The species are *T. delanonis* (left) , *T. duncanensis* (middle) , and *T. albemarlensis* (right) . The karyotypes are printed to the same magnification.

In *Tropidurus* (Fig. 1, upper; Fig. 2) pairs one through five show a fairly even gradation in length, with pair six being conspicuously smaller than five. Comparing the arm ratios to those of *Conolophus, Tropidurus* pair two is more submetacentric, with the long arm being slightly more than twice the length of the short; and *Tropidurus* pair five, rather than being metacentric, is almost subacrocentric, with the long arm about 2.5 times the length of the short. Again, some of the microchromosomes appear to be metacentric or submetacentric, but they are not adequately resolved to allow accurate pairing.

PRIMITIVE KARYOTYPES

(E. E. Williams and W. P. Hall)

Comparisons with other iguanid genera and other families of lizards suggest that the *Tropidurus* pattern is derived with respect to the *Conolophus* pattern, which may be primitive for several families, including the Iguanidae.

As Gorman (1973) in the latest review of reptilian chromosomes has emphasized, our knowledge of lizard karyotypes and especially of iguanid karyotypes has increased immensely since the early work of Matthey (1931, 1933). In the iguanids even such very speciose genera as *Sceloporus* and *Anolis* have now been sampled very extensively and at least one or two species have been examined in all major subgroups of the family (Table 2). The more species studied, the more widely one chromosomal arrangement is demonstrated: that with a 2n of 36, with 12 metacentric macrochromosomes and 24 microchromosomes.

The kind of 2n = 36 karyotype characteristic of the Galapagos *Tropidurus* (i.e. 2n, arm ratios, etc.) has also been reported for representatives of this genus in eastern South America (Gorman et al., 1967; Peccinini, 1969; and Becak et al., 1972); however, we are not aware of its occurrence in any other genera. On the other hand, the 2n = 36 *Conolophus* karyotype, or at least the details of its macrochromosomal pattern, is found in many different lizard groups. In the Iguanidae (Table 2) precisely this macrochromosomal pattern is found in such diverse groups as the anolines (Gorman, 1973), sceloporines (Cole, 1970; Pennock et al., 1969; Gorman, 1973; Hall, 1973), *Crotaphytus* (Montanucci, 1970), iguanines (Cohen et al., 1967; Gorman et al., 1967; Robinson, 1974), oplurines (Gor-

Table 2

Genera are those in Peters and Donoso-Barros, 1970 unless otherwise noted. Reference for number of species karyotyped and diploid number is Gorman 1973 or this paper unless otherwise noted.

Genus	Number of species in genus	Number of species karyotyped	Range of known 2n
Amblyrhynchus	1[1]	——	——
Anisolepis	2	1	2n=36
Anolis	ca 200[2]	80+[3]	2n=25–48
Aperopristis[4]	1	——	——
Aptycholaemus	1	——	——
Basiliscus	4	1	2n=36
Brachylophus	2[5]	——	——
Callisaurus	2[6]	2	2n=34
Chalarodon	1[7]	——	——
Chamaeleolis	2[8]	1	2n=36
Chamaelinorops	1[9]	1	2n=36[3]
Conolophus	2	1	2n=36
Corytophanes	3	——	——
Crotaphytus	5[10]	3	2n=36
Ctenoblepharis	8[11]	——	——
Ctenosaura[12]	7	1	2n=36
Cyclura	8[13]	1	2n=36
Diplolaemus	3	——	——
Dipsosaurus	3[14]	1	2n=36[3]
Enyalioides	7	1	2n=36[3]
Enyalius	8[15]	——	——
Holbrookia	3[16]	2	2n=34[3]
Hoplocercus	1	——	——
Iguana	2	1	2n=34
Laemanctus	2	——	——
Leiocephalus[17]	20	5	2n=32–36[3]
Leiosaurus	4	——	——
Liolaemus	50+[18]	8	2n=30–40
Morunasaurus	2	——	——
Ophryoessoides	8[19]	——	——
Oplurus	6[7]	1	2n=36
Petrosaurus	2	2	2n=34[3]
Phenacosaurus	3[20]	1	2n=36

Table 2 (Continued)

Genus	Number of species in genus	Number of species karyotyped	Range of known 2n
Phrynosaura	3	——	——
Phrynosoma	14[21]	9	$2n=34$
Phymaturus	2[22]	——	——
Plica	2	1	$2n=40$
Platynotus[23]	1	——	——
Polychrus	6[24]	4	$2n=20\text{--}30$[25]
Pristidactylus[26]	4	1	$2n=36$
Proctotretus	3	——	——
Sator	2[6]	1	$2n=34$[27]
Sauromalus	7[6]	4[28]	$2n=36$
Sceloporus	64+[29]	45+	$2n=22\text{--}46$[3]
Stenocercus[19]	29	——	——
Strobilurus[30]	1	——	——
Tropidurus	20	4	$2n=36$
Uma	5[31]	3	$2n=34$
Urocentron	4[30]	——	——
Uranoscodon	4	——	——
Urosaurus	10[6]	5	$2n=34$[3]
Urostrophus	3	——	——
Uta	6[32]	6	$2n=34$

Because they do not appear on the Etheridge dendrogram, two recently described genera have been omitted from the table:

Vilcunia Donoso-Barros and Cei, J. Herp. *5:* 90. 1971.

Pelusaurus Donoso-Barros, Neotropica *19:* 132. 1973.

Both are said to be allied to *Liolaemus* and *Proctotretus.* Etheridge (personal communication) infers from their descriptions that they are allied to the *Liolaemus-Phrynosaura-Ctenoblepharis* complex and not to *Proctotretus.*

[1]Eibl-Eibesfeldt, I. 1962. Neue Unterarten der Meerechse, *Amblyrhynchus cristatus,* nebst weiteren Angaben zur Biologie der Art. Senckenbergiana, Biol. **43:** 177–199.

[2]This is only a rough approximation. Continental members of the genus are in general poorly understood, and species are still being discovered in Hispaniola and Cuba.

[3]We include unpublished data from material in the Museum of Comparative Zoology.

[4]Etheridge (personal communication) after examination of specimens prefers to recognize the genus as distinct from *Leiosaurus*. Cf Müller, L., 1922: Über *Aperopristis paronae* Peracca und die Genera *Aperopristis* Peracca und *Leiosaurus* Dumeril and Bibron. Senckenbergiana 4: 153–159.

[5]Avery, D. and W. W. Tanner, 1970. Speciation in the Fijian and Tongan iguana *Brachylophus* (Sauria, Iguanidae) with description of a new species. Great Basin Nat. 30: 166–172.

[6]Smith, H. and E. H. Taylor, 1950. An annotated checklist and key to the reptiles of Mexico, exclusive of the snakes. Bull. U. S. Nat. Mus. 199: 1–253. *Cophosaurus (Holbrookia) texana* is placed with *Callisaurus* here. See Norris, K. S., 1958. The evolution and systematics of the iguanid genus *Uma* and its relation to the evolution of other North American desert reptiles. Bull. Amer. Mus. Nat. Hist. 114: 247–326, and Axtell, quoted by Norris. The only important character separating the two genera is the condition of the ear opening, which is evaluated as less important than characters separating other sceloporine genera. In fact, it would not be unreasonable to lump the three sand-swimming genera, *Callisaurus*, *Holbrookia* and *Uma*. This larger genus would still have only 10 species.

[7]Angel, F. 1942. Les Lezards de Madagascar. Mem. L'Acad. Malgache 34: 1–193.

[8]Garrido, O. H. and A. Schwartz, 1968. Cuban lizards of the genus *Chamaeleolis*. Quart. J. Fla. Acad. Sci. 30: 197–220.

[9]Thomas, R. 1966. A reassessment of the herpetofauna of Navassa Island. J. Ohio Herp. Soc. 5: 73–89.

[10]Montanucci, R. 1969. Remarks on the *Crotaphytus-Gambelia* controversy (Sauria: Iguanidae). Herpetologica 25: 308–314. Montanucci, R. 1970. Analysis of hybridization between *Crotaphytus wislizenii* and *Crotaphytus silus* (Sauria, Iguanidae) in California. Copeia 1970: 104–123.

[11]Cei, J. 1974. Two new species of *Ctenoblepharis* (Reptilia, Iguanidae) from the arid environments of Central Argentina (Mendoza Province). J. Herp. 8: 71. In contrast to Cei, we continue to recognize *Phrynosaura* as distinct from *Ctenoblepharis*. On the key character of juxtaposed versus imbricate dorsals, Cei's two new species are *Ctenoblepharis*.

[12]Etheridge follows an unpublished MS by Clayton E. Ray in uniting *Enyaliosaurus* and *Ctenosaura*.

[13]*fide* Albert Schwartz and Michael Carey, who are preparing a revision of the genus.

[14]Smith and Taylor 1950, as in footnote 6 above.

[15]Etheridge, R. 1969. A review of the iguanid genus *Enyalius*. Bull. Brit. Mus. (N.H.), Zool. 18: 233–260.

[16]Williams, K. L. and H. M. Smith, 1958. Herpetologica 13: 265–267.

[17]Etheridge, R. 1966 (The systematic relationships of West Indian and South American lizards referred to the iguanid genus *Leiocephalus*. Copeia 1966: 79–91) listed 16 species in his restricted genus *Leiocephalus*. Subsequent to 1966, Schwartz, by reinterpretation of already described forms, has raised the number to 20. O. H. Garrido, 1973 (Nueva especies de *Leio-*

cephalus (Lacertilia, Iguanidae) para Cuba. Poeyana No. 116: 1-19) has added a 21st species.

[18]Richard Sage (personal communication) believes the taxonomy of *Liolaemus* to be still in a very primitive state. He suggests that the genus may contain as many as 100 biological species.

[19]Fritts, T. H. 1974. A multivariate evolutionary analysis of the Andean iguanid lizards of the genus *Stenocercus*. Mem. San Diego Soc. Nat. Hist. 7: 1-89. Fritts reallocates to *Stenocercus* a number of the species formerly placed in *Ophryoessoides*, leaving only six described and two undescribed species in the genus.

[20]Lazell, J. D. 1969. The genus *Phenacosaurus* (Sauria: Iguanidae). Breviora No. 325: 1-24.

[21]Presch, W. 1969. Evolutionary osteology and relationships of the horned lizard genus *Phrynosoma* (family Iguanidae). Copeia 1969: 250-275.

[22]Cei, J. M. and L. P. Castro, 1973. Taxonomic and serological researches on the *Phymaturus patagonicus* complex. J. Herp. 7: 237-247.

[23]Etheridge (in a letter): "I know of no reference that presents evidence for or against recognition of this genus. Most, but not all, recent authors include the species *semitaeniatus* in *Tropidurus*.

[24]Gorman, G. C., R. B. Huey and E. E. Williams, 1969. Cytotaxonomic studies on some unusual iguanid lizards assigned to the genera *Chamaeleolis*, *Polychrus*, *Polychroides* and *Phenacosaurus*, with behavioral notes. Breviora No. 316: 1-17. *Polychroides* synonymized with *Polychrus*.

[25]Peccinini, D. 1969. Variação nos cromossomos do lagarto *Polychrus marmoratus* (Sauria, Iguanidae) de diferentes localidodes (*Nota preliminar*). Rev. Brasil. Biol. 30: 1-4. (The *Polychrus* from São Paulo with $2n=20$ is actually *P. acutirostris* [P. Vanzolini, pers. comm.]. See also Peccinini, D., Beçak, O. Frota-Pessoa and Iris Ferrari, 1971. Sex determination of the "pseudo-XO/XX" type in the Brazilian lizard *Polychrus* sp. (Sauria, Iguanidae). Caryologia 24: 129-139, and Beçak, M. L., W. Beçak and L. Denaro, 1972. Chromosome polymorphism, geographical variation and karyotypes in Sauria. Caryologia 25: 313-326.

[26]"Barrio (1969) has demonstrated *Cupriguanus araucanus* Gallardo 1964 is conspecific with *Leiosaurus fasciatus* Dorbigny in Dumeril and Bibron 1837. Barrio used the combination *Cupriguanus fasciatus*. However, *Leiosaurus fasciatus* was in 1843 designated the type of *Pristidactylus* by Fitzinger. If *fasciatus* is congeneric with *achalensis*, the type of *Cupriguanus*, the latter becomes a junior synonym of *Pristidactylus* which then would be regarded as having four species, *fasciatus* Dorbigny 1837, *scapulatus* Burmeister 1861, *achalensis* Gallardo 1964 and *casuhatiensis* Gallardo 1968." Etheridge (personal communication).

[27]Lowe, C. H. and M. D. Robinson, 1971. The chromosome pattern in *Sator grandaevus* (Reptilia: Iguanidae), Baja California, Mexico. J. Arizona Acad. Sci. 6: 282.

[28]Robinson, M. D. 1974. Chromosomes of the insular species of the

chuckwalla lizards (genus *Sauromalus*) in the Gulf of California, Mexico. Herpetologica **30**: 162–167.

[29]Sixty-four *Sceloporus* species are currently recognized. When taxonomic revisions suggested by Hall, 1973 are incorporated, this number will be raised to about 72, with considerable uncertainty remaining concerning the number of biological species to be recognized within the *torquatus* and *formosus* species groups.

[30]Etheridge, R. 1968. A review of the iguanid lizard genera *Uracentron* and *Strobilurus*. Bull. Brit. Mus. (N.H.), Zool. **17**: 48–64.

[31]Williams, K. L., P. S. Chrapliwy and H. M. Smith, 1959. A new fringe-footed lizard from Mexico. Trans. Kans. Acad. Sci. **62**: 166–162; Mayhew, W. W. 1964. Taxonomic status of California populations of the lizard genus *Uma*. Herpetologica **20**: 170–183.

[32]Ballinger, R. E. and D. W. Tinkle, 1972. Systematics and evolution of the genus *Uta* (Sauria: Iguanidae). Misc. Publ. Mus. Zool. Univ. Michigan No. 141: 1–83.

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man et al., 1967) and the tropidurines (Gorman et al., 1967). In other families (Table 3) this pattern has been demonstrated in the Agamidae (Arronet, 1965; Gorman and Schochat, 1972; Hall, 1970; Sokolovsky, 1972), in the Teiidae (Gorman, 1970), in the Gerrhosauridae (Matthey, 1933; Hall, unpub.) and in the Amphisbaenidae (Huang et al., 1967).

This most widely distributed *Conolophus*-like karyotype is a source of controversy. On the one hand, it has been called "primitive" (Gorman and others). On the other hand, it has been interpreted, as by Cole (1970, 1971b), as derived in at least some iguanids, or, as by M. J. D. White, as a possible example of an exceptionally stable configuration that has been repeatedly evolved within a group. (White at one time called this "the principle of homologous change," but he now prefers to call it "karyotypic orthoselection" [see White, 1973 for discussion].)

Those who deny the primitiveness of the $2n = 36$ pattern hold very firmly to the concept that primitive karyotypes in lizards consist entirely of acrocentrics with karyotypic evolution then occurring by centric fusions of them.

This view, that acrocentrics are *prima facie* primitive, has rested on the belief that fusion is cytologically much easier than fission and hence much more common (Matthey, 1949; White, 1954, 1959; Reiger et al., 1968). In particular, the generation of a new centromere, which supposedly occurs in fission, has seemed to lack any mechanism that would readily permit the

event, while fusion has been interpreted as the result of the (conceptually) less difficult process of reciprocal translocation followed by loss of a centromere carrying small segments of one or both chromosomes.

However, there are now many cases for which fission is an obligatory explanation of the origin of the karyotypes of highly derived groups and species — too many cases to allow any doubt of the reality of fission as one possible path of karyotypic evolution — whatever its mechanism. Even White (1973) now admits its existence under the name "centric dissociation" in certain cases. Morescalchi (1973) finds fission the hypothesis of choice for the origin of the karyotypes of certain species of *Hyla* and *Eleutherodactylus*. In reptiles, Webster et al. (1972)

Table 3

Karyotypes in Non-Iguanid Lizard Families

12V + 24m or direct derivatives occur in some member	Only karyotypes *not* readily related to 12V + 24m known
Agamidae	Gekkonidae
Chamaeleontidae	Pygopodidae
Xantusiidae (6V + 12I + 24m)	Lacertidae
	Anniellidae
Gerrhosauridae	
Teiidae (see Gorman, 1970)	
Anguidae	
Helodermatidae (10V + 4I + 24m)	
Varanidae	
Scincidae (see Greer et al., in prep.)	

Based on karyotypic data in Gorman (1973), unless otherwise noted.

presented evidence for the highly derived phyletic position of *Anolis monticola*, the one species within that very large genus that has a 2n as high as 48. It is similarly inescapable that fissioning has occurred several times in *Sceloporus* (Hall and Selander, 1973; Hall, 1973). A recent discussion in the journal *Evolution* has summarized some of the mammalian evidence for fission (Lawlor, 1974; Baker et al., 1975). It is no longer reasonable to peremptorily reject fission as a plausible mode of Robertsonian karyotypic evolution.

The argument for the primitiveness of the 12 macro- and 24 microchromosome pattern for iguanids and for lizards, however, does not depend on the supposed plausibility or implausibility of fission. The argument becomes easier to accept if fission is admitted in certain cases, but primitiveness for a karyotype, as for any other character state, can be determined on its own merits, independent of any theoretical mechanism for the evolution of that character state.

A large literature now exists dealing with objective recognition of primitiveness. Kluge and Farris (1969) may stand as an example. They would use the following criteria (1969:5), listed in order of reliability:

(1) The primitive state for any particular group is likely to be present in many representatives of closely related groups.

(2) A primitive state is more likely to be widespread within a group than is any one more advanced state.

(3) The primitive state is likely to be associated with states of other characters known from other evidence to be primitive.

They add that "closely related groups can be selected through estimates of overall similarity that make no assumptions about primitive conditions."

"Widespread" they define not by counting taxa but as occurring in several taxa that otherwise would have little in common. They would also use "available fossil material."

At least in intention these criteria have merit, but, in general, such criteria are especially difficult to use in our present stage of knowledge of karyotypes. Fossils are clearly unavailable. It is still rare for karyotypes to be known for even a substantial number of any group and, on the contrary, those at hand may be a very biased sample. The problem of real similarity may

be serious; diploid number by itself is meaningless; there must be near identity in chromosome morphology paralleling taxonomic relationships inferred on other grounds.

When a group has been as well sampled as the Iguanidae now are, however, the Kluge and Farris criteria begin to be applicable and the comparative method can lead to sound results when appropriately applied. Cole misrepresents, indeed caricatures, the comparative approach when, in opposing the concept of the 12 + 24 karyotype as ancestral in iguanids, he says (1970:31):

> "These conclusions are based on the assumption that the general karyotypic condition found in the majority of species that were available for sampling, at whatever level of the taxonomic hierarchy one happened to be working with, was, therefore, the most primitive,"

and, again (1970:31):

> "If I were to simply employ the principal [sic] on which these authors' arguments are based, I would reach a rather different conclusion for the *spinosus* group, for in this group the karyotype of the *lundelli* subgroup (12 biarmed macrochromosomes plus 10 smaller chromosomes, most of which are clearly biarmed; a 12 + 10 karyotype) would then be considered ancestral because it occurs in five of the nine species in the species group and none of the three remaining general karyotypes of the group is represented in more than two species."

Our own reasoning has a quite different base than that portrayed by Cole. We start from a base that is broad and quite independent of the ideas of Cole or ourselves.

Figure 3 provides a dendrogram of the phylogenetic relationships of the genera of the Iguanidae which represents the present

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Figure 3. Phylogeny and karyotype distribution in the family Iguanidae. The base dendrogram summarizes phylogenetic conclusions of Richard Etheridge from his osteological studies and is reproduced here with his permission from a privately circulated figure. The available karyotypic information for the family (references cited in Table 3) is superimposed on this dendrogram and indicates (1) the basic diploid karyotype for each genus chromosomed or (2) in karyotypically variable genera, the most primitive karyotype in the genus plus the range of 2n known for it. "V" chromosomes are metacentric macrochromosomes, "I" are acrocentric macrochromosomes, and "m" are microchromosomes. Thus, an 8V,8I+24m karyotype has a 2n of 40 with eight metacentric macrochromosomes, eight acrocentric macrochromosomes, and 24 microchromosomes.

Uracentron

Strobilurus

Platynotus

Plica
8V,8I +24m

eastern Tropidurus
12V+24m

Uranoscodon

Ophryoessoides
Stenocercus

Proctotretus

Galapagos
Tropidurus
12V+24m

western Tropidurus

Phrynosaura
Ctenoblepharis

Liolaemus
2n:30-40
(inc. 12V+22m)

Phymaturus

Leiocephalus
12V+24m
12V+20m

Crotaphytus
12V+24m

Sceloporus
2n: 22-46
(inc. 12V+22m)

Uta
12V+22m

Urosaurus
12V+22m

Sator
12V+22m

Uma
12V+22m

Holbrookia
12V+22m

Callisaurus
12V+22m

Phrynosoma
12V+22m

Petrosaurus
12V+22m

α Anolis
2n: 25-48
(inc.12V+24m)
SOUTH AMERICA,
CENTRAL AMERICA,
WEST INDIES

Aptycholaemus
Anisolepis
12V+24m

Urostrophus

Enyalius

Phenacosaurus
12V+24m
NORTHERN
SOUTH AMERICA

β Anolis
2n: 29-40
MEXICO TO
SOUTH AMERICA,
CUBA, JAMAICA

Chamaelinorops
12V+24m
HISPANIOLA

Chamaeleolis
12V+24m
CUBA

SOUTH
AMERICA

NORTH AMERICA

tropidurines

sceloporines

Iguana
12V+22m

Cyclura
12V+24m

Amblyrhynchus

Conolophus
12V+24m

Sauromalus
12V+24m

Dipsosaurus
12V+24m

Ctenosaura
12V+24m

NORTH AMERICA,
CENTRAL AMERICA,
NORTHERN SOUTH
AMERICA, WEST INDIES

anolines

SOUTH AMERICA
CENTRAL AMERICA

Polychrus
2n: ♂ =29
♀ =30
♀ =28
♀ =26
♀ =20

Diplolaemus
Leiosaurus
Aperopristis
Pristidactylus
12V+24m

5

4

6

7

GALAPAGOS

Brachylophus
FIJI

Hoplocercus
Morunasaurus
Enyalioides
12V+24m
SOUTH AMERICA

3

iguanines

2

basiliscines

1 oplurines

Corythophanes
Laemanctus
Basiliscus
12V+24m
CENTRAL AMERICA,
NORTHERN SOUTH
AMERICA

Oplurus
12V+24m

Chalarodon
MADAGASCAR

views of Richard Etheridge and Richard Estes, extending those of Savage (1958), Etheridge (1964) and Presch (1969). This has been based wholly on osteology and thus it gives us a picture of relationships constructed without knowledge of or reference to karyotypes. We have then superimposed on this dendrogram the range of karyotypes for each iguanid genus for which these are known. We use both the published reports summarized by Gorman, 1973 (most references cited by Gorman are not repeated) and our still unpublished data. We use the latter despite the lack of formal (and especially pictorial) documentation because it fills out much of the picture of karyotypic variation in the Iguanidae without significantly altering it.

The Etheridge scheme recognizes a basal stock (called "morunasaurines" by Estes and Price, 1973) from which seven major lineages arise (Polychrus, the *Anolis-Enyalius-Diplolaemus* lineage, the "tropidurines," the "sceloporines" plus *Crotaphytus*, the "iguanines," the "basiliscines," and the "oplurines").

Karyotypes are known for one genus of morunasaurines (one species of *Enyalioides* — our unpublished data); in this and in six of the seven derived lineages (*all* except *Polychrus*) the "primitive" 12 + 24 karyotype is known to occur or is the only karyotype known. Furthermore, in every one of the derived lineages (except *Polychrus*) those genera closest to the base on Etheridge's diagram — i.e. those believed for osteological reasons to be the more primitive members of each lineage (and, in fact, each sublineage) — have either the 12 + 24 karyotype or a 12 + 22 karyotype that differs from the primitive condition by the absence (by loss or fusion) of a pair of microchromosomes. In the iguanine line, for example, all genera in the sublineage containing *Iguana, Ctenosaura, Dipsosaurus* and *Sauromalus* have a 12 + 24 or (*Iguana*) 12 + 22 karyotype.

The sceloporine line is especially instructive in this and other respects. *Crotaphytus,* an early offshoot of this line, has 12 + 24 (Cohen et al., 1967; Montanucci, 1970). *Every* primitive sceloporine and some *Sceloporus* have 12 + 22 (several authors, summarized in Hall, 1973). Within *Sceloporus* (a morphologically more derived genus) numbers range from 12 + 10 to 24 + 22; if the 12 + 22 pattern is accepted as primitive for the genus, it is clear that both fusions and fissions must have been involved in the evolution of its karyotypic diversity.

The tropidurine line is not well sampled, but as we have shown above, *Tropidurus* from eastern South America and the

Galapagoan *Tropidurus* (derived from western South American stock) have the basic 12 + 24 pattern, although their karyotypes are slightly derived in non-Robertsonian ways. The only West Indian *Leiocephalus* published (Gorman et al., 1967) also has the basic pattern. Besides confirming the 12 + 24 pattern in Hispaniolan species, Hall (unpub.) has found representatives of the Cuban branch of the genus to have 12 + 20 patterns. In the speciose genus *Liolaemus*, the single species so far reported (Gorman et al., 1967) has 12 + 22, although slides made by Richard Sage and examined by Hall indicate the presence of considerable karyotypic variation in this genus (2n ~ 30–40)[1].

In the line leading to *Anolis*, the primitive genera *Chamaeleolis*, *Phenacosaurus* and *Chamaelinorops* (Hall and Williams, in preparation) have 12 + 24 karyotypes, as do many of the alpha section of the genus *Anolis* itself. The 12 + 24 pattern is also found in the related lineage including the genera *Pristidactylus* and *Anisolepis*.

Given this evidence, it is difficult to contest the hypothesis that the 12 + 24 pattern is primitive in the Iguanidae. It is possible to go to greater detail: arguments similar to those above support the idea that even the detailed chromosome size and arm ratios found in *Conolophus* must be primitive for iguanids.

Additionally, when we notice (1) that quite similar 12 + 24 karyotypes are found in other lizard families (Table 3), both in families that everyone agrees are closely related to the Iguanidae, i.e. the Agamidae and the Chamaeleontidae, and in families that are just as universally regarded as not closely related (Gerrhosauridae, Anguidae, Amphisbaenidae); (2) that still other families (Scincidae, Helodermatidae, Varanidae) have karyotypes easily derivable from 12V + 24m (Gorman, 1973), it then becomes clear that, using the most neutral descriptive terms, the 12 + 24 karyotype is an extraordinarily stable and conservative pattern. To us it is evident that the most careful and skeptical use of the Kluge and Farris criteria of primitive-

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[1]Although variation in chromosome number was clearly demonstrated in this material, the preparations were not of good quality and the data were complicated by the inclusion of unnamed taxa (clearly *Liolaemus*, however). Further work will be required before publication is warranted. However, we think that the existence of substantial karyotypic variation in this genus should be noted.

ness points unequivocally to the ancestral position of the 12 + 24 karyotype not only for iguanids, but for all lizards.

On the other hand, there is no doubt that some lizard families and at least one group within the Iguanidae have karyotypes that are very difficult to reconcile with derivation from a 12 + 24 pattern (Gorman, 1973). The Gekkonidae will serve as an example of the first case; *Polychrus* is, of course, the second. We are impressed that these deviant families and groups are in general isolated cases, neither closely related to one another, nor arguable as ancestral to forms with the 12 + 24 karyotype. In all of these cases, morphological and other evidence suggests long separation from plausible basal stocks, and hence leads all the more strongly to the conclusion that the *Conolophus*-like 12 + 24 pattern is the one primitive for lizards.

EVOLUTIONARY ROLE OF ROBERTSONIAN CHANGE

(W. P. HALL AND E. E. WILLIAMS)

Let us point out immediately that there is no antithesis between primitiveness and stability — the two explanations that have been proposed for the iteration of one chromosome pattern throughout a large number of species. On the contrary, the genera which show only the widespread chromosome patterns which we believe to be primitive seem *not* to be the ones that have radiated widely. This is a point which we want to stress, especially for the Iguanidae. Karyotypically conservative groups, so far as we can see, have produced only few species. Of the more than 50 genera of iguanids, only three — *Anolis, Sceloporus* and *Liolaemus* — are very large, each including more than 50 species (several times 50 in *Anolis*), or have produced high levels of sympatry (5 + syntopic species in several areas of the ranges of *Anolis* or *Sceloporus*). Of the others, only *Stenocerus* (as revised by Fritts, 1974), *Tropidurus* (if the Galapagos species are included), and *Leiocephalus* (a purely insular radiation in the West Indies) have as many as 20 species, and no others have as many as 15. Excepting *Polychrus*, whose several karyotypes bear little obvious relationship to one another and none to any other iguanid, the other small, conservatively speciating genera show on current evidence little or no intrageneric variation in karyotypes, and indeed very little variation among genera. Of the 14 non-sceloporine small iguanid genera (in-

cluding *Crotaphytus*) sampled, 11 have the 12 + 24 pattern. All of the primitive sceloporines (eight genera) and *Iguana* among the iguanines have 12 + 22. Only *Plica*, aside from *Polychrus*, stands out in showing a notably different karyotype (16 + 24), and its modifications seem relatively simple (presumably fissions of four of the primitive metacentric macrochromosomes). Of the genera of middle size (20–29 species), the four sampled species of *Tropidurus* have again the 12 + 24 pattern but differ somewhat in arm ratios from the usual condition, and while some *Leiocephalus* have the 12 + 24 pattern, others have 12 + 20 (reduction in two pairs of microchromosomes — Hall, unpublished). *Stenocercus* has not yet been sampled.

Contrasting strongly with this picture of conservative speciation and karyotypic evolution in the small iguanid genera is a picture showing extensive, usually Robertsonian karyotypic variation in each of the three prolifically speciose genera. In *Anolis* 2n's range from 25 to 48 (Gorman, 1973; Hall, unpub.), in *Sceloporus* they range from 22 to 46 (Gorman, 1973; Hall, 1973), and in a few *Liolaemus* they range from 30 to 40 (Sage and Hall, unpublished).

The apparent association of conservative speciation with conservative karyotypic evolution, and prolific speciation with remarkable karyotypic diversity suggests the possibility of an evolutionarily important causal relationship between karyotypic differentiation and speciation. Though there are undoubtedly other possibilities and explanations that might be raised, it is this possibility of causal relationship that we here want to evaluate. We offer the following arguments to demonstrate that the relationship between speciation and karyotypic diversity is genuine.

(1) *Intrageneric variation in karyotypes.* Since few small genera from six of the seven major iguanid lineages are represented by karyotypes from more than one species, we must agree that we cannot safely compare the amounts of *intra*generic variation between small and large genera in these lineages. This defect, however, most certainly does not apply to the sceloporine lineage: all nine sceloporine genera and the related *Crotaphytus* are cytologically well known. Half or more of the species from each of these 10 genera have been karyotyped: 3/5 from *Crotaphytus*, 2/2 from *Petrosaurus*, 9/14 from *Phrynosoma*, 2/2 from *Callisaurus*, 3/3 from *Uma*, 2/3 from *Holbrookia*, 1/2 from *Sator*, 6/6 from *Uta*, 5/10 from *Urosaurus*, and 45 + /

Table 4

Distribution of karyotypic variation in Iguanidae: interspecies comparisons (large genera except *Sceloporus* omitted).

2n	*Sceloporus*[1]	Other scelo-porines[2]	Other *small* iguanid genera		All small iguanid genera
48	0	0	0		0
46	2	0	0		0
44	2	0	0		0
42	1	0	0		0
40	3	0	1	*Plica plica*	1
38	0	0	0		0
36	1	0	13		13
34	18	33	1		34
32	15	0	0		0
30	2	0	1	*Polychrus marmoratus*	1
28	0	0	1	*Polychrus peruvianus*	1
26	1	0	1	*Polychrus femoralis*	1
24	3	0	0		0
22	13	0	0		0
20	0	0	1	*Polychrus acutirostris*	1
species karyotyped	45+	33	19		52
species known	64+	49	122		171
% karyotyped species with 2n=36 or 34	42%	100%	74%		90%

[1] includes polymorphisms within currently recognized "species."
[2] here including *Crotaphytus*.

64+ from *Sceloporus* (data summarized from Table 2). None of these genera (except *Sceloporus*) shows any intrageneric variation, and the only intergeneric difference is between the 12 + 24 *Crotaphytus* and the 12 + 22 sceloporines. Within *Sceloporus* only 13 species (15 after taxonomic revisions by Hall) are known to have the primitive sceloporine condition (2n = 34), while the remaining 32 (40 or 41 after revisions) karyotyped species have derived patterns — and most of these belong to the phylogenetically more advanced large-scaled branch as defined by Smith (1939). In the sceloporine lineage (Table 4), the correlation between chromosomal diversity and prolific speciation is clear cut and does indeed appear to be fundamental. And even with our poor sampling of the small non-sceloporine genera, the association between chromosomal conservation and few species per genus is, at the least, suggestive.

(2) *Intergeneric diversity in karyotypes.* Although comparatively few species of the small, non-sceloporine genera have been karyotyped, still there is less intergeneric diversity observed than we would expect if variation were randomly distributed in the family. Phylogenetic relationships inferred from morphology (Fig. 3) show that many of these genera must have been evolving as independent lineages for comparatively long times, possibly since the Cretaceous (Estes and Price, 1973). Given so long a period of evolution, they show remarkably little evidence of the acquisition or accumulation of chromosomal differentiation. As we have said, there are very few known differences among genera, and, in fact, few departures from the 12 + 24 pattern. In the 25 small genera sampled (Table 5), the few observed cases of *inter*generic variation are slight indeed compared to the known *intra*generic variation of the phylogenetically more recent large genera. Unless the sampling of the small genera has been biased in some unknown way, this should be quite significant.

The deviations from the 12 + 24 pattern among the small genera are again: *Plica* (16 + 24 in no more than four mutational events, and possibly in only one, *fide* Todd, 1970), *Iguana* (12 + 22 in one event), all of the "primitive" sceloporines (12 + 22 in one event in the common ancestry for all species), and *Polychrus* (2n's = 20–30 resulting from an undetermined number of events producing karyotypes derived in relation both to one another and the 12 + 24 pattern). Contrasted to the limited intergeneric variation in the family as a

whole is the remarkable interspecific diversity involving many mutational events found *within* each of the three especially speciose genera (cf. Fig. 3). Again, this relationship is clearest in the well-investigated sceloporine lineage (Hall, 1973, in prep.).

Table 5

Distribution of intergeneric comparisons in the Iguanidae

lineage	small genera			large genera		
	no. genera	no. karyotyped[1]	Any k'types other than 12 + 24 or 12 + 22[2]	no. genera	no. karyotyped	Any k'types other than 12 + 24 or 12 + 22
basal stock	3	1	0	0	–	–
oplurines	2	1	0	0	–	–
basiliscines	3	1	0	0	–	–
iguanines	8	6	0	0	–	–
sceloporines & *Crotaphytus*	9	9	0	1	1	1
tropidurines[3]	11	1	1	4	3	2
anolines	3	2	0	1	1	1
anoline relatives	8	3	0	0	–	–
Polychrus	1	1	1	0	–	–
Totals	49	25	2	6	5	4

[1]The number of genera in the lineage for which karyotypic data exist.
[2]The number of genera in the lineage containing one or more species with a karyotype deviating from the 12 + 24 or 12 + 22 pattern.
[3]*Stenocercus, Tropidurus, Leiocephalus,* and *Liolaemus,* each with 20 or more species, are treated as large genera.

(3) *Relative recency of species and of karyotypic diversity.* If rates of fixation of Robertsonian mutations were independent of the process of speciation, one expectation might be that many of the older genera would accumulate karyotypic variants while phylogenetically recent groups might show little variation, even though they include many species.

Hall (1973) would adduce *Sceloporus* as a counter-example, since he believes it to be a phylogenetically quite recent genus. We summarize Hall's views and arguments here.

(A) While the Iguanidae may have originated in the Cretaceous (Estes and Price, 1973), the differentiation of the present sceloporine genera probably did not antedate the development of the xeric habitats in North America during the Miocene (Axelrod, 1950, 1958). This conclusion is supported by the facts: (1) that *Crotaphytus* and all sceloporine genera are largely or entirely restricted to the North American deserts (except *Sceloporus* itself, which has extensively radiated in mesic habitats as well as in deserts); (2) that all sceloporine genera except for the osteologically primitive *Crotaphytus* and *Petrosaurus* (Etheridge, 1964; Presch, 1969) and *Sator* (which simply has not been tested) will "shimmy bury" (Axtell, 1956) in loose soil or sand for escape or sleeping cover (Stebbins, 1943, 1948; Axtell, 1956; Norris, 1958), a behavior not seen in any of the other North American or West Indian iguanids (we know nothing about South American iguanids in this respect); and (3) that all sceloporines but no other North American iguanid genera (including *Crotaphytus*) show a "sink-trap" type of nasal passage and almost always an associated valvular nostril[1] (Stebbins, 1943, 1948; Savage, 1958; Hall, unpub.), which clearly seems to have been evolved in relationship to the use of shimmy burial for cover in xeric environments where loose soil is likely to be more readily available for cover than that provided by plants or permanent burrows in firm soil.

(B) Within the sceloporines, *Sceloporus* seems to be one of the most recently differentiated genera. Osteological data clearly show four groups within the sceloporines (Savage, 1958; Etheridge, 1964; Presch, 1969): the primitive *Petrosaurus;* the specialized *Phrynosoma;* the group of "sand-swimming" (Norris, 1958) genera, *Callisaurus, Holbrookia* and *Uma;* and the group

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[1]*Petrosaurus,* which lives in xeric habitats but which does not shimmy bury under experimental conditions, has the nasal sink trap but lacks the nasal valve (Hall, personal observation).

of four genera, *Sceloporus, Urosaurus, Sator* and *Uta.* According to Etheridge (1964), these last four genera cannot be distinguished osteologically. However, comparisons suggest that *Sceloporus,* with its mucronate imbricate scales developed to a degree not found in any of the other North American iguanids (where granular scales seem to be the primitive condition) and with its loss of the gular fold found in all other sceloporines, is the phylogenetically most recent of these four genera.

(C) Within *Sceloporus,* again based on characteristics of the squamation, it seems clear that Smith's (1939) small-sized, small-scaled species are more closely related to the other sceloporines than is the large-sized, large-scaled branch. To summarize the cytosystematics of these two divisions, the phylogenetically more primitive small-scaled branch contains 20 species by present taxonomy: 12 of these are karyotypically conservative,[1] five have not been karyotyped, and the three that are karyotypically derived are also highly derived ecologically (*merriami,* $2n = 46$, is a specialized cliff-face dweller and *scalaris* and *aeneus,* $2n = 24$, are specialized montane bunch grass dwellers). Within the morphologically more advanced large-scale branch, according to present taxonomy, *only* the single species, *S. orcutti,* has the primitive $12 + 22$ pattern, while all other karyotyped species are derived. At present (very conservative taxonomy) this branch contains a minimum of 43 species, of which all but 13 (all 13 are in chromosomally highly derived species groups) have been karyotyped.

This phylogenetically most recent radiation of the sceloporines (the large-scaled *Sceloporus*) has covered the entire ecological and geographical range of lizards in North America (Smith, 1939) and shows simultaneously a truly remarkable karyotypic diversity (2n's from 22 to 46). It is also notable that the most ecologically differentiated small-scaled species in the genus (the *scalaris* group species $[2n = 24]$ and the *merriami* $[2n = 46]$) are also among the karyotypically most highly derived forms.

The one egregious example of chromosomal diversity in a small genus, *Polychrus,* seems in the very fact of its uniqueness equally a counter-example to the generality of the proposition that deviant karyotypes tend to accumulate in all genera with time.

[1]Karyotypically at least to a first approximation: Cole (1971) notes that *maculosus* has a $2n = 31$, $X_1X_2Y \, \delta$ (based on three specimens, only one a male) and that in *pyrocephalus* chromosome 1 shows a pericentric inversion.

Polychrus is seen on Etheridge's diagram as an isolated basal twig, truly very old and very distinct, entirely suitable as a group in which deviant karyotypes might accumulate. But each of the other six major groups is as old in Etheridgean terms. If karyotypic diversity is a product only of time, even a random and superficial sampling of the other small genera should, so it seems to us, have resulted in more cases of highly derived karyotypes than are in fact in front of us.

Our own surmise regarding *Polychrus* is that the six forms currently recognized, all highly arboreal, may represent only the few survivors of an old and formerly more prolific lineage of tree dwellers that, perhaps, has been largely replaced by the radiation of *Anolis* in the arboreal habitat.

Chromosomal evolution in the Iguanidae: two major patterns

We do not deny that the history of karyotypic change is not now and never will be known from direct evidence, that the real and unique historical process must be inferred from its products, nor that the survey of iguanid karyotypes, though it is already impressive, is incomplete. We insist, however, that the present sample is large enough to justify conjecture and to point to the kinds of evidence that will verify or negate postulated sequences.

Our picture of chromosomal evolution in lizards, and perhaps also in many other groups, is that there are both periods of chromosome conservatism with usually slow geographic modes of speciation (Mayr, 1963) and episodes of karyotypic instability associated with rapid proliferations of new species (Hall, 1973). We believe that both *Anolis* and *Sceloporus* exhibit these phenomena (cf. especially Webster et al., 1972; Williams and Webster, 1973; and Hall and Selander, 1973), and presumably *Liolaemus* also does. Todd (1970) suggests a similar relationship between karyotypic diversification and prolific speciation in the Canidae.

To us the comparative data strongly suggest that karyotypic diversification and speciation are in many cases functionally related, such that the temporal and/or geographic requirement for the separation of populations is somehow minimized (not eliminated but very greatly reduced) when chromosomal differences become fixed between them. White's model of "stasi-

patric" speciation (White et al., 1967; White, 1968; Key, 1968)
offers one mechanism, and others are possible (Hall, 1973; in
prep.). Here we wish to emphasize only that Robertsonian
mutations frequently are found fixed between species of rapidly
proliferating groups but only rarely are found as intrapopula-
tion polymorphisms. (Wallace, 1959, provided an early note of
this phenomenon in *Drosophila*.) Given this distribution of
Robertsonian mutations, we think it especially significant that,
among the varieties of chromosomal rearrangements, the Robert-
sonian ones probably have the least impact on the meiotic as-
sortment or recombination of *balanced* genomes; but, on the
other hand, at least in mammals where breeding and cytological
studies have been made, these mutations are increasingly impli-
cated as a significant source of chromosomal malassortment in
meiosis serving to reduce the effective fertility of chromosomally
heterozygous individuals (Polani et al., 1965; Gustavsson, 1971a,
b; Cattanach and Mosely, 1973). Once a chromosomal differ-
ence is established, reduced heterozygote fertility could then
serve in appropriate circumstances as an *intrinsic* partial barrier
to gene flow between karyotypically differentiated homozygous
populations, thereby reducing the requirement for extrinsic bar-
riers to gene flow before speciation could ensue (Hall, 1973; in
prep.).

Then, assuming some model of chromosomal speciation based
on cytogenetically reduced fertility in heterozygotes, the proba-
bility or frequency of such speciation in given lineages should
be highly dependent on parameters of their genetic systems such
as: mutation rates, malassortment rates, population structures,
mating systems, ets. Chromosomal speciation might then be
precluded in some lineages because of unfavorable genetic sys-
tems that would allow speciation only by conservative geographic
modes; on the other hand, genetic systems of other lineages may
especially favor chromosomal speciation, and thus allow great
proliferations of species, even in the absence of strong extrinsic
barriers to gene flow. Such a chromosomal speciation theory can
easily account for the associations of karyotypic diversity and
prolific speciation found in *Sceloporus, Anolis,* and apparently
in *Liolaemus.*

The test of the chromosomal speciation model of karyotypic
evolution as it pertains to the iguanids will be found in the still
unsampled or inadequately sampled iguanid radiations, par-
ticularly those of South America. *Stenocercus,* now with 29

recognized species and with notable sympatry, is certainly crucial. The karyotypic variation in *Liolaemus* and *Leiocephalus* must be confirmed, and the karyotypic patterns in these two genera adequately documented. We suggest that the species of mainland *Tropidurus*, which seem to have rather complicated distributions (Peters and Donoso-Barros, 1970), may also repay careful attention. Only such a wider survey of the karyotypes of the Iguanidae can provide either a verification of the evolutionary patterns we have suggested here, or, by demonstrating new patterns, require alternative models.

RESUMEN

Los iguanidos: *Conolophus subcristatus, Tropidurus albemarlensis, T. delanonis,* y *T. duncanensis* tienen cariotipos similares de 36 cromosomas. *C. subcristatus,* con 12 macrocromosomas metacéntricos y 24 microcromosomas, tiene un cariotipo que se demuenstra ser "primitivo" dentro la familia Iguanidae, y que probablemente es también primitivo entre todos de los lagartijos. Los cariotipos 2n = 36 de los tres *Tropidurus* son iguales y también al *Tropidurus* del este de Suramérica, pero ellos son diferentes del cariotipo primitivo porque hay modificaciones "no-Robertsonianas" de tres pares de los macrocromosomas.

La filogénia y todos de los datos cromosómicos de la Iguanidae están resumidos para una discusión sobre la determinación de que cariotipos son "primitivos" dentro radiaciones de especies, y también sobre los funciones que sirven las mutaciones de Robertson en el proceso de evolución. Análisis de la información sobre los cariotipos y sistemática demuenstra una conexión causal y cerca entre la diferenciación cariotipica y la proliferación rápida de especies nuevas, donde el requisito para aislamiento geográfico se minimiza a causa de la diferenciación cromosómica.

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NOTE ADDED IN PRESS

Since we wrote the above, Vegni Talluri et al. (1975) published karyotypes identical to those *Tropidurus* karyotypes given here for the additional two species, *T. jacobi* (James Bay, James Id.) and *T. indefatigabilis* (Academy Bay, Indefatigable Id.); and for two additional populations of *T. albemarlensis* (Villamil, Albemarle Id. and Punta Espinoza, Narborough Id.). These data further support our conclusion that chromosomal differentiation plays no functional role in classical geographic speciation and add contrast to the situations of frequent association between the fixation of chromosomal differences and speciation which does not involve obvious geographic separation.

ADDITIONAL REFERENCE

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B R E V I O R A

Museum of Comparative Zoology

A LABORATORY STUDY OF THE TURKISH HAMSTER
MESOCRICETUS BRANDTI

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ABSTRACT. Ten years of laboratory observations of a breeding colony of *Mesocricetus* from central Turkey are summarized. From morphological and karyological evidence, as well as cross-breeding experiments, it is concluded that *Mesocricetus brandti* is distributed in specific areas throughout Asiatic Turkey, south into Palestine, Syria, the northern part of Iraq, northwest Iran, and over the Caucasus into Daghestan. The chromosomal polymorphism noted in this species may be due to the isolation of groups to these specific types of terrain.

The reproductive cycle, growth, and care and behavior in the laboratory are described. Records of hibernation are detailed and compared with those of *Mesocricetus auratus*. It is emphasized that *M. brandti* offers a unique opportunity to study the factors which influence hibernation using matched animals of known age and lineage.

INTRODUCTION

The study of hibernation in mammals has long been hampered by the lack of an animal which could be bred and raised readily under laboratory conditions. Ground squirrels, marmots, dormice, European hamsters, hedgehogs and microchiropteran bats have been used extensively as experimental animals, but all of these species are usually obtained by collecting them in the wild.

The Syrian hamster is easily raised in the laboratory and has been used as an experimental animal for more than forty years. However, hibernation in this species is extremely unpredictable, and many individuals fail to hibernate even when exposed to cold for many months (Lyman, 1948, 1954).

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In August, 1965, we obtained 13 hamsters trapped in central Turkey.[1] These animals hibernated readily when exposed to cold ($5 \pm 2°C$) the following winter and bred in the laboratory during the next spring. Since that time, the colony has been continued, detailed notes have been maintained, and various experiments have been undertaken. In 1971, we received an additional 29 animals. We maintained and bred these animals separately from the original group for comparative data.

The two groups resembled each other closely, and clearly differed from laboratory specimens of the Syrian or golden hamster, *Mesocricetus auratus*. As information concerning the Turkish hamsters accumulated, it became apparent that this species is the best experimental animal for the study of certain aspects of hibernation, particularly those which require animals of known history and lineage. Offspring of the two original colonies have been distributed to several investigators and we hope that the Turkish hamster is now established as an experimental animal. For this reason, our knowledge concerning this hamster is detailed below.

Identification is, of course, of critical importance in animals used for experimental studies. However, because of the limited amount of comparative material available, comparisons of skins and skulls have led to conflicting opinions on the taxonomy of *Mesocricetus* (Ognev and Heptner, 1927; Aharoni, 1932; Ellerman, 1941, 1948; Vinogradov and Argiropulo, 1941; Ellerman and Morrison-Scott, 1951; Vereshchagin, 1959; Hamar and Schutowa, 1966; Ivanov, 1969; Raicu et al., 1969; Vorontsov and Krjukova, 1969; Todd et al., 1972). The genus exhibits chromosomal polymorphism while showing relatively few morphological differences over a wide geographic area. Emphasis by some investigators on the analysis of karyotypes has led to divergent taxonomic views which can not be fully reconciled until more definitive data such as chromosomal banding studies and cross-breeding experiments in the laboratory have accumulated. For this reason we have limited ourselves to a consideration of the identity of the Turkish animals and have attempted to delineate their distribution in their natural habitat.

TAXONOMIC MATERIALS

The animals which formed our original colony in 1965 were captured by Mr. Haluk Anat in Malya, near Kirsehir (39°N, 34°E)[2] about 125 kilometers (km) southeast of Ankara, Turkey (Fig. 1). Mr. Anat trapped the second group six years later near the city of Ankara. We refer to these two groups collectively as "Turkish" hamsters in this text.

Skins and skulls of hamsters from Malya which had been trapped alive and kept in captivity for varying periods of time were used for comparison with the specimens of *Mesocricetus* in the British Museum.[3] As far as we have been able to determine, the British Museum collection is the only representative collection of this genus in the United Kingdom or the United States. It contains specimens from a now defunct colony in the Wistar Institute which were obtained from Pirbadan [m] (35°N, 48°E), Iranian Kurdistan, a small village 125 km north-northwest of Hamadan, Iran (Fig. 1). Hamsters from this colony have been the subject of karyological and breeding studies and have been referred to as "Kurdistan" or "K" hamsters[4] (Lehman and Macpherson, 1967; Palm, Silvers and Billingham, 1967; Todd et al., 1972; Raicu et al., 1972).

We observed four hamsters originating from a colony of Rumanian hamsters maintained by Dr. Petre Raicu, University of Budapest[5], alive in our laboratory. We used two skins and skulls from the Rumanian colony to compare with the specimens in the British Museum. In addition, hamsters trapped for Dr. Michael Murphy[6] in Aleppo, Syria were maintained in our laboratory for comparative studies and breeding experiments.

Breeding crosses were usually attempted by placing the female in the cage of the male, though occasionally the reverse process was used. In many instances we used vaginal smears to determine the estrous cycle, and exposed the female to the male in the afternoon

[2]The report that these animals came from Aksehir, Turkey (Todd et al., 1972) is an error derived from faulty original information.

[3]We thank Drs. J. E. Hill and G. B. Corbet of the British Museum for making these specimens available

[4]All place names in this paper are those given in the original articles.

[5]We are grateful to Dr. William Nixon of Randolph, Mass. for supplying these animals.

[6]Dr. Murphy made a trip to Aleppo to obtain this colony and observe their behavior. We acknowledge his gift with thanks.
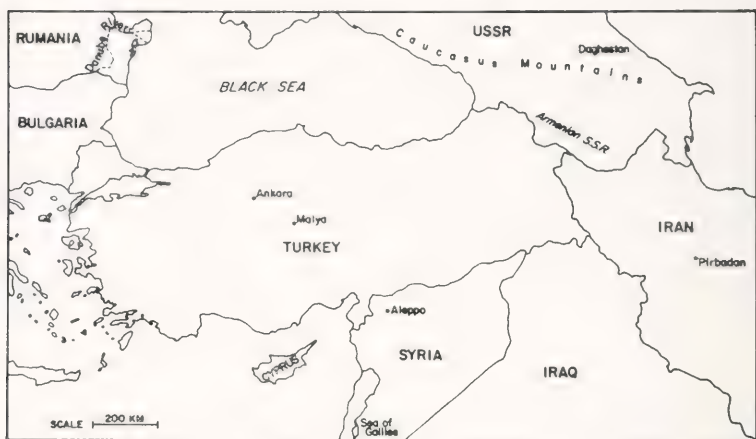
Figure 1.   Map showing distribution of *Mesocricetus.*

prior to estrus. If the animals fought, they were separated temporarily, and pairing was attempted at later dates. Otherwise, the animals were left together for three or four days and then separated. The animals were observed for copulatory behavior and vaginal smears were often made if copulation was suspected but not observed.

We prepared karyotypes from metaphase spreads obtained from normally dividing primary skin cultures. The cells were harvested on the seventh to ninth day of culture. After exposure to colchicine (final dilution 36 micrograms per milliliter of medium) for five hours, and hypotonic solution for 10–15 minutes, cells were fixed in 3:1 methanol:glacial acetic acid and stained with Wright-Giemsa stain.

Chromosomes were counted in at least 100 cells per animal. Selected metaphase spreads were photographed and homologous chromosomes were paired in the conventional manner according to their length and position of the centromere.

DISCUSSION OF TAXONOMY

It is generally agreed that the distribution of the genus *Mesocricetus* includes the eastern parts of Rumania and Bulgaria, across Anatolian Turkey into the Caucasus, and south into Syria, the northern tip of Iraq and the northwest part of Iran.

Hamar and Schutowa (1966) have presented the most complete taxonomic investigation of the genus in recent time. They had

available for comparison 102 specimens from the Moscow and Leningrad Zoology Museums as well as the Humbolt Museum in Berlin. Based on morphological data, they recognized three species of one group. They proposed that *Mesocricetus newtoni* was found in eastern Rumania and Bulgaria and that *Mesocricetus auratus* was confined to the type locality of Aleppo, Syria. *Mesocricetus brandti* appeared to occupy the rest of the range of *Mesocricetus* except for an area north of the Caucasus which was occupied by *Mesocricetus raddei* and *M. r. nigriculus*.

Based on cranial measurements, they found little difference between *newtoni, auratus* and *brandti*, but the two forms of *raddei* were distinctly different, with relatively massive skulls and larger molar teeth. The bodies of animals of the *raddei* group were also larger in size, and the black color of their bellies contrasted with the grey or white of the smaller *newtoni-auratus-brandti* group.

Our examination of specimens of *raddei* from the Caucasus in the British Museum and the Museum of Comparative Zoology confirmed the observations of Hamar and Schutowa (1966). These authors summarized their findings by suggesting that *raddei* should be separated from the other group at the subgeneric level, and the evidence presented for this view is convincing.

When compared to specimens from Rumania or Turkey, the dorsal pelage of the Syrian or golden hamster is notably different. The color of the latter is a rich Sanford's brown (Ridgway, 1912) while our animals from Turkey are tawny-olive to Saccardo's umber dorsally, with an overlay of black-tipped guard and pile hair which darkens the pelage. Although Hamar and Schutowa do not emphasize this, our animals from Rumania were darker dorsally than our animals from central Turkey, as were several of the seven Rumanian specimens in the British Museum. The subauricular stripe in the Syrian animals is poorly defined, being a mixture of brown and black hairs, while in the Turkish and Rumanian animals it is pure black. There is a difference in the coloring of the chest, for in the Syrian hamster it is brownish with a narrow white mid-stripe, while in the Turkish and Rumanian animals there is a pronounced bar of black, as illustrated by Hamar and Schutowa (1966). The Kurdistan or "K" specimens were paler on the dorsal surface but otherwise closely resembled our animals, which were trapped approximately 1350 km to the west-northwest.

It is of incidental interest that the pelage of the type specimen of *M. auratus* in the British Museum is indistinguishable from speci-

mens which Dr. Murphy collected in Syria in 1971 and these in turn match the common laboratory Syrian hamster. Thus, laboratory breeding since 1930, when the first animals were captured (Adler, 1948), has not altered the natural coat color of this animal, though many mutations in coat color have occurred.

More than one thousand Turkish hamsters have been raised in our laboratory, and slight differences in the pelage have been observed. Some individuals have darker dorsal pelage than others, and the ventral surface may vary from grey-white to grey, particularly on the abdomen. There are no consistent differences in color between the colony which originated from Malya and the colony from Ankara.

The four living animals from Rumania were about the same size as laboratory strains of Syrian hamsters, but our Turkish hamsters were bigger as full-grown adults. Twenty-one two-year-old Turkish hamsters chosen at random averaged 163 grams (g) with a range of 137 to 258 g. In comparison, 111 two-year-old Syrian hamsters averaged 105 g with a range of 97 to 113 g (Altman and Dittmer, 1964). The heads of the living animals from Rumania differed from the others, for the face was more pointed and ratlike, though the nasal portion of the skulls of Rumanian animals is not narrower.

Laboratory interbreeding experiments have been detailed by Todd et al. (1972) and can be briefly summarized. No offspring have resulted from matings between our animals from Malya or Ankara in Turkey laboratory animals originating in Syria (Todd et al., 1972; present study), though copulation has been observed (Murphy, personal communication; present study). Attempts to cross Kurdistan animals with laboratory Syrian hamsters have been similarly unsuccessful (Palm et al., 1967).

The cross between Rumanian female and Malya male hamsters has produced viable offspring, but the reciprocal cross has not been attempted. Todd et al. (1972) report the survival of five females, with a male living only two weeks. In our laboratory, a female killed her first litter and two females survived in the second litter, both of which had developed diabetes mellitus by the age of nine weeks. Diabetes was not the invariable result of this cross, however, for we tested a female raised by Todd et al. and found the urine negative for glucose. The hybrids were larger than either parent, with one weighing 293 g as an adult. Todd et al. report copulation between a hybrid Rumanian-Turkish female and a Malya male, but presented no evidence that the hybrid was fertile.

Viable hybrids have been produced in the cross between female hamsters from Kurdistan and males from Rumania, but the reciprocal cross was unsuccessful (Raicu et al., 1972). (Dr. M. Bahmanyar of the Pasteur Institute of Iran collected both Dr. Raicu's and the Wistar Institute hamsters. He writes that the former animals were trapped 25 km west of Pirbadan.) The number of young per litter was small and averaged about 50 per cent of the number expected in non-hybrid litters. Histological examination revealed that both the male and female reproductive organs of the adult hybrids were atrophic, and on this basis both sexes were considered to be totally sterile.

Raicu and Bratosin (1968) and Raicu et al. (1969) have obtained reciprocal crosses between Syrian and Rumanian hamsters. Though the litters were small, the individual animals were large and the gonads of the hybrids appeared histologically atrophic, leading to the conclusion that the animals were sterile. Todd et al. (1972) found that the hybrid females resulting from crosses between Rumanian males and Syrian females would mate with Syrian males. No viable young were produced, though reabsorbing embryos were found at autopsy in three cases.

In contrast, there was no indication of lack of fertility between the two groups of animals from Turkey. Reciprocal crosses in our laboratory between hamsters originating in the Ankara and Malya areas result in normal healthy litters and the F_1 generations are fertile, producing normal young.

The karyotypes of the various groups of hamsters, including hamsters in our laboratory which originated in Malya, have been reported by Todd et al. (1972). Since that time we have established the karyotype of hamsters from the area of Ankara. The latter animals have a diploid number (2N) of 44 chromosomes with a fundamental number of autosomal arms (FN) of 80 (Fig. 2), while in the hamsters from Malya 2N = 42 and FN = 78 (Fig. 3). Hybrids of both sexes were examined and in these 2N = 43 and FN = 79.

In the animals from Ankara, the autosomal complement is composed of two pairs of metacentric chromosomes (#3 and #13), two pairs of acrocentric chromosomes (#19 and #21) and the remaining 16 pairs, which are a graduated series of submetacentric and subtelocentric chromosomes. Because of the similarity and gradation in size of the majority of the chromosomes, it was not possible to identify with complete certainty many individual chromosomes, including X and Y.
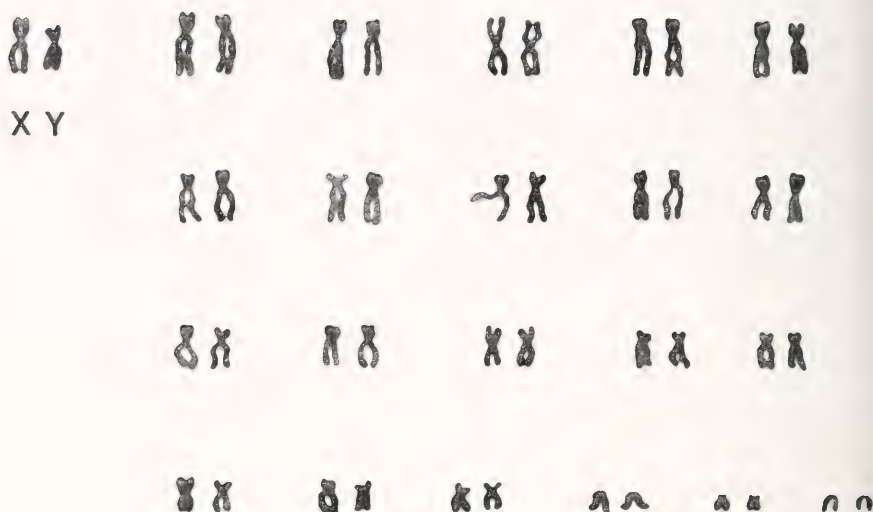
Figure 2. Representative karyotype of *Mesocricetus brandti* from the area of Ankara, Turkey. Autosomes are arranged sequentially from upper left to lower right.

In comparing the karyotype of the Ankara hamsters with that of the Malya group the same difficulty obtained, yet it is obvious that the difference in diploid number between the two groups is the result of the absence of the acrocentric pair #19 in the Malya hamsters leaving only one pair of acrocentric chromosomes. The hybrid animals have three acrocentric chromosomes, two small ones and one slightly larger. The X chromosome of the Malya hamster is unmistakably larger than that of the hamster from Ankara.

Comparison of the karyotype of the Ankara hamster with that of the Kurdistan hamster (Lehman and Macpherson, 1967) reveals certain differences. In the Kurdistan hamster $2N = 42$ and $FN = 80$. The smallest autosomal pair appears similar to #20 in the Ankara karyotype and there are no acrocentric elements. The Y chromo-
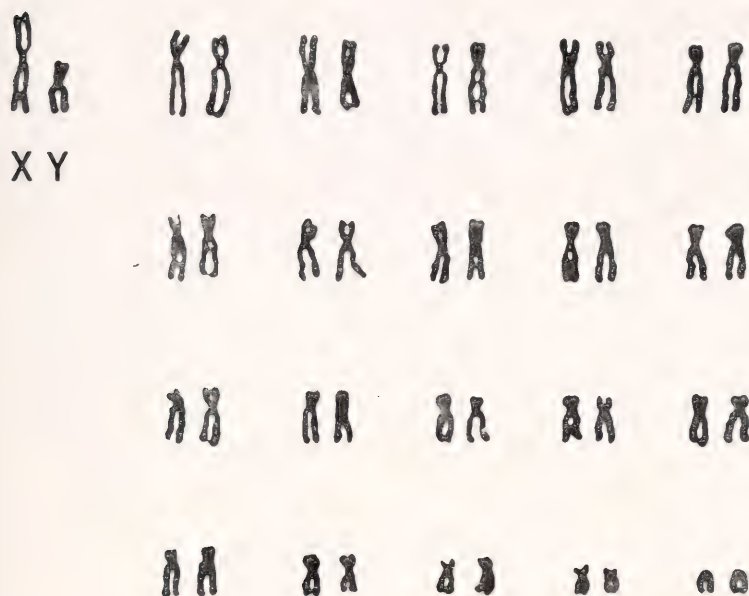
Figure 3.   Representative karyotype of *Mesocricetus brandti* from Malya, Turkey. Autosomes are arranged sequentially from upper left to lower right.

some of the Kurdistan hamster is obviously much larger than that of the Ankara animals.

From the evidence which has accumulated to date, a few conclusions can be drawn. It is apparent that the hamsters of the genus *Mesocricetus* from Anatolia to at least as far east as Iran are not subspecies of the Syrian hamster, *Mesocricetus auratus*, as some authors have suggested (Ellerman and Morrison-Scott, 1951; Vereshchagin, 1959). While wild-caught Syrian, Turkish, or Rumanian hamsters breed readily in captivity with animals from the same area, all attempts to cross the Syrian with the Turkish or Kurdistan hamster have failed. If the animals will not breed in the laboratory under a wide series of conditions, it is unlikely that they would breed in the field. The bright golden brown color of the back,

the absence of black subauricular and chest patches and the creamy white belly plus the smaller size of the Syrian hamster reinforce the concept that *M. auratus* is a separate species.

When Syrian and Rumanian hamsters are compared, the difference in pelage is equally striking. These animals are similar in size, but the Rumanian animals are much darker dorsally and on the belly, have darker chest patches, and the ratlike face is obvious in the live animals. Although viable crosses have been produced in the laboratory, both histological data and attempts at breeding indicate that the F_1 generation is sterile. On the basis of karyological studies (Raicu and Bratosin, 1968) as well as electrophoretic and chromatographic analysis of the blood serum, Raicu et al. (1968, 1969) stated that the Rumanian hamster, *Mesocricetus newtoni,* was a different species from the Syrian hamster, *Mesocricetus auratus,* and the data given above reinforce this conclusion.

The Rumanian hamster is smaller and darker than the Turkish and Kurdistan animals, and the facial appearance in the live Rumanian animals is distinctive, but these differences are not sufficient for specific separation. Crosses between Rumanian hamsters and animals from Malya in central Turkey or from Kurdistan produce viable young, but the F_1 generation is sterile. Furthermore, the occurrence of diabetes in the Rumanian-Turkish cross, and the small litters and failure of reciprocal crossing in the Rumanian-Kurdistan matings, are evidence that the crosses encounter biological barriers sufficient to separate them as species.

When Lehman and Macpherson (1967) described the karyotype of their hamsters from Kurdistan, the animals were tentatively identified by the British Museum as *Mesocricetus brandti* from skins and skulls. Our subsequent comparison with skins and skulls of hamsters from Malya reveal that the two groups resemble each other closely, though the Kurdistan animals are lighter on the dorsal surface. Color photographs of these animals alive, lent through the kindness of Dr. R. E. Billingham of the Wistar Institute, indicate that the animals do not possess the ratlike face which seems to be typical of hamsters from Rumania. After karyotypic examination of hamsters from Kurdistan, Malya, Rumania and Syria, Todd et al. (1972) concluded that the karyotypes of animals from Kurdistan and Malya most closely resembled one another.

The evidence is persuasive that the animals from Malya and Ankara and the Kurdistan hamsters are all *Mesocricetus brandti.* The lighter dorsal pelage of the Kurdistan animals, when compared

to the two colonies from central Turkey and the specimens in the British Museum, suggest that the Kurdistan animals may be a subspecies of *M. brandti*. In this regard, it is of interest that Mr. Anat, who is a trained field naturalist, has written us that the animals in the northeast area of Turkey near Kars are larger and darker than hamsters from central Turkey. Several subspecies of *M. brandti* may exist in Turkey, Armenia and northwest Iran, separated by various geographic barriers.

We conclude that there are three distinct species of small hamsters of the genus *Mesocricetus* in areas south and west of the Caucasus. *Mesocricetus newtoni* inhabits the Dobruja area in the eastern part of Rumania and Bulgaria and, according to Hamar and Schutowa (1966), probably is not found west of the Danube in Rumania. *Mesocricetus brandti* ranges across Anatolian Turkey into the northern part of Iraq and the northwestern portion of Iran. Hamar and Schutowa (1966) and Aharoni (1932) report that *M. brandti* is found south of Aleppo and Aharoni indicates the southern limit is at the latitude of the Sea of Galilee. In contrast to this wide distribution, *M. auratus* appears to be restricted to the area of the type locality of Aleppo, Syria.

For definitive information on the distribution of *Mesocricetus* in and north of the Caucasus, one must turn to investigators who had access to live specimens or collections in Russia. Although there are differences of opinion on the number of subspecies involved, Ognev and Heptner (1927), Vinogradov and Argiropulo (1941), Hamar and Schutowa (1966) and Gromov et al. (1963) all agree that the genus in this area is clearly separable into two species, referred to here as *M. brandti* and M. *raddei*. *M. brandti* are smaller than *M. raddei* and there is no black on their bellies. In their karyological studies, Vorontsov and Krjukova (1969) and Ivanov (1969) also concluded that *M. brandti* and *M. raddei* were specifically different. The *M. brandti* studied by Ivanov came from the Daghestan area and Gromov et al. (1963) state that this species is found in the plains and foothills of Daghestan. Gromov et al. (1963) and several other Russian investigators remark on the discontinuity of the distribution of *M. brandti* in the Caucasus, and we find nothing in the literature to indicate that it is actually sympatric with *M. raddei* in any area.

Todd et al. (1972) reviewed the reported karyotypes of *M. brandti* from Daghestan, Armenia, Iranian Azerbajzan and Erevan, and of a specimen which was probably from Iran. They presented a haploid idiogram comparing the karyotypes of the Kurdistan animals with

our hamsters from Malya, *M. newtoni* from Rumania and laboratory *M. auratus*. The diploid number (2N) of *M. newtoni* was 38, that of *M. auratus* was 44, and that of the various specimens of *M. brandti* was 42. They concluded that the differences in the karyotypes of the samples of *M. brandti*, including the fundamental numbers, was sufficient to suggest that the designation *M. brandti* was being applied to a group of "cryptic" species. At the time their data was collected, it was not known that the karyotypes of hamsters from Malya and Ankara differed both in diploid and in fundamental numbers, though the animals appeared phenotypically similar and produced fertile crosses in the laboratory. Zimmerman (1970) emphasizes the frailty of karyological data when used by itself to determine taxonomic relationships and the breeding success between the Malya and Ankara group reinforces this concept.

Recent evidence indicates that some rodents may be genetically isolated though phenotypically similar. *Spalax* (Nevo and Shkolnik, 1974), *Perognathus* (Patton, 1972), *Thomomys* (Patton, 1973) and *Peromyscus* (Schmidly and Schroeter, 1974) are some of the rodents which have marked chromosomal differences in groups from restricted, contiguous areas. Patton and Dingman (1970) point out that the diversity in karyology often occurs in burrowing rodents with limited dispersibility and small breeding populations. Field reports, particularly those of Argiropulo (1939), and our observations of "field" conditions in the laboratory indicate that hamsters are fossorial rodents, though their way of life is not comparable to that of an animal such as *Thomomys*, which spends virtually its whole existence underground. Aharoni (1932) and Argiropulo (1939) both emphasize that *Mesocricetus* is found in very specific types of habitat and Argiropulo states that the distribution of *brandti* in Armenia is limited to specific altitudes. Mr. Anat has written us that there was no available open water in the areas where he trapped our animals, yet we find that hamsters in the laboratory which are fed laboratory rat chow cannot survive without water to drink. Thus, *brandti* in some areas must depend on metabolic water and water in their food, and this must limit their distribution. Furthermore, Argiropulo states that they never live in wooded areas. These factors, coupled with their slow locomotion, may limit *brandti* to very specific types of habitat and isolate one group from another, which may explain why the karyotype of each population of this species examined to date differs from the other.

Aharoni (1932) points out that the Syrian hamster is confined to the immediate vicinity of Aleppo and suggests that the very dry climate has resulted in the recognizably different *M. auratus.* This population appears to have been isolated long enough to become specifically distinct, a conclusion that is supported by the cross-breeding experiments. Evolutionary factors of less influence may be causing the differences in karyotypes of *M. brandti* without producing reproductive isolation or obvious differences in phenotype.

NATURAL HISTORY

Published observations of *M. brandti* under natural conditions are scanty, the most complete being that of Argiropulo (1939) who studied this species in the Caucasus. Because his paper is written in Russian, a brief summary is included here, supplemented with field notes taken by Mr. Anat when he was trapping hamsters for us in Turkey. Both sources agree that the habitat of *M. brandti* consists of dry, rocky steppe country sometimes bordering culti-vated fields. These hamsters do not inhabit wooded or bushy areas, and appear to avoid areas of high humidity and dampness. In the Caucasus they are found at altitudes as high as 2800 meters. Al-though they may be seen at dawn and dusk, they are mainly noc-turnal and feed principally at night. In the wild, they are relatively fearless, for Argiropulo observed that they were apt to stand on their hind legs facing an intruder in the agonistic posture so often seen in the Syrian hamster.

In order to observe these animals under as natural conditions as possible, a compound measuring 160 × 280 centimeters (cm) and filled with clay soil to an average of 30 cm was set up in our labo-ratory. One part of the area was made higher than the remainder by the addition of rocks up to three kilograms in weight, and part of the flatter surface was planted with ground pine. A sunken dish served as a water supply and the bare soil was moistened periodically. During the month of July, two male and three female five-week-old *M. brandti* were released simultaneously into the compound. Within a few hours there were numerous holes in the soil and all of the animals were underground. For the next four months, no animal was ever seen in the broad daylight, though they were seen above ground when light was failing in the evening or under dim artificial illumination at night.

During the period of observation, the animals were given Purina laboratory chow (Ralston Purina Co., St. Louis, Mo.) as food, which was thrown at random on the ground. Most of the food which was not eaten was stored underground during the night. Argiropulo noted that *M. brandti* stores both grain and grasses in its burrows. M. R. Murphy (personal communication) reports that *Mesocricetus auratus* obtains grain by standing on its hind legs, grasping the stalk with its front feet or pushing it down, and cutting the stalk with its incisors. The animal then eats the fallen grain or puts it in its cheek pouches. Numerous stalks of tall grasses with ripened ears were pushed into the soil of the compound to simulate growing grain and the animals were observed in the evening under dim illumination. In spite of the fact that these hamsters were the sixth generation of animals raised in the laboratory, with no exposure to any growing grain, they cut down the stalk and consumed the kernels as described above.

After the five hamsters had been in the compound for 130 days, they were removed using box traps, and a diagram of their tunnel system was constructed by squirting silicone foam (Froth Pak, Insta-foam Products Inc., Addison, Ill.) down the various holes and permitting it to harden. Once hardened, the earth was scraped away and a positive cast of the underground galleries was obtained. Although these casts show several points of interest, it must be borne in mind that the hamsters were limited in the depth of their digging by the floor of the room.

At the time that the casts of the burrows were made, we were unaware of the work of Argiropulo (1939) with detailed descriptions of burrows which he excavated in the Caucasus. However, within the limitations imposed by the artificiality of the compound, the two series of burrows were remarkably similar. Both Argiropulo and Anat note that the main entrance of the burrow, when on a flat surface, is an almost vertical shaft extending a meter or more in depth. The vertical shaft usually curves quite abruptly to a horizontal plane, and the galleries and rooms branch from this shaft. Mr. Anat indicates that the hamster burrows can always be distinguished from those of *Microtus* or *Citellus*, which may inhabit the same area, because the burrows of the latter two enter the ground at a slant. When a hamster burrow was made in a bank, Argiropulo found that it was nearly horizontal. This type of tunnel was usually abandoned in a few days after other tunnels had been dug and the space filled in

with dirt and feces. Both in the artificial situation and in the natural state there were several underground chambers. One or more of these chambers were used for storage of food. Another chamber was a nesting area which in the natural state was filled with dried grass. In the artificial compound, the nesting material was ground pine and shreds of a cardboard box that had been placed in the area as a surface shelter. Argiropulo found that one chamber was used exclusively as a latrine, but no such chamber was found in the artificial compound.

To observe the method of digging employed by the hamster, a narrow, rectangular, clear Plexiglas box measuring $62 \times 31 \times 3.5$ cm (inside dimensions) was constructed. The box was placed on edge with its long side down and filled with earth to a depth of 17 cm. A hamster placed on top of the earth was squeezed so that both of its sides touched the sides of the box. The animal was capable of moving forward or backward, or of turning around, but it could only rest comfortably with its body parallel to the long axis of the box.

After several minutes of exploration, the hamster always commenced digging in the earth. The rapidly moving front feet were used to displace the earth, with motions like a dog burying a bone. The loose dirt accumulated under the chest and abdomen. To move this dirt, the hind feet were thrust backward together, while the front feet were braced. During this maneuver, the hamster arched its back and lifted its head. If the animal was in a tunnel, the head-lifting served to tamp the earth on the roof of the tunnel. As the tunnel or the surface excavation became longer, the earth at the head of the excavation was moved to the tail by a series of parallel kicks of the hind feet accompanied by back arching and head lifting, as described above. After each set of kicks, the hamster moved backward about one-half the length of its body and resumed moving the earth. Use of the mouth and cheek pouches for moving dirt was not observed, though the animals often took small quantities of earth in their mouth as if to taste it.

The rapidity with which hamsters can move earth and dig tunnels marks these rodents as truly fossorial, and indicates that hamsters kept in laboratory cages are denied a significant part of their normal behavioral pattern. The lifting of the head to tamp the roof of the tunnel apparently has functional significance, for Argiropulo observed that the inside of the tunnels which he excavated were very smooth.

LABORATORY CARE AND REPRODUCTION

Turkish hamsters in this colony are now kept in individual 17 ×
17 × 24 cm floored cages and given ample shavings for bedding.
During breeding 23 × 23 × 38 cm cages are used. The hamsters do
not thrive in wire bottomed cages. The animals are given water
and Purina laboratory rat chow *ad lib.* with a slice of raw apple
and 30 g rolled oats weekly.

In 1968–1969 the colony was greatly reduced due to "wet tail" diar-
rhea and osteomalacia. The diarrhea was partially controlled by
adding 0.05 per cent tetracycline hydrochloride (Polyotic, Cyana-
mid) to the drinking water for a period of not longer than two weeks.
Various diets, one consisting wholly of Purina mouse breeder
chow, have been experimentally tested, but the diet outlined above
has been most satisfactory. The cause of osteomalacia has not
been determined, but since it no longer occurs in the colony, it proba-
bly was due to an insufficiency in the diet exacerbated by an intes-
tinal infection which, in its most virulent form, resulted in "wet
tail" and death.

Although it rarely occurs in *M. auratus*, several *M. brandti* suf-
fered from malocclusion, so that the upper and lower incisors grew
unchecked by wear. The unrestrained growth was remarkably rapid.
In a three-month-old hamster the upper incisors had grown slightly
more than a full circle with one incisor penetrating and exiting
from the roof of the mouth. The lower incisors of a one-year-old
hamster with malocclusion were trimmed periodically and the ex-
cess tooth material was measured. Growth averaged 1 cm per month
compared to growth of approximately 0.4 cm per month reported
by Sarnat and Hook (1941) in the much larger thirteen-lined ground
squirrel (*Citellus tridecemlineatus*).

Pairs of hamsters from five weeks to two years of age were exposed
to each other for breeding in every month of the year. The young-
est female to produce a litter was 50 days old when she gave birth,
and animals seven to eight weeks of age reproduce successfully
though they have not yet attained full growth. Hamsters reach
their peak of fecundity at about one year of age, and most of our
breeding is carried out with animals of this age. The tests of one-
year-old males are large during the breeding season and histological
examination shows active spermatogenesis. Females of this age
almost invariably have normal estrous cycles. In the second year,
the female estrous cycles are less regular during the breeding season

though active spermatogenesis usually occurs in the males. Breeding is notably less successful in these animals. We have not attempted to breed three-year-old hamsters.

In our laboratory (Boston, Mass.), animals exposed to natural day length usually were not in breeding condition between the months of November and March. During this period the females which were examined were apt to have anestrous vaginal smears with a preponderance of non-nucleated squamous cells. The testes of some males were atrophic with no histological evidence of spermatogenesis, and no stored sperm in the epididymides. Other animals of both sexes had all the anatomical indications of full breeding condition. The testes were the same size as those of summer animals and histological examination revealed spermatogenesis, while biopsy of the epididymides showed motile sperm. Vaginal smears indicated normal estrous cycles.

In 1971, pairs of hamsters were exposed to each other from January to September. As was expected, successful breeding was low for the first three months of the year, improved in the next two months and then declined. Thus, from January 20 to April 3 there were 11 litters out of 33 exposures. Successful matings peaked in May, with seven litters born out of 13 exposures. From June 1 to September 3, there were only 11 litters born in 34 exposures.

From 1966 to 1971 various changes in daily illumination and diet were carried out in order to discover the optimum conditions for breeding this species in the laboratory. During the first two years after their arrival, the animals were maintained on 10 hours of illumination in each 24 hour period. Breeding success was high during the first summer (1966) with a total of 109 young in 16 litters being produced by 23 pairings from the wild-caught group of six males and seven females. During the next summer there was a notable decline in successful matings. Of a total of 79 pairings with 42 males and 45 females, only 111 young in 15 litters were produced. In the case of unsuccessful pairings, the female always appeared to be the unwilling one of the pair.

In the difficult years of 1968 and 1969 the colony barely maintained a steady population, but by 1970 a successful diet had been developed, the daily lighting had been standardized to the illumination of this latitude, and attempted breedings were usually limited to the spring and summer months. Under this regime, breeding success improved, with 17 litters in 34 matings in 1974.

Hoffman and Reiter (1965) and Elliott et al. (1972) have reported that the reproductive cycle of the male Syrian hamster is responsive to photoperiod. A controlled experiment to test this responsiveness in the Turkish hamster has not been carried out, but the birth of litters in January and February, with the day length near the minimum, shows that the photoperiodic effect is not absolute. Data presented below indicate that hibernation is involved in a much larger segment of the yearly life of the Turkish hamster than is the case in the Syrian species. Turkish hamsters which are exposed to a constant temperature of $22°C$ in the laboratory during the winter months are living in an environment which they would never encounter for long periods in the natural state. It is not surprising that photoperiod alone does not control the seasonal sexual cycle under these circumstances.

The breeding behavior of the Syrian hamster has been described by Murphy and Schneider (1970) and the behavior of the Turkish hamster is similar. When the animals were paired in the afternoon, there was usually some preliminary exploration, but not much activity occurred until nightfall. In some cases, however, an immediate antipathy developed and violent fighting occurred at once.

After the first half hour of exposure, fighting was not as frequent, but it could occur at any time. If the animals were kept together for more than four days the chances of fighting increased, perhaps because the female was pregnant. Fighting was always violent, with the female biting the male near the head region and then clawing him with both front and rear feet. The male, in spite of the punishment he received, often followed the female and attempted to copulate, only to be attacked again. If the male retreated, the female often pursued him and bit him on the flanks and hind quarters. Attempts to reduce the damage to the male by providing various shelters were unsuccessful because of the male's persistence in pursuing the female. Often the punishment received by the male was fatal. At autopsy the cuts and bruises did not seem sufficiently severe to cause death and it is possible that exhaustion was a contributing cause.

The estrous cycle of the Turkish hamster is similar to that described by Kent (1968) for the golden hamster. The cycle is of four days duration and estrus is characterized by the appearance of large numbers of nucleated epithelial cells in the vaginal smear.

Gestation is 15 days in length and the litter size has varied from one to 13 with the average being six (N young = 1021, N litters = 177).

No female has produced more than three litters during one breeding season and Argiropulo (1939) reports that two litters a year is maximum for wild animals in the Caucasus. The female becomes extremely apprehensive before the birth of her litter, and partial darkness and ample bedding are a necessity. Even if left undisturbed she may kill and eat the young, and if she is handled during parturition the destruction of the litter is inevitable. Perhaps a littering cage which approximated the fossorial existence in the wild would reduce this nervousness, but this has not been tested.

Hamsters are born blind and naked, but they quickly grow a protective coat. By the twelfth to thirteenth day the eyes open and the young eat rolled oats, ground laboratory chow and drink from the water bottle. The young are weaned by the mother before the twentieth day, and we routinely separate the young from the mother at four weeks of age.

The young live together amicably until about the seventh week, when fighting starts to occur. Usually one animal is the aggressor, but if it is removed from the litter, another soon takes up the role. The attacked animal is bitten violently, resulting in large wounds from tears in the tender skin, and these are often fatal. Presumably, under natural conditions this aggressive behavior causes dispersion of the litter with little harm to its members, but in the laboratory it is a serious problem. Although we have used several types of shelters, we have not been able to keep Turkish hamsters in collective cages and must separate and maintain them in single cages at about six weeks of age. Obviously this is a serious disadvantage for maintaining a large colony.

The young hamsters grow rapidly, and healthy litters average 91 g in weight with a range of 50 to 141 g (N = 411) at six to seven weeks of age. Animals born after June do not attain sexual maturity until the following spring.

AGING

Turkish hamsters in captivity tend to become obese after the first year of life and sometimes weigh over 200 g, with our heaviest recorded animal attaining 285 g. It is unlikely that hamsters in the wild, with limited food supply and an active life, would ever reach this weight.

The median life-span of 43 animals which were bred and kept in the laboratory at a room temperature of $22 \pm 3°C$ was 670 days with a range of 231 to 1399 days. After about two years of age, the

pelage usually loses its glossy smoothness and the animals present a scruffy appearance. The effect of hibernation on aging in this or any other species of mammal is unknown and an experiment is in progress to determine if these hamsters age less rapidly during hibernation.

HIBERNATION

During the past ten years, quite complete records of the colony of *M. brandti* have been maintained, so that some information can be gleaned concerning the putative factors which control hibernation. Previous observations on *M. auratus* in this laboratory (Lyman, 1954; Lyman, unpublished observations) provide comparison between the two species.

In those studies, all hamsters were moved to a cold room kept at $5 \pm 2°C$ and lighted 8 to 10 hours a day. The animals were housed in individual cages with ample shavings and food and water *ad lib*. Hibernation was monitored by dusting the backs of hibernating Syrian hamsters with shavings. If the shavings were still in place at the next observation, hibernation was assumed to be continuous. This technique is common among students of hibernation (Mrosovsky, 1971) but is not always accurate. Because hamsters often burrow in their bedding before hibernation, shavings occasionally become lodged on the back and the hamster may be erroneously scored as being in continuous hibernation. Following the technique of Johnson (1931), extraneous material (rolled oats) was placed on the backs of the hibernating Turkish hamsters. Arousal from hibernation invariably displaced this material. The result of this difference in technique is to make the Syrian hamsters appear to be "better" hibernators than they actually are.

The timing and period of cold exposure was not the same for *M. auratus* and *M. brandti*. The former were moved to the cold at various times of year and remained there until they hibernated or died. In contrast, because it was necessary to enlarge the *M. brandti* colony, most of these animals were exposed to cold in the autumn and removed to the warm room for breeding in the spring. The fact that the *M. auratus* were moved to the cold in all seasons of the year should have no effect on the comparisons given below. Smit-vis and Smit (1963) have theorized that there is a seasonal preparation in this species which results in a greater tendency for

hibernation in February. The evidence is not persuasive, however, for it is based on 26 animals, two of which are excluded from the basic computations. The paper relates the month in which the animals were exposed to cold to the lapse of time before hibernation occurred, but there are no data for April through July or for September and October, and there is data for only one animal in August and two in March. From our records of over 2800 Syrian hamsters, placed in the cold in every month of the year, we adduce no convincing evidence that the tendency to hibernate is seasonal in this species.

In studies such as this, an as yet unresolved problem concerns the criteria which should be used to distinguish "good" from "poor" hibernators. There are at least five interdependent factors which can be considered in such a comparison. These are: 1) the number of animals in a group which hibernate during the period of exposure to cold, 2) the span of time between cold exposure and hibernation, 3) the length of the hibernating season, 4) the amount of time spent in hibernation compared to the amount of time in the cold, and 5) the length of the period during which an animal remains in continuous hibernation. Concerning the fifth factor, Pengelley and Fisher (1961) have shown that the lengths of the periods or bouts of hibernation are quite predictable with individual *Citellus lateralis*, but these lengths may vary greatly in a group. We find that the same situation obtains in *Mesocricetus* so that the maximum time of uninterrupted hibernation is more definitive than an average of the lengths of the bouts of hibernation. Until more is known about the subtle physiological nuances which determine whether an animal does or does not hibernate, it is not practical to attempt to assign meaningful values to the five factors listed above, nor to make statistical comparisons. Therefore, in the following studies as many factors as possible are considered but no attempt is made to weight their importance.

In a group of 373 Syrian hamsters exposed to the cold, 68 per cent or 252 hibernated and 121 animals died before ever entering the hibernating state. The shortest period before hibernation occurred was three days of cold exposure and the longest was 218 days (Lyman, 1954). Once hibernation occurred, the period during which *M. auratus* hibernated lasted about three months. An accurate figure on the percentage of time spent in hibernation cannot be obtained because many of the animals were used in acute experiments and the best hibernators were usually chosen. The longest

recorded bout of hibernation was 21 days and the usual period of hibernation was a week or less (Lyman, 1954).

The hamsters from which these data were collected were originally obtained from commercial dealers and hence must be descendants of the trio which were the foundation stock of the laboratory hamsters used today (Adler, 1948). Twelve *M. auratus*, which were the first generation of animals obtained in the field near Aleppo by Dr. M. Murphy, were exposed to the cold in the autumn of 1971 under the conditions described above. Although the sample is small, there was no detectable difference in the tendency of this group of animals to hibernate when compared to laboratory animals. Thus, forty years of domestic breeding with no selection pressure for hibernation has not changed the pattern of hibernation in *M. auratus*.

These "native" Syrian hamsters provide some information concerning the percentage of time spent in hibernation. The group was moved to the cold on November 15, 1971 and taken from the cold on May 26, 1972. No animal hibernated before January and hibernation occurred only 11.3 per cent of the total time. The best months for hibernation were January through April, during which time the animals were in hibernation 13.7 per cent of the time.

Between the years 1971 and 1975, a group of 318 *M. brandti* were exposed to cold for periods of 145 to 172 days. Two hundred ninety-three or 92 per cent hibernated at some time during this period. Eight animals died without hibernating and the remaining 17 did not hibernate at all. Thirty-one animals entered hibernation within 24 hours after exposure to cold. Once hibernation started, the period during which this species hibernated lasted about five months, but for some animals the hibernating season was as long as 10 months. In the entire group, 36 per cent of the time in the cold between November 15 and April 15 was spent in hibernation. The longest period of uninterrupted hibernation was 28 days, with the average bout of approximately the same duration as *M. auratus*. Thus *M. brandti* is a "better" hibernator than *M. auratus* in all categories except the average length of the bout of hibernation.

The records of over 400 *M. brandti* which have been exposed to cold reveal no obvious factors which control or influence hibernation in this species. However, they do give a clearer picture of the pattern of hibernation and its variability, and obviate the need for further research in some aspects of the problem.

As reported for *M. auratus* (Lyman, 1948), *M. brandti* does not undergo the period of autumnal fattening and lethargy which is so typical of the Marmotini that hibernate. Like *M. auratus, M. brandti* almost invariably lose weight during the first two or three weeks of exposure to cold, with the heavier animals losing the greater amount. Some animals, especially the young of the year, are apt to regain and exceed the original weight if kept in the cold for several months. The amount of hibernation which occurs during this time is not correlated with the change in body weight.

Examples from the spring and summer months demonstrate that this species will hibernate at any time of the year. Certainly, if compared to Marmotini such as *Citellus lateralis* or *C. tridecemlineatus*, any seasonal change in the tendency to hibernate is very poorly defined. These citellids, if experimentally naive, rarely hibernate when exposed to cold during the spring and summer months and almost invariably hibernate in the autumn. In contrast, of 66 *M. brandti* which were in the cold in June, 75 per cent hibernated at some time during the period and, in July, 77 per cent of 53 cold-exposed animals hibernated.

The majority of our animals were placed in the hibernaculum between October 1 and January 2. In a sample of 257 animals, no particular one of the four months was favored for onset of hibernation or for the number of days spent in the hibernating state. Whether exposure to cold was begun in early October or in January, hibernation became much less frequent by the beginning of April and, when removed from the cold room in May, most of the animals had ceased hibernating.

No organized experiment to test the effect of photoperiod has been carried out, but it is clear that the timing of the onset of hibernation does not depend exclusively on this factor, since hamsters hibernated in June when the daily illumination was close to its peak.

Although 9.7 per cent of a sample of 318 animals hibernated within 24 hours after being exposed to cold, these animals did not necessarily hibernate for a greater number of days than animals which started hibernation at a later date. Age does not affect the ability to hibernate, for a comparison between animals ranging from 3.5 to 36 months of age revealed no differences in the onset or pattern of hibernation.

In spite of efforts to standardize conditions, the frequency and pattern of hibernation changed from year to year in the colony as

a whole and with individual animals. There is no simple explanation for the fact that individuals failed to hibernate with six months of cold exposure one year, and hibernated under the same conditions the following year. Nor can the observation that the colony exposed to cold hibernated only 16 per cent of the time in 1970 and 39 per cent in 1971 be readily explained. Conditions in the cold room are maintained as identically as possible from year to year, but changes such as shifts in caretaking personnel are inevitable. Even differences in handling the animals during cleaning of the cages might influence the onset of hibernation.

It was observed that the first shipment of *M. brandti* hibernated 67 per cent of the first sojourn in the cold and only 42 per cent in the second. This suggested that environmental factors might play an important role in the control of hibernation. The ability of animals to store food had already been shown to have an effect on hibernation in *M. auratus* (Lyman, 1954) and this factor was included in the experimental design.

M. brandti between five weeks and six months of age were placed in the following experimental conditions. As often as possible, sexes and litter mates were matched. On July 8 five animals were placed in the "natural" compound described above. For all other groups, each individual was put in a separate cage ($23 \times 23 \times 38$ cm) and given ample shavings for bedding, and water *ad lib*. A control group of 13 animals was given Purina rat chow pellets *ad lib*., which they were able to store in a corner of the cage, while another group of six was given ground chow in unspillable food cups which prevented these animals from storing food. Twelve other cages were fitted with exercise wheels, and the number of revolutions for each wheel was monitored by an event recorder (model A620X, Esterline Angus Instrument Co., Indianapolis, Ind.). The animals in six of these cages were given rat chow pellets *ad lib*. while the others were fed from unspillable food cups. All animals received 14 hours of light daily at the start of the experiment, and this was reduced by one hour approximately every 16 days. On November 12 all animals were moved to smaller individual cages ($17 \times 17 \times 24$ cm) with shavings, water and rat chow pellets *ad lib*., and on November 15 all were moved in these cages to the cold room, where the daily illumination was 9 hours. Thus, after the preparation period, all animals were exposed to the same conditions. Records of hibernation were kept for the following 137 days.

As has been reported for many other species, the use of the activity wheel varied greatly from animal to animal. The nocturnal habits of *M. brandti* were verified, for virtually no activity was recorded during the daylight hours. There was no correlation between the tendency of an animal to run in the wheel and its subsequent hibernation. All of the hamsters hibernated at some time during their exposure to cold, but no one group showed a tendency to enter hibernation earlier or to have longer bouts of hibernation. The percentage of time spent in hibernation was as follows: "natural" enclosure, 56 per cent; activity wheel, food hoarding, 43 per cent; no wheel, food hoarding, 37 per cent; wheel, no hoarding, 34 per cent; no wheel, no hoarding, 25 per cent. These results suggest that the conditions prior to cold exposure may have an influence on the subsequent amount of hibernation and that "natural" conditions increase the tendency to hibernate. However, none of the factors tested are crucial to the onset of hibernation.

Experiments such as these are easily carried out with *M. brandti*. Because this animal hibernates readily and can be bred in the laboratory, it offers a unique opportunity to study the effects of various factors using matched pairs of known age and lineage.

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EPIGONUS TREWAVASAE POLL, A JUNIOR SYNONYM OF *EPIGONUS CONSTANCIAE* (GIGLIOLI) (PERCIFORMES, APOGONIDAE)

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ABSTRACT. The holotype of *Pomatomichthys constanciae* Giglioli was reexamined and compared with specimens of *Epigonus trewavasae* Poll from equatorial west Africa, northwest Africa, Madeira, and the western Mediterranean. The two nominal forms were not distinguishable at the species level; thus, the name *Epigonus constanciae* should be used for the species under consideration. A description and discussion of the geographic variability of *E. constanciae* is provided.

INTRODUCTION

Questions about the status of *Pomatomichthys constanciae* have recently arisen as the result of increased interest in deep-sea members of the family Apogonidae. *P. constanciae* was originally described from a single specimen from the Straits of Messina (Giglioli, 1880). The description was incomplete, unillustrated and included several inaccuracies. Although Giglioli designated the fish a new species, he indicated that the specimen resembled juveniles of the more common Mediterranean apogonid, *Epigonus telescopus* (Risso).

Perhaps because of Giglioli's comment and because of the dearth of information about Mediterranean continental slope ichthyofaunas, *P. constanciae* was generally accepted as a junior

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synonym of *E. telescopus* (e.g., Jordan and Evermann, 1896; Jordan, Evermann and Clark, 1930; Schultz, 1940; Tortonese and Queirolo, 1970; Tortonese, 1973). Goode and Bean (1896) were the last authors of a comprehensive treatise to give *P. constanciae* consideration as a separate species. Cavaliere (1956) claimed to have compared the juveniles of *Epigonus telescopus* and *Pomatomichthys constanciae*, but Tortonese and Queirolo (1970) and Tortonese (1973) deemed the study of doubtful validity.

In 1974, Mayer published a revision of the genus *Epigonus*. Although the paper included *P. constanciae* as a synonym of *E. telescopus*, it pointed out that several features of *P. constanciae* were reminiscent of traits characteristic of *Epigonus trewavasae* Poll. The same work reported *E. trewavasae* from the Mediterranean for the first time and urged that further studies be undertaken on the relationship between *E. trewavasae* and *P. constanciae*.

The current paper stems from a reexamination of the *P. constanciae* holotype and a comparison of this specimen with *E. trewavasae* from equatorial west Africa, Mauritania, Madeira and the western Mediterranean. Our findings indicate that *P. constanciae* and *E. trewavasae* are conspecific and that the correct name for the species should be *Epigonus constanciae* (Giglioli).

METHODS

Specimens were examined according to techniques outlined by Mayer (1974, 1975) and by Hubbs and Lagler (1958). Statistical analyses were performed on a Wang Model 720 Programmable Calculator at the Department of Marine Science, University of South Florida. A package program was used to calculate routine meristic parameters, such as means and standard deviations. Linear regression analyses were undertaken on mensural data using Ricker's method for Functional (GM) Regressions (1973: 412–414). To insure linearity, scatter diagrams were plotted for all morphometric data. Characters exhibiting non-linear scatters, as determined by inspection, were excluded from consideration.

Meristic characters exhibiting slight variability are reported in the text as the value of the character followed by the number of individuals exhibiting that character. Data exhibiting greater variability are presented in tabular form. Mensural data are

presented as linear regressions and/or as ratios on standard length (SL) or head length (HL).

Specimens for this study were obtained from the following institutions:

IRSN: Institut Royal des Sciences Naturelles de Belgique, Brussels
ISH: Institut für Seefischerei, Hamburg
ISTPM: Institut Scientifique et Technique des Pêches Maritimes, La Rochelle
MCZ: Museum of Comparative Zoology, Cambridge, Massachusetts
MF: Museo Municipal do Funchal, Madeira
MSNG: Museo Civico di Storia Naturale, Genoa
MZF: Zoological Museum, Florence
USNM: National Museum of Natural History, Washington, D.C.
ZMB: Zoologisches Museum der Humboldt Universität, Berlin

SYSTEMATICS

Mayer (1974: 183–186) provided a comprehensive description of *Epigonus trewavasae*. The following discussion of *E. constanciae* represents a recapitulation of the former account, modified to reflect data obtained from a larger, more representative sample of individuals. Readers are referred to Mayer (1974) for synonymies, accounts of ontogenetic change and in-depth comparisons with congeners.
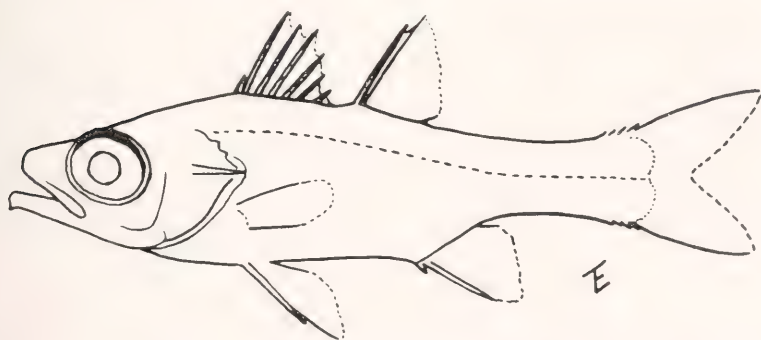

Figure 1.   *Epigonus constanciae* holotype, MZF 3089, 115 mm SL.

Epigonus constanciae (Giglioli, 1880). Figure 1.

Pomatomichthys constanciae Giglioli, 1880: p. 20; original description; Straits of Messina. Holotype examined: MZF 3089.

Epigonus trewavasae Poll, 1954: p. 91; figure 27; original description; NOORENDE III, Sta. 52: 06°08′S, 11°30′E, 280–290 m. Holotype examined: IRSN 209.

MATERIAL EXAMINED

IRSN 209 (1: 153.9 mm, holotype *Epigonus trewavasae*, NO-ORDENDE III Sta. 52, 06°08′S, 11°30′E, 280–290 m); IRSN 16549 (1: 97.1 mm, Golfe de Cagliari, 540 m); IRSN 16550 (4: 75.5–98.6 mm, Golfe d'Oristano, no depth recorded); ISH 386/64 (3: 144.6–153.2 mm, WALTHER HERWIG Sta. 137/64, 15°51′N, 16°51′W, 200 m); ISTPM uncatalogued (10: 129.9–158.9 mm, THALASSA Sta. U30, 17°56′N, 16°32′W, 224–322 m); ISTPM uncatalogued (1: 149.0 mm, THALASSA Sta. X007, 20°59′N, 17°37′W, 250–330 m); ISTPM uncatalogued (1: 148.0 mm, THALASSA Sta. X020, 19°08′N, 16°48′W, 280–468 m); MCZ 48849 (1: 76.9 mm, LA RAFALE Cr. I, Sta. 27, 11°25′N, 17°21′W, 200 m); MF 3694 (1: 117.6 mm, from stomach of *Polymixia nobilis*); MF 7231 (1: no SL, from stomach of *Aphanopus carbo*); MF 8213 (1: no SL, from stomach of *P. nobilis*); MF 12518 (1: 124.5 mm, from stomach of *P. nobilis*); MF 14695 (1: 131.3 mm, from stomach of *A. carbo*); MF 15650 (1: no SL, from stomach of *A. carbo*); MF 16067 (2: 120–127 mm, from stomach of *A. carbo*); MF 17088 (1: 125.5 mm, from stomach of *A. carbo*); MF 18204 (1: 97.0 mm, from stomach of *A. carbo*); MF 20599 (1: no SL, from stomach of *A. carbo*); MSNG 38155 (1: 89 mm, Messina, Sicily); MZF 3089 (1: 117 mm, holotype of *Pomatomichthys constanciae*, Straits of Messina); USNM 207723 (2: 98.6–100.9 mm, LA RAFALE Cr. I, Sta. 27, 11°25′N, 17°21′W, 200 m); USNM 207724 (1: 70.9 mm, LA RAFALE Cr. I, Sta. 27, 11°25′N, 17°21′W, 200 m); ZMB 23101 (1: 148.9 mm, MORS Sta. 136/72, 18°36′S, 11°29′E, 275 m); ZMB 23102 (1: 116.5 mm, MORS Sta. 175/72, 18°05′S, 11°27′E, 360 m).

DIAGNOSIS

In the past, *E. constanciae* has been mistaken for *E. telescopus* (Risso) and *E. pandionis* (Goode and Bean). The distribution

of *E. constanciae* also makes confusion likely with *E. denticulatus* Dieuzeide. *E. constanciae* may be distinguished from the above species by the presence of VII–I, 9 dorsal fin elements, a pungent opercular spine, lingual teeth and six to eight pyloric caeca.

E. constanciae most closely resembles *E. pectinifer* Mayer, a species found in the Caribbean Sea, the Gulf of Mexico and the western Pacific Ocean. The former is distinguished by the presence of numerous awl-like fill rakers (29–36) and elongate D_2I and AII fin spines (12.7–16.5 per cent and 13.5–16.8 per cent SL, respectively).

DESCRIPTION

See Tables 1 and 2 for morphometric and meristic data.

Body elongate, fusiform in larger individuals; body depth 21.1–30.0 per cent SL. Head moderate, length 32.2–38.9 per cent SL; height 16.2–18.7 per cent SL. Snout tapering to a rounded point, 7.0–9.1 per cent SL. Lower jaw 13.9–17.6 per cent SL; equal to or projecting slightly beyond upper jaw; bearing two nubs of variable prominence on anterior surface of mandible near symphysis. Maxilla reaching 1/3–1/2 length of eye; ventro-lateral surface of maxillary head bearing sharp, posteriorly re-

Table 1. *Epigonus constanciae* regression parameters. u = functional (GM) regression coefficient; v = Y intercept of GM regression line, Y = uX + v; b = predictive regression coefficient ±95 per cent confidence interval; a = Y intercept of predictive regression line, Y = bX + a; n = number of specimens.

	u	v	b	a	n
HL	0.391	–4.033	0.348 ± 0.026	–3.240	33
Head height	0.191	–1.810	0.189 ± 0.011	–1.566	30
Body depth	0.332	–8.043	0.324 ± 0.027	7.062	33
Eye diameter	0.168	0.976	0.164 ± 0.015	·0.367	32
Snout length	0.078	0.333	0.074 ± 0.010	⌡0.922	32
Maxillary length	0.161	–0.384	0.157 ± 0.013	0.076	34
Lower jaw length	0.174	1.280	0.167 ± 0.017	0.428	36
Interorbital width	0.090	0.910	0.087 ± 0.008	1.300	36
Caudal peduncle length	0.269	0.333	0.264 ± 0.018	0.242	35
Caudal peduncle depth	0.145	3.418	0.139 ± 0.015	2.673	34
D_2I	0.156	1.219	0.150 ± 0.015	0.546	31
AII	0.156	0.547	0.149 ± 0.019	0.282	27
P_2I	0.145	0.298	0.142 ± 0.009	0.233	35

Table 2. *Epigonus constanciae* meristic data. $\overline{X}$ = mean; SD = standard deviation; n = number of specimens.

	$\overline{X}$	Range	SD	n
Pectoral fin rays	17.65	16 19	0.62	40
Gill rakers				
Total	32.43	29 36	1.75	40
Upper arch	9.18	8 10	0.64	39
Lower arch	22.31	20 25	1.30	39
Lateral line scales	47.74	46 50	0.93	34
Pyloric caeca	7.00	6 8	0.64	35

curved process, may be obscured by overlying skin. Eye longer than high, reaching upper profile of head, 41.1–49.1 per cent HL. Interorbital width 8.7–10.9 per cent SL. Caudal peduncle moderate, length 24.3–28.8 per cent SL; depth 9.7–13.8 per cent SL.

Dentition subject to ontogenetic and geographic variation (see Mayer, 1974: 185 and below). Teeth small, conical; present on premaxillae, mandibles and vomer; palatines edentulous or dentigerous; tongue dentigerous, bearing triangular patch of glossohyal teeth along midline and broad, closely-spaced patches of teeth parallel to margins; endo- and ectopterygoids edentulous.

Opercle dominated by pungent, bony spine; surmounted by one or more poorly ossified spinelets. Preopercle well-ossified; angle narrowly produced; ornamentation subject to geographic variation (see below). Interopercle and subopercle weakly serrated or unserrated.

Gill rakers awl-like, 29–36 on first gill arch, 8–10 on upper portion, 20–25 on lower portion (see Table 2).

First dorsal fin VII (38); second dorsal fin I, 8 (2), I, 9 (36), I, 10 (1). Anal fin I, 8 (1), II, 9 (36); ventral fins I, 5 (40), soft rays extending to level of anus. Pectoral fin 16 19 (see Table 2). D_1I variable, 1.7 3.2 per cent SL; D_2I, AII, and P_2I long and pungent; 12.7 16.5 per cent, 13.5 16.8 per cent and 13.0 15.5 per cent SL, respectively.

Preserved specimens yellow-brown; mouth light; branchial and peritoneal membranes black; dorsal fin membranes dark. Viscera often sheathed by heavy, yellow-brown fat deposits.

Description based on forty specimens 70.9 158.9 mm SL.

NOTES ON THE HOLOTYPE OF E. CONSTANCIAE

As mentioned earlier, Giglioli's description of *Pomatomichthys constanciae* is incomplete and includes a number of inaccuracies. Tortonese and Queirolo (1970) figured and redescribed the holotype but did not fully characterize the fish. One aspect of the present investigation involved reexamining Giglioli's type specimen, now in rather poor condition. Measurements and counts obtained from the holotype appear in the Appendix. Qualitative features not mentioned in previous descriptions include:

1. Lower jaw slightly prominent with two nubs at symphysis.

2. Small teeth on premaxillae, mandibles, vomer, palatines and tongue; lingual dentition composed of a central tooth patch and a series of elongate tooth patches parallel to the borders of the tongue.

3. Opercular spine well-developed; two poorly developed spinelets above, but well-separated from the spine.

4. D_1I and AI spines short; D_2I, AII and P_2I spines long. Longest ventral fin rays reach anus.

If previous *E. trewavasae* descriptions (e.g., Mayer, 1974; Poll, 1954) are compared with *P. constanciae* data presented in the Appendix and above, it becomes apparent that the two forms are synonymous. Giglioli's holotype bears all characters diagnostic of *E. trewavasae* including VII–I, 9 dorsal fin elements, long fin spines, 18 pectoral rays, numerous awl-like gill rakers, a pungent, bony opercular spine, mandibular chin nubs and lingual teeth. The species is correctly called *E. constanciae* because *Pomatomichthys* is a junior synonym of *Epigonus*, and *constanciae* has precedence over *trewavasae*.

The fish was named after Giglioli's wife, Costanza.

DISTRIBUTION

E. constanciae is found from the coast of equatorial west Arfica to the Straits of Messina. The species has also been taken off Madeira and probably occurs off the Canaries and Azores. *E. constanciae* appears most abundant on upper portions of the continental slope between 200 and 400 m.

GEOGRAPHIC VARIATION

Mayer (1974: 185 186) briefly commented on geographic variation in *Epigonus trewavasae* and suggested that Mediterranean and African populations may represent subspecies. At the time, sufficient material was not available to draw firm conclusions about the validity of infraspecific categories. Nevertheless, variations were noted in qualitative characters such as the prominence of chin nubs, the development of vomerine and palatine teeth and the occurrence of preopercular armor.

The consolidation of *Pomatomichthys constanciae* and *Epigonus trewavasae* brings the question of geographic variation into sharper focus, because holotypes of the nominal species were taken from opposite ends of the *E. constanciae* range. An analysis of geographic variation in *E. constanciae* was accomplished by dividing the specimens examined for this study into three geographic groups: a Mediterranean series, a Madeiran series and an African series. The African series was the largest group and included fishes taken along the west African coast from 18°S to 21°N. The lumping of west-central African and northwest African populations follows Maurin's conclusion (1968: 78) that the Cape Blanc-Arguin Bank region represents a major northern faunal limit for demersal forms with tropical affinities.

Table 3. Comparisons of meristic data from African, Mediterranean and Madeiran populations of *Epigonus constanciae*. Afr. = African population; Med. = Mediterranean population; Mad. = Madeiran population. See text for explanation.

COEFFICIENTS OF DIFFERENCE

	Afr. vs. Med.	Afr. vs. Mad.	Med. vs. Mad.
Pectoral fin rays	0.33	0.48	0.20
Gill rakers			
Total	0.63	1.24	0.26
Upper arch	0.28	0.59	0.14
Lower arch	0.57	1.27	0.39
Lateral line scales	0.50	0.61	0.16
Pyloric caeca	0.12	0.38	0.09

MERISTIC CHARACTERS

Meristic data comparisons were accomplished by calculating Coefficients of Difference (C.D.'s) (Mayr, 1969: 189–193) for the three geographic groups. The index indicates the degree of non-overlap between two populations for a given character. Populations exhibiting a non-overlap of 90 per cent or more (C.D. ≥ 1.28) are considered distinct at the subspecies level. Table 3 presents data from the current study. As indicated, none of the differences observed are significant at the subspecies level.

MORPHOMETRIC CHARACTERS

Analogous examinations of mensural data were undertaken using regression techniques. Individual values obtained from Mediterranean and Madeiran specimens were compared to regression data from African populations by means of Student's t-tests. Results of the tests are summarized below.

Mediterranean and African populations are very similar and do not appear distinct at the subspecies level. Only one Mediterranean data point fell outside the 99 per cent confidence limits of the African group and most data points fell within the 95 per cent or 98 per cent limits.

The Madeiran population is more distinct. Madeiran *E. constanciae* appear characterized by shallower bodies, shorter heads and shorter jaws than African forms. However, part of the divergence may be an artifact of the Madeiran specimens' poor condition. All were obtained from the stomachs of large, predatory fishes and many were considerably damaged. Additional data are required to assess the taxonomic significance of differences exhibited by the Madeiran specimens.

QUALITATIVE CHARACTERS

Geographic variability reported by Mayer (1974) for qualitative characters was confirmed by the present study. Character states such as prominent chin nubs, weakly armored preopercular margins, edentulous palatines and vomerine tooth patches lacking posterior median extensions are prevalent, but not uniform among fishes from equatorial west Africa. In contrast, poorly

developed chin nubs, spinous preopercular margins, dentigerous
palatines and vomerine tooth patches with posterior median
extensions are common among Mediterranean specimens. The
frequency of "northern" and "southern" character states varies
with latitude. Madeiran and Mauritanian specimens tend to be
intermediate, with the former more closely resembling Mediter-
ranean fish and the latter more similar to specimens from equa-
torial Africa. Because characters exhibit continuous variation
along the range of the species, and because populations at spe-
cies' distribution limits exhibit a mixture of character states and
are not uniformly "northern" or "southern", qualitative characters
do not support the division of *E. constanciae* into formal sub-
species.

CONCLUSIONS

The picture that emerges for *Epigonus constanciae* is one of a
polymorphic species whose range extends from the eastern equa-
torial Atlantic to the western Mediterranean. This pattern has
been reported for other organisms by many authors (e.g., Briggs,
1974; Maurin, 1968; Tortonese, 1964, 1960; Ekman, 1953). The
prevalence of polymorphism among Atlantic and Mediterranean
populations has been discussed by Tortonese (1964: 103–104; 1959
387). Although genetic differences between populations cannot
be ruled out, Tortonese suggests that Atlantic-Mediterranean phe-
notypic dissimilarities may be induced by regional differences in
temperature regime and food availability.

It has been suggested elsewhere (Mayer, 1972) that *E. constan-
ciae* may be among the least vagile species of the genus *Epigonus*.
Adults appear strongly associated with the substrate. Neither
pelagic larvae nor pelagic juveniles are known for this species,
although such forms have been discovered for several congeners.
The smallest known specimen of *E. constanciae* is a 29.8 mm SL
juvenile (IRSN 16548) taken by a bottom trawl off Sardinia.
The latter data suggest that *E. constanciae* may have either a
short-lived pelagic phase or may lack a pelagic phase entirely.

The hypothesis of limited vagility fits the pattern of phenotypic
variability observed for *E. constanciae*. Individual populations
adapt to local conditions and evolve characteristic traits. Breeding
may be assumed to occur primarily between members of the same or

neighboring populations, thus preserving local phenotypes. Relatively isolated populations, such as that from Madeira, are more unique in appearance but still conform to phenotypic patterns resulting from latitudinal gradients in environmental or genetic factors.

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APPENDIX

Meristic and morphometric data obtained from the holotype of *Epigonus constanciae*. MZF 3089. Measurements are in millimeters.

Meristic data

Dorsal fin	VII I, 9	Pelvic fin	I,5
Anal fin	II, 9	Lateral line	46
Pectoral fin	18	Gill rakers	30

Morphometric data

SL	115	Interorbital width	12.5
HL	37	Maxilla	16
Head height	19.5	Caudal peduncle length	29
Body depth	30	Caudal peduncle depth	13
Eye	17	D_2I	16
Snout	8	AII	17
		P_2I	15

STATIONS OF THE THAYER EXPEDITION TO BRAZIL
1865 — 1866

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ABSTRACT. In April of 1865, a group of scientists from the Museum of Comparative Zoology led by Louis Agassiz embarked for Brazil. The purpose of this expedition was to study, *in situ*, the fauna and flora of that country. Members of the expedition, divided into three groups, explored the major part of Brazil from the Rio Tocantins eastward to the coast. Although the major part of the work was done on the distribution and relationships of the fresh water fishes (Agassiz's prime interest) many superb collections were made of plants, invertebrates and vertebrates. Thorough geological surveys provided much information on the structure of Brazil. This paper traces and maps the numerous stations where specimens were collected. Based on modern and nineteenth century maps, and on notes and papers recording the routes followed and collections made by the expedition, it represents a compilation of all this information into a single, indexed directory. This directory should facilitate the future labors of individuals working with the Thayer Expedition material.

INTRODUCTION

Louis Agassiz had for many years wanted to observe *in situ* the fauna and flora of Brazil, a study that he knew would be substantially encouraged by the Brazilian government. The opportunity to do so, however, had never presented itself. This cherished dream became a reality in 1865 through the understanding and generosity of Nathaniel Thayer, a Boston businessman keenly interested in science. Thayer assumed the expenses of Professor and Mrs. Agassiz and six assistants for an expedition to Brazil lasting several months.

The scientific staff from the Museum of Comparative Zoology

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[1]Museum of Comparative Zoology

included John G. Anthony, Assistant Curator of Molluscs (who
was with Agassiz in Rio de Janeiro and made extensive collections
in this area before illness forced his return to Cambridge); Joel
Asaph Allen, Assistant Curator of Birds (later the noted Curator
of Birds at the American Museum of Natural History); Frederick
C. Hartt and Orestes St. John, geologists trained by Agassiz; George
Sceva, Preparator and collector primarily of fossil material; and
James Burkhardt, an artist who had worked for many years with
Aggassiz. In spite of poor health, Burkhardt was an indefatigable
worker and made, according to Agassiz, over eight hundred illus-
trations during the expedition. Most of these unfortunately have
disappeared, but the remaining examples, which are in the Museum
of Comparative Zoology, indicate the high quality of his draft-
manship.

Agassiz also had extremely able and enthusiastic young volun-
teers in his party: Edward Copeland, who accompanied Hartt
from Rio de Janeiro to Bahia; Newton Dexter; Walter Hunnewell;
William James, the future great professor of philosophy at Harvard
University; Stephen Thayer, the son of Nathaniel Thayer; and
Thomas Ward.

On 2 April 1865 the group left Boston aboard the S.S. Colorado,
guests of the Pacific Mail Steamship Company. While at sea,
Agassiz gave a series of lectures giving background for the work
planned for the months ahead. On 23 April 1865 the S.S. Colorado
docked in Rio de Janeiro. Agassiz had arrived at the threshold of
his longed-for goal.

The area covered by the members of the expedition was extensive.
They divided into three groups and explored the major part of Brazil
from the Rio Tocantins eastward to the coast; they also explored
some of its tributaries, to the borders of Colombia and Peru. Al-
though the major part of the work was done on the distribution
and relationships of the fresh water fishes (Agassiz's prime interest),
many superb collections were made of plants, invertebrates and
vertebrates. Thorough geological surveys provided much infor-
mation on the structure of Brazil.

The numerous stations where specimens were collected have
been difficult to locate because several were small villages or clusters
of dwellings on the edge of a river or lake. Many no longer exist
and some have names other than those used in 1865. Rivers and

lakes that were recognized a hundred years ago are frequently overlooked in recent atlases. Researchers involved with the Thayer Expedition have devoted many hours to tracing these stations and collections. Using both modern and nineteenth century maps, it has been possible to locate them fairly accurately. Information concerning the routes followed and the collections made by members and associates of the expedition was obtained from publications listed in the bibliography. The locality names used in the text and on the maps are almost always those employed during the period of the Thayer Expedition. Subsequent changes in locality names or spelling are italicized in the index. Having this information incorporated in a single directory should facilitate the future labors of individuals working with the Thayer Expedition material.

Much work needs to be done with the material collected by Agassiz and his corps, especially with the collections of fishes. Many other groups, both plant and animal, also need comprehensive study and evaluation to complete the survey of Brazil envisaged by Louis Agassiz so long ago.

MEMBERS OF THE THAYER EXPEDITION
1865 — 1866

MUSEUM STAFF:

Louis Agassiz	
Elizabeth Cary Agassiz	
Joel A. Allen	Ornithologist
John G. Anthony	Malacologist
James Burkhardt	Artist
Frederick C. Hartt	Geologist
George Sceva	Preparator
Orestes St. John	Geologist

VOLUNTEERS:
Edward Copeland
Newton Dexter
Walter Hunnewell
William James
Stephen Van R. Thayer
Thomas Ward

MEMBERS ADDED IN BRAZIL

Major M. Coutinho	Brazilian Government Corps of Engineers
Monsieur D. Bourget	French naturalist residing in Rio de Janeiro
Mr. Talisman	Officer, Amazonian Steamship Company

COLLECTIONS ALSO MADE BY:

Captain Anacleto	Fishes, Amazon River
Senhor Augustinho	Fishes, Amazon River
Senhor Barrosa	Miscellaneous, Amazon River
Colonel Bentos	Fishes, Rio Trombetas
Senhor S. E. Pimento Bueno	Forest and river fishes, Amazon River
Dr. Pacheco de Silva	Fishes, Rio de Janeiro
Major Estolano	Fishes, Amazon River
Senhor Felice	Geological observations, miscellaneous, Ceará
Senhor Joao Baptista da Fonseca	Fishes, mammals, environs of Rio de Janeiro
Senhor Glaziou	Plants, palms, Organ Mountains
Senhor Honorio	Miscellaneous, Amazon River
Dr. Justa	Fishes, Rio Parahyba do Norte
Mr. Kaulfuss	Andean fossils
Senhor Antonio de Lacerda	Miscellaneous, Bahia
Senhor Mariano P. F. Lage	Plants, animals, fishes, Rio Novo, basin Rio Parahyba
Senhor Cicero de Lima	Fishes, insects, interior Brazil
Dr. Couto de Magalhaes	Miscellaneous, at his direction, upper Amazon River
Dr. Malcher	Birds, Amazon River
Dr. Mendes	Miscellaneous, Ceará
Senhor Penna	Fishes, Amazon River
Senhor Joachim Rodriguez	Fishes, Santarém
Senhor Sepeda	Miscellaneous, Amazon River
Mr. Charles Taylor	Drawings and collections of fishes and insects, Posse
Father Torquata	Fishes, Amazon River
Senhor Vinhas	Fishes, Rio Xingú

The Emperor, Dom Pedro II, had extensive collections of fishes made for Professor Agassiz from several rivers in southern Brazil.

Thomas G. Cary, Mrs. Agassiz's brother, though not connected with the expedition, contributed material from Montevideo, Buenos Aires and other localities.

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THE THAYER EXPEDITION

Louis Agassiz established a laboratory in Rio de Janeiro which the members of the expedition used as a base for their work during the weeks prior to their departure for other areas of Brazil. Numerous brief trips were made at this time, including one over the route of Dom Pedro II Railroad, which Agassiz believed would be of great future value for the transportation of large geological and zoological specimens. Zoologists and geologists thoroughly investigated the railroad from its origin in Rio de Janeiro to its terminus in Parahyba, a distance of one hundred miles. On 27 April Professor and Mrs. Agassiz enjoyed their first journey on the railroad as guests of Major Ellison, chief engineer. Two specimens from the fresh waters of Brazil were collected at this time, inaugurating what was to be an outstanding assemblage of Brazilian fishes.

An excursion of several days duration was made by the Agassizes in May, 1865; it was the first extending any distance from Rio de Janeiro. They went by ferry to Mauá then by railroad and post coach to Petrópolis. From Petrópolis they continued along the valley of the Rio Piabanha to Posse, crossed the Rio Parahyba at

Entre Rios, soon reached the Rio Parahybuna, then went on to Juiz de Fora. This trip provided an excellent opportunity to study the plant life and geological formations and to collect numerous specimens of fishes and other vertebrates.

Examples of the peculiarities of Brazilian geological formations were observed in Tijuca, about eight miles from Rio de Janeiro, 26 27 May. On 21 June the Agassizes again went to Juiz de Fora, arrived there 22 June, then continued thirty miles farther where they were guests of Senhor Lage at his fazenda. Senhor Lage accompanied the Agassizes to the Serra da Babylonia. On 27 June they returned to Rio de Janeiro.

In June the party divided into units to facilitate the exploration of Brazil. St. John, Allen, Ward and Sceva left for the interior the first week of June and Hartt and Copeland left to explore the coast from the Rio Parahyba to Bahia the following wee. On 25 July, the Agassizes, Major Coutinho, Burkhardt, Monsieur Bourget (a French naturalist residing in Rio de Janeiro engaged by Agassiz as a collector and preparator), Hunnewell and James left Rio de Janeiro on the "Cruzeiro do Sul" for Bahia, where they arrived 28 July. In Bahia they were joined by Dexter and Thayer, who had preceded them. Antonio de Lacerda, their host, had greatly assisted Dexter and Thayer in their collecting. The next collecting station was Maceió on 30 July, then Pernambuco 31 July and on 2 August the Parahyba do Norte as far as the town of Parahyba. They arrived at Ceará 5 August, the guests of Dr. Mendes, and were at Maranhão 6 August. They arrived at Pará 10 August, where Mr. Pimenta Bueno arranged living and working quarters from 10 August to 19 August, and the use of a steamer, the "Icambiaba", for a month between Pará and Manáos. In Pará, Mr. Talisman, a young Brazilian officer of the Amazonian Steamship Company, joined the group. Breves, 20 August, was the first station in Amazonas. Leaving Aturia, they passed into the Rio Tajapurú and stopped at the village of Tajapurú.

On 21 August, after two days spent skirting the island of Marajó, they left the Pará River and turned into the mainstream of the Amazon. They went to Gurupá, 22 August, where a collection of forest fishes was made, and on to Porto de Moz on the Rio Xingu, 23 August. A brief non-collecting halt was made at Prainha on 24 August, and they were at Monte Alégre, at the mouth of the Rio Gurupatuba on 25 August.

From Santarém, at the mouth of the Rio Tapajoz, Dexter, James and Talisman left, 26 August, to explore the Rio Tapajoz. Bourget and Hunnewell remained in Santarém, Bourget to make collections, Hunnewell to repair his photographic equipment. Agassiz, Burkhardt, Thayer and Coutinho continued on to Obydos. Before leaving the Rio Tapajoz to join the Amazon, the "Icambiaba" detoured through a narrow channel, Igarapé-Assú. A brief stop was made at Obydos, 26 August. On 27 August they landed at Villa Bella, at the mouth of the Rio Tupinambaranas. By canoe, the group left Villa Bella to explore Lago José Assú until 30 August, proceeding from there to a branch of the Rio Ramos, which connects the Amazon to the Rio Madeira. They returned to Villa Bella on 2 September.

A rest period was taken from 4 to 11 September at Manáos, on the Rio Negro. There they were joined by Dexter, James and Talisman. A brief halt was made at Barreira das Cudajas on 12 September and on 13 September they made another short halt at Coarí. Teffé stands beside a small lake formed by the Rio Teffé before it joins the Amazon. This site was visited on 14 September, then Fonte Boa, 15 September and São Paulo de Olivença, 17 September. Here James and Talisman left the group to continue from there to the Rios Içá and Hyutahy by canoe. The farthest point reached by Agassiz was Tabatinga, 19 September. Bourget remained in Tabatinga for a month, collecting there and in the surrounding country. Agassiz and the rest of the party returned to Teffé, remaining there until 22 October. Agassiz and Coutinho were at a station on a branch of the Rio Solimoens from 4 October to 6 October. James and Talisman rejoined them at Teffé, 16 October and Bourget boarded the "Icambiaba" 22 October.

While in Teffé, Dexter made an extensive collection of birds and, with the assistance of Hunnewell, Thayer and local sportsmen, added to the reptile and animal specimens. Agassiz also purchased a large collection of insects at this station.

Manáos was reached on 23 October. While at this station, Agassiz, Coutinho, Burkhardt, Dexter and James, preceded by their host, Senhor Honorio, had a two day, 27 October to 29 October, collecting excursion to Lago Hyanuary on the western side of the Rio Negro. Talisman and Dexter explored the Branco and Negro rivers for six weeks, returning to Manáos 10 December. Thayer and Bourget were at Lago Cudajas for ten days, 27 November to

6 December (Thayer also collected at Lago Alexo), and James went to Manacapuru for ten days.

The Agassizes, Coutinho and Burkhardt left Manáos 10 December to spen ten days at Mauhes. They proceeded down the Rio Ramos to the Rio Mauhes, which runs almost parallel with the Amazon, to the Rio Madeira (which joins the Amazon opposite Serpa). The land encircled by these rivers is the island of Tupinambaranas. Mucaja-Tuba and another small settlement on the Rio Mauhes were visited 13 15 December, and on 21 December the group returned to Manáos.

On 26 December the party left Manáos and went up the Rio Negro as far as Pedreira on the "Ibicuhy," arriving there 28 December. A collection of palms had been made at Taua Péassu and they were picked up on the return to Manáos 31 December.

The stay at Manáos ended about 12 January 1866 and the party returned to Villa Bella 16 January. Collections were made 18 January at Lago Maximo, a short walk overland from Villa Bella. A narrow outlet connects this lake to the Rio Ramos. On 21 January the party was again at Obydos, and 22 January at Santarém, which is situated on a point of land separating the Rio Tapajos and the Amazon. They left Santarém 24 January for Monte Alégre, where they stayed until 29 January. Agassiz, Coutinho and a few friends went to the Serra d'Ereré, northwest of Monte Alégre, to see the geological formations. Coutinho went by horseback and Agassiz by canoe, along the Rio Gurupatuba, up a narrow stream known as the Rio Ererê to a point on a line with the Serra and from there proceeded on foot.

Senhor Vinhas, a resident of Porto de Moz, had a collection of fishes from the Rio Xingu ready for Agassiz upon his arrival 29 January, so the group quickly continued on to Gurupá, arriving 30 January. They reached Tajapuru 31 January and spent two days there.

From 4–27 February they were at Pará. On 28 February they left on the steamer "Tabatinga" to explore the great island of Marajó. They visited Soures, then, 29 February to 4 March, Vigia, Baia do Sul and the small island of Tatuatuba. They returned to Pará 5 March.

On 26 March the party left Pará for Ceará where they arrived 31 March. A stop was made en route at Maranhão so that Agassiz and Coutinho might examine the coastal geology with more care

than on their previous visit. An excursion to Pacatuba and the Serra da Aratanha, 6–12 April, included the Agassizes, Coutinho and Senhor Pompeo, Government Engineer of the Province. Collections were made in the vicinity of Ceará by various people including Senhor Felice and Senhor Cicero de Lima. They left Ceará 16 April and continued, with a brief stop at Pernambuco, to Rio de Janeiro, where they arrived 25 April.

During the time in Rio de Janeiro, 25 April to 2 July, collections were packed and shipped to Cambridge. A few short trips were made, to Petrópolis and again along the Dom Pedro II Railroad. The last excursion made by Agassiz was 9–12 June, to the Organ Mountains, accompanied by Mrs. Agassiz, Mr. Glaziou and Dr. Nageli. The group went by boat to Piedade, then walked from there to Theresopolis, collecting along the way.

On 2 July Burkhardt, Hartt, Copeland, Sceva, Dexter, James, Hunnewell and Thayer embarked for the United States.

Allen, Ward and Sceva left Rio de Janeiro 9 June 1865 under the leadership of Orestes St. John. Their route led to Juiz de Fora, then across the Serra da Mantiqueira to Barbacena (where Ward left the group) through Lagoa Dourada, across the Rio Carandahy and the Rio Paraopeba just above the water gap of the Serras da Piedade and Itatiaiassú, to the village of Morro Velho. They traversed the basins of the Rio Parahyba, Rio Grande (Rio de La Plata) and Rio São Francisco. By way of Saburá, Santa Luzia, Lagoa Sancta and Sette Lagoas they reached Gequitiba.

Sceva remained in Lagoa Santa to search for fossils in the caves of the region, but a previous collector had taken most of the material. He did, nonetheless, prepare an excellent series of mammals before returning to Rio de Janeiro. After a few days in Rio de Janeiro, devoted to preparing and packing specimens collected by other members of the expedition, Sceva went to Cantagallo to collect until he rejoined Agassiz in Rio de Janeiro to return to the United States.

St. John and Allen left Gequitiba 31 July 1865 and travelled by canoe down the Rio das Velhas, arriving at the junction of the Rio São Francisco 28 August. After three days here they continued by boat to Januária, reaching there 9 September and remaining until 19 September.

Allen, in ill health, decided at this point to continue on alone to Bahia, taking with him the material so far collected. Still trav-

elling by boat he followed the Rio São Francisco past Urubú to Chique-Chique, where he arrived 8 October and stayed for several weeks. From Chique-Chique his route led overland to the coast by way of Engenho Velho, Jacaré and Olhos d'Agua, across an arid plain, to Taboleiro de Jacobina, down the "Tombador" (a precipitous defile) to Jacobina valley. From Jacobina he went to the Serra da Terra Dura, Arraial do Riacho do Jacuhype, Feira de Sta. Anna, Espelto (Espelho?) and Cachoeira, then to Bahia, a journey of many weeks. He did not reach Bahia until the end of November. On 15 December Allen left Bahia for Cambridge.

St. John followed the Rio São Francisco to Barra, then went along the valley of the Rio Grande to the Rio Prêto, Santa Rita and Paranaguá. Several days were spent at Paranaguá before continuing on along the valley of the Rio Gurgueia to Manga. The party followed the Rio Paranahyba to São Gonçallo where many specimens (primarily birds, reptiles and insects) were taken. Therezina, capitol of the state of Piaui, was the next station and excellent collections of fishes were made from the Rio Poty, a tributary of the Rio Parnahyba. From Therezina St. John continued on to Caxias, proceeded to Maranhão by way of the Rio Itapicuru and arrived at Maranhão 8 January 1866. Illness kept St. John in Maranhão until February, when he left to join Agassiz in Pará. His geological observations were as careful and as valuable as his zoological collections.

After Ward separated from his associates at Barbacena he continued on to Ouro-Prêto, Mariana and Santa Bárbara, then down the Rio Piracicaba to the Rio Doce. He followed the river almost to the point where it meets the Rio Antonio. Crossing the Serra das Esmeraldas he arrived at the basin of the Rio Jequitinhonha and explored several branches of the river after passing Diamantina. He proceeded cross-country to the town of Rio Pardo and the Rio Pardo. He crossed the Rio São Francisco at Januária, then continued northwestward until he reached the Rio Tocantins, which he followed to Pará. From Pará Ward returned to the United States.

Hartt visited Brazil twice, first as a member of the Thayer Expedition, and, later, on a private expedition. Although he and Copeland made extensive collections, particularly of marine invertebrates and fishes, their major interest was the geology of Brazil. This has been comprehensively treated by Hartt, both from per-

sonal observation and from the work of other geologists, in his book, *The Scientific Results of a Journey in Brazil,* 1870. Considerable information is also included on the common species of plants and animals and areas of fossil beds.

Hartt and Copeland did not go directly from Rio de Janeiro to Bahia as planned. Their first attempt took them as far as Nova Almeida north of Victoria, but they were forced to return to Rio de Janeiro for lack of mules and money. After again working near Rio de Janeiro they embarked on a sailing vessel for São Matheos, stopping wherever possible along the coast. From São Matheos they went to the Rio Doce, returned to its mouth and then back to São Matheos. They proceeded north to Belmonte via the Rio Jequitinhonha and then returned to Porto Alegre, then north to Bahia.

Rather than complicate the survey of the area covered by Hartt and Copeland the following route description is given (with the exception of their return to Porto Alegre) in direct sequence.

The environs of Rio de Janeiro were thoroughly explored by Hartt and Copeland. They examined the area of the Serra do Mar, which borders the coast from the state of São Paola to the state of Rio de Janeiro, and also the Serra da Mantiqueira, partly separated from the Serra do Mar by the valley of the Rio Parahyba do Sul. Within the bay of Rio de Janeiro the Ilha de Paquetá, Ilha das Cobras, Ilha das Enxadas and Ilha do Governador were explored. They visited several places near Rio de Janeiro, including the hills that run westward to Lagoa de Freitas, separated from Corcovado by the valley of Botafogo. They also explored Três Irmãos, southwest of Corcovado, the Gaira to the west and the Tijuca range to the north, which is separated from Corcovado by the pass of Boa Vista. They covered the entire length of the Dom Pedro II railroad. The Rio Macacu was followed to Porto Villa Nova, then along the Cantagallo Railway to Porto das Caixas and the terminus at Cachoeria.

Between Rio Janeiro and Cabo Frio observations were made at Maricá, Lagoa de Maricá, Lagoa de Saquarema (east of Porto Negra) and Lagoa de Araruama. After Cabo Frio they stopped at Os Búzios, Cabo de São Thomé, Macahé, the Ilhas de Santa Ana (which are a few miles offshore from Macahé) and Campos on the Rio Parahyba do Sul. Just south of Campos is the Lagoa Feia into which the Rio Macacu empties. Several lagoons have formed

along this coast, including large ones such as Rio Iguassu and Lagoa do Campello.

They followed the Rio Muriahé, a tributary of the Rio Parahyba, for several miles then followed the Rio Parahyba from Campos to São Fidélis. From here they travelled northward through the valley of Vallão Grande to Bom Jesus on the Rio Itabapuana, which divides the states of Rio de Janeiro and Espíritu Santo. They went down the Rio Itabapuana, past Porto da Limeira, to the mouth of the river.

Hartt and Copeland continued northward to Lago Marobá, then along the coast to the town and river of Itapémirim and the surrounding area, then on to Piuma, the Rio Benevente and Guarapary. Stops were made at Ponta da Fructa and Ponta de Jecú en route to the bay of Espíritu Santo, Villa Telha (on the bay of Espíritu Santo) and Victoria. Fifty miles northwest of Victoria they explored the Rio Santa Maria and São Leopoldina then went on to Carapina, Santa Cruz and the Rio Doce, which they traversed from its mouth to Porto do Souza. They went down the river to Linhares and Lagoa Juparanãa (connected to the Rio Doce by a deep channel called the Rio Juparanãa).

Returning to the coast they continued northward, stayed briefly during November 1865 in the vicinity of Barra Secca, then passed the Lagoa Marircu and the Rio Azeites at As Azeites on the way to São Matheos. Hartt journeyed to the Fazenda do Capitão Grande on the Rio Braço do Norte, which joins with the Braço do Sul to form the Rio São Matheos. On the return trip he mapped the river as far as São Matheos. Further north along the coast they noted the Rio Itahunas.

From Porto Alégre they went up the Rio Mucury to Santa Clara and from that point travelled westward, using the Minas road, to the headwaters of the Rio Mucury near Poté. Farther west they passed the watershed dividing the Rio Mucury and the Rio Jequitinhonha. They arrived at the valley of Jequitinhonha in April 1866 via the Rio Setubal. A detour was made from the Rio Setubal to Alto do Bois before they proceeded cross-country to Calháo. After arriving at Calháo, Hartt made a visit to Minas Novas, returned to Calháo, and with Copeland, went down the Rio Arassuahy and the Rio Jequitinhonha to Belmonte. From Belmonte, Hartt and Copeland returned to Porto Alégre, before again following the coast north.

Observations were made of the terrain between the Mucury and Peruhype rivers. They visited São Leopoldina, about ten miles upstream, and Villa Viçosa, four miles below. The route continued northward along the coast to the Rio Caravellas, Prado, the Rio Jucurucú, Porto Seguro and Santa Cruz. After again reaching Belmonte they went on to Cannavieiras and the Rio Pardo. They ascended the river to the head of navigation, passing Cachoeirinha do Rio Pardo and the fazenda of Sisterio.

They stopped briefly in Ilhéos on the Rio Cachoeira and in Camamu, en route to Bahia. From Bahia they ascended the Rio Paraguassú as far as Cachoeira, passing the valley of Iguapé. The area surrounding Bahia received close attention before Hartt and Copeland returned to Rio de Janeiro, where they joined Agassiz and other members of the expedition for departure to the United States.

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Lago Curupira	9
Lago do Bota	10
Lago Hyanuary (*January*)	10
Lago Irandubo	10
Lago *January* (Hyanuary)	10
Lago José Assú (*Açu*)	9
Lago José Fernandes	10
Lago Manacapuru	10
Lago Marobá	3B
Lago Saracá	9

Name	Map
La Plata (*Grande?*), Rio	6
Linhares	3B
Macacos, Rio dos	9
Macacu, Rio	2
Macahé (*Macaé*)	3B
Maceió	11
Madeira, Rio	9
Mamuru (Tupinambaranas), Rio	9
Manacapuru	10
Manáos (*Manaus*)	9, 10
Manga	5
Manhuassú (*Manhuaçu*), Rio	3B
Mantena (Braço do Sul), Rio	3A
Marajó, Ilha de	9
Maranhão (*São Luís*)	11
Marañon, Rio	10
Mariana	7
Maricá, Lagoa do, Ilhas	3B
Mateus, Rio	3A
Mauá (*Barão de Mauá*)	2
Mauhes (*Maués*), Rio	9
Minas Novas	3A
Monte Alegre	9
Morro Velho	4, 6
Moura (Pedreira)	10
Mucaja-Tuba (*Mucajá*)	9
Mucury (*Mucuri*), Rio	3A
Mucury Pequeno, Rio	3A
Mugiquisaba (*Mogiquiçaba*)	3A
Muriache (Muriahé) (*Muriaé*), Rio	3B
Mutum, Rio	3B
Nazareth	9
Negro, Rio	10
Novo, Rio	3B
Obydos (*Óbidos*)	9
Olhos d'Água	6
Organ Mountains (*Serra dos Órgãos*)	2
Os Búzios (*Cabo dos Búzios*)	3B

Name	Map
Ouro-Prêto (*Ouro Prêto*)	7
Pacatuba	11
Paquetá, Ilha de	1, 3
Pará (*Belém*)	8, 9
Parahyba (*Paraíba*) do Norte, Rio	11
Parahyba (*Paraíba*) do Sul, Rio	3B, 4
Parahybuna (*Paraibuna*), Rio	3B
Paramirim, Rio	6
Paranaguá	5
Paraopeba, Rio	6
Parcel dos Abrolhos	3A
Pardo	3A, 7
Pardo, Rio	3A, 7
Parguassú (*Parguaçu*), Rio	3A
Parintins (Villa Bella)	9
Parnaíba (Parnahyba), Rio	5
Pedreira (*Moura*)	10
Pernambuco (*Recife*)	11
Peruhype (*Peruípe*), Rio	3A
Petrópolis	2, 6
Philadelphia (*Teófilo Otoni*)	3A
Piabanha, Rio	2, 3B
Piauhy (*Piauí*), Rio	3A
Piedade	1
Piracicaba, Rio	7
Pirahy (*Piraí*), Rio	2
Po-Assú (*Canal de Poaçu*)	3A
Ponta da Fructa (*Fruta*)	3B
Ponta de Jecú	3B
Ponta Negra	2
Porto Alegre	3A
Porto da Limeira	3B
Porto das Caixas	2
Porto de Moz	9
Porto do Souza	3B
Porto Nacional	7, 8
Porto Seguro	3A
Posse	3B

Name	Map
Poté	3A
Poty (Puty) (*Poti*), Rio	5
Prado	3A
Prados	4
Prainha	9
Prêto, Rio	2, 4
Puty (*Poti*), (Poty), Rio	5
Ramos, Rio (*Paraná do Ramos*)	9
Recife (Pernambuco)	11
Rio Antonio (*Santo Antônio*)	7
Rio Arupuana	9
Rio Arassuahy (*Araçuaí*)	3A
Rio Azeites	3B
Rio Aturiá (*Furo do Aturiá*)	9
Rio Belmonte (*Jequitinhonha*)	3A, 7
Rio Benevente	3B
Rio Braço do Norte	3A
Rio Braço do Sul (*Rio Mantena*)	3A
Rio Branco	10
Rio Caninde	5
Rio Carandahy (*Carandaí*)	4
Rio Caravellas (*Caravelas*)	3A
Rio Caxoeira	3A
Rio Coeira	3A
Rio das Velhas	3A, 4, 6, 7
Rio de Contas	3A
Rio de Janeiro	1, 3, 4, 6, 7
Rio Doce	3B, 7
Rio dos Macacos	9
Rio Ererê	9
Rio Gongogi	3A
Rio Grande	6
Rio Grande (La Plata?)	4
Rio Guaxindiba or Itahunas (*Itaúnas*)	3B
Rio *Gurgueia* (Gurugueia)	5
Rio Gurupatuba (*Parieutuba*)	9
Rio Hyapura (*Japurá*)	10
Rio Hyavary (Javary) (*Javari*)	10

Name	Map
Rio Hyutahy	10
Rio Iça	10
Rio Iguapé	3A
Rio Iguassú	3B
Rio Itabapuana (*Itabapoana*)	3B
Rio Itanheim	3A
Rio Itapemérim	3B
Rio Itapicurú	5, 11
Rio *Itaúnas* (Itahunas or Guaxindiba)	3B
Rio Itim	5
Rio Jacaré	6
Rio *Jacuípe* (Jacuhype)	3A
Rio *Japurá* (Hyapura)	10
Rio Javary (Hyavary) (*Javari*)	10
Rio *Jequitinhonha* (Belmonte)	3A, 7
Rio Jucururú	3A
Rio Juparanãa (*Lagoa Juparanã*)	3B
Rio Jutahy (*Jutai*)	10
Rio Macacu	2
Rio Madeira	9
Rio *Manhuaçu* (Manhuassú)	3B
Rio Mantena (Braço do Sul)	3A
Rio Marañon	10
Rio Mateus	3B
Rio Mauhes (*Maués*)	9
Rio Mucury (*Mucuri*)	3A
Rio Mucury Pequeno	3A
Rio Muriahé (*Muriaé*) (Muriache)	3B
Rio Mutum	3B
Rio Negro	10
Rio Novo	3B
Rio Paraguassú	3A
Rio Parahyba (*Paraíba*) do Norte	11
Rio Parahyba (*Paraíba*) do Sul	2, 3B, 4
Rio Parahybuna (*Paraibuna*)	3B
Rio Paramirim	6
Rio Parnahyba (*Parnaíba*)	11
Rio Paraopeba	6

Name	Map
Rio Pardo	3A
Rio *Parnaíba* (Parnahyba)	5
Rio Peruhype (*Peruípe*)	3A
Rio Piabanha	2, 3A
Rio Piauhy	3A, 5
Rio Piracicaba	7,
Rio Pirahy	2
Rio Piuma	3B
Rio Poty (*Poti*) (Puty)	5
Rio Prêto	2, 3A, 4
Rio Ramos (*Paraná de Ramos*)	9
Rio *Samambaia* (Sambaia)	2
Rio *Santo Antônio* (Antonio)	7
Rio São Francisco	3A, 4, 5, 6, 7
Rio São Matheos (*São Mateus*)	3B
Rio Setubal	3A
Rio Solimoens (*Solimões*)	10
Rio Tajipurú (*Furo do Tajipurú*)	9
Rio Tapajoz (*Tapajós*)	9
Rio Tocantins	7, 8
Rio Trombetas	9
Rio Tupinambaranas (*Mamuru*)	9
Rio Una	3B
Rio Vacaria	7
Rio Xingu	9
Saburá (*Sabará*)	4
Salvaterra	9
Samambaia (Sambaia), Rio	2
San Gonçallo (*Amarante*)	5
San Luiz (Maranhão)	11
San Mateo (*São Mateus*) (Matheos)	3B
San Paolo (*São Paulo de Olivença*)	10
Santa Anna Islands (*Ilhas de Santana*)	3B
Santa Bárbara	3A, 3B, 7
Santa Caterina (Catherina)	3B
Santa Clara	3A
Santa Cruz (*Cabralia*)	3B
Santa Luzia	4, 6

Name	Map
Santarém	9
Santa Rita de Cassia (Villa da Santa Rita)	4
Santo Antônio (Antonio), Rio	7
São Fidélis	3B
São Francisco, Rio	3A, 4, 5, 6, 7
São Leopoldina (Colônia Leopoldina)	3B
São Matheos (*São Mateus*)	3B
São Paulo de Olivença (San Paola)	10
São Tomé, Cabo de	3B
Serpa (*Itacoatiare*)	9
Serra da Aratanha	11
Serra da Babylônia (*Babilonia*)	3B
Serra da Mantiqueira	3B, 4, 7
Serra da Piedade	4, 6
Serra das Esmaraldas	7
Serra da Terra Dura	6
Serra de Cupati	10
Serra de Monguba	11
Serra d'Ereré (*Ereré*)	9
Serra do Itatiaiassú (*Itatiaiuçu*)	4, 6
Serra do Mar	3B
Serra dos Orgãos (Organ Mountains)	3B
Sette Lassas	4, 6
Setúbal, Rio	3A
Silva	9
Sisterio	3A
Solimoens (*Solimões*), Rio	10
Soures (*Soure*)	9
Tabatinga	10
Taboleiro de Jacobina	6
Tajipuru, Rio (*Furo do Tajipuru*)	9
Tapajóz (*Tapajós*), Rio	9
Tatuatuba	9
Taua Péassu (*Tauapeçaçu*)	10
Teffé (Ega) (*Tefé*)	10
Teófilo Otoni (Philadelphia)	3A
Teresopolis (Theresopolis)	3B
Therezina (*Teresina*)	5

Name	Map
Tijuca	1
Tocantins, Rio	7, 8
Tombador	6
Tonantins	10
Três Irmãos	1
Três Rios (Estaçao d'Entre Rios)	2
Trombetas, Rio	9
Tupinambaranas (*Tupinambarama*)	9
Tupinambaranas (*Mamuru*), Rio	9
Una, Rio	3B
Urubú	6
Vacaria, Rio	7
Vallão Grande (*Valão Grande*)	3B
Velhas, Rio das	3A, 4, 6, 7
Vereda do Mocambo (Mocambo)	4
Victoria (*Vitória*)	6
Vigia	9
Villa Bella (*Parintins*)	9
Villa da Santa Rita (*Santa Rita de Cassia*)	4
Villa do Barra (*Barra*)	4, 6
Villa (*Vila*) Velha	3B
Villa (*Vila*) Viçosa	3A
Vitória (Victoria)	6
Xingú, Rio	9
Xique Xique (Chique Chique)	4, 5, 6
Ypiranga (*Ipiranga*)	2

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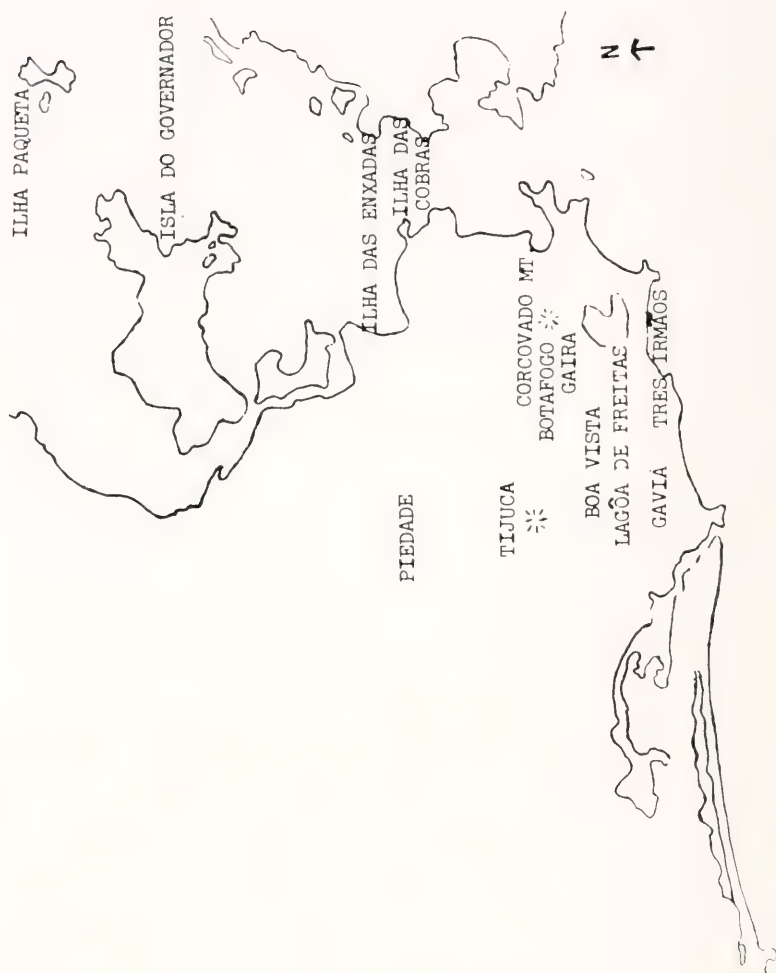Figure 1. Rio de Janeiro

Figure 2. Dom Pedro II Railroad (after Hart, 1870)

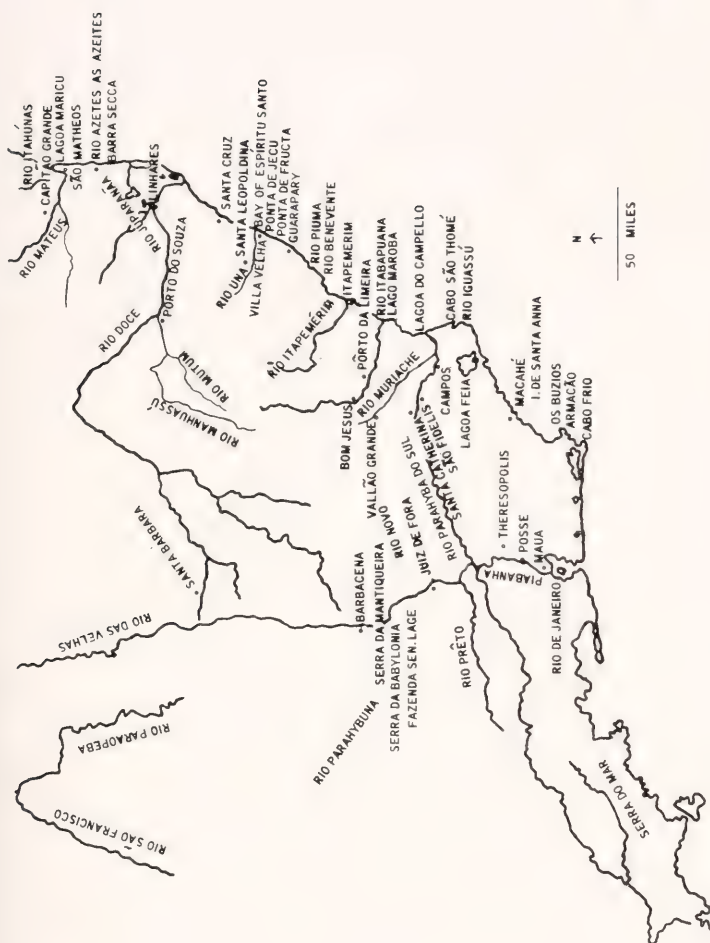Figure 3 A. Coast from Bahia to Porto Alegre — Hartt and Copeland

Figure 3 B.   Coast from Rio Itahunas to Rio de Janeiro — Hartt and Copeland

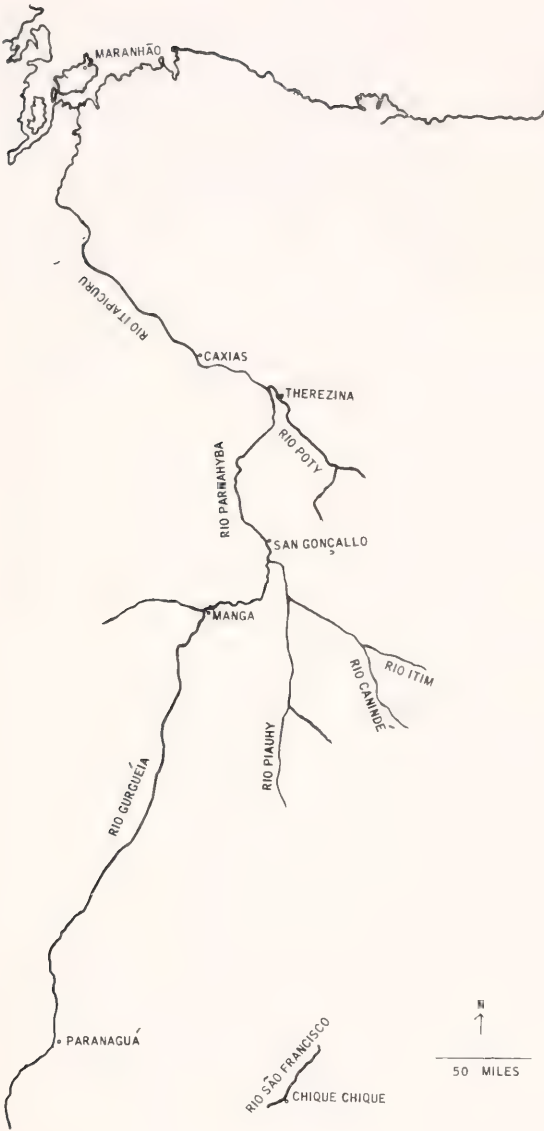Figure 4.　Rio de Janeiro to Paranaguá — St. John

Figure 5.   Paranaguá to Maranhão — St. John

Figure 6.   Rio de Janeiro, Chique Chique, to Bahia — Allen

Figure 7.   Rio de Janeiro to Rio Tocantins — Ward
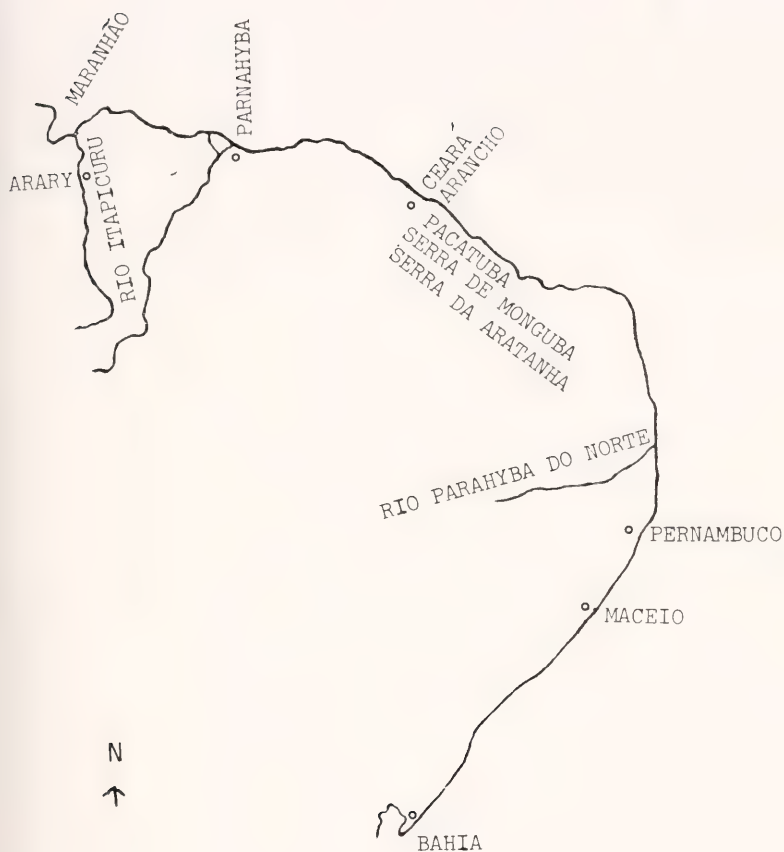
Figure 8.   Rio Tocantins to Pára — Ward

Figure 9. Amazonas, Pará to Manaus — Agassiz et al.

Figure 10. Amazonas, Manaus to Tabatinga — Agassiz et al.

Figure 11.   Coast, Maranhão to Bahia — Agassiz et al.

B R E V I O R A

Museum of Comparative Zoology

NATURAL HISTORY OF *CERION*. VII. GEOGRAPHIC VARIATION OF *CERION* (MOLLUSCA: PULMONATA) FROM THE EASTERN END OF ITS RANGE (HISPANIOLA TO THE VIRGIN ISLANDS): COHERENT PATTERNS AND TAXONOMIC SIMPLIFICATION.

STEPHEN JAY GOULD[1] AND CHARLES PAULL[2]

ABSTRACT. The eastern cerions (Hispaniola to the Virgin Islands) have, following the conventional practice for this diverse genus, been split into seven allopatric taxa. We reject this traditional scheme on the basis of a multivariate morphometric analysis (19 characters, 20 shells per sample) of 23 samples from all major areas of *Cerion's* eastern range. We first show that eastern cerions are distinct from other members of the genus by patterns of covariation among their morphometric measures. We then demonstrate by canonical analysis that populations of each island have a distinct morphology. Were there no coherent patterns among islands, current nomenclature might be supported. However, the first canonical axis (59 per cent of all information) for an analysis by islands arrays the populations in perfect geographic order — from egg-shaped, finely and copiously ribbed shells in the east, to more cylindrical, apically pointed shells with fewer, stronger ribs in the west. The morphological direction of this cline approaches common cerion forms further west (particularly on Cuba); unique morphologies are isolated at the eastern extreme of the range. In addition, a plot of Mahalanobis vs. geographical distance shows a remarkably tight relationship ($r = 0.96$) between geographic and morphological distance. Therefore, we synonymize all living eastern cerions into the single taxon *C. striatellum* ("Férrusac" Guerin-Meneville), reserving *C. rude* (Pfeiffer) for the rather different St. Croix fossil.

I. INTRODUCTION

Cerion has attracted the attention of eminent naturalists ever since Linnaeus designated its type species in 1758. W. H. Dall (1905), H. A. Pilsbry (1902), P. Bartsch (1920), Ludwig Plate

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(1906, 1907), W. J. Clench (1957), and Ernst Mayr (1956, 1963) invested substantial segments of their careers trying to understand the protean diversity of this unusual genus containing more than 600 described species and subspecies. So far *Cerion* has stood firm against all efforts to find coherence in the geographic distribution of its exuberant morphological variation. Elegant, oversimplified stories have collapsed (Plate, 1906), while more circumspect evolutionists speak of "crazy-quilt" distributions and random transport by hurricanes (Mayr and Rosen, 1956). The burden of available names has generally precluded a search for order and simplicity in the areas of *Cerion's* greatest diversity — Cuba, the Bahamas, and the Cayman Islands. Yet order and simplicity demonstrably exist when we trade museum trays and lists of names for the mapping of recognizable elements and their interactions in the field (Gould and Woodruff, in press, and in preparation on Little Bahama Bank, New Providence, Great Exuma, and Long Island, Bahamas).

As another strategy, we might wage some preliminary skirmishes before attacking the central areas of Cuba and the Bahamas, since *Cerion* displays markedly less variation in three peripheral areas of its distribution. The isolated populations on Aruba, Bonaire, and Curaçao have received much attention (Baker, 1924; Hummelinck, 1940; de Vries, 1974; Gould, 1969). Geographic variation in the single species, *Cerion uva* (L.), reflects both isolation (each island has a characteristic, if subtly differentiated, morphology) and local habitat; patterns have been stable for at least 50 years (Baker, 1924; Gould, 1969). This coherence allows hope for sensible interpretations elsewhere. The second peripheral area is contiguous with central regions: the Florida Keys with their single species, *Cerion incanum* (Binney). The third peripheral area is larger, more diverse, also contiguous to major centers, and equally unstudied: the essentially linear array of islands running from Hispaniola through Mona Island and Puerto Rico, to Necker and Anegada in the Virgin Islands (Fig. 1). Here 11 names are available for a basic morphology that all students of *Cerion* have recognized as unique to this Eastern area (Pilsbry, 1902). These eastern cerions provide a superb opportunity for modern study; they represent a situation intermediate between the relative simplicity of *Cerion uva* in the Leeward Islands (where we cannot practice the

art of taxonomic rectification, since no one ever successfully split the single species) to the complexity of New Providence Island with its 82 named species.
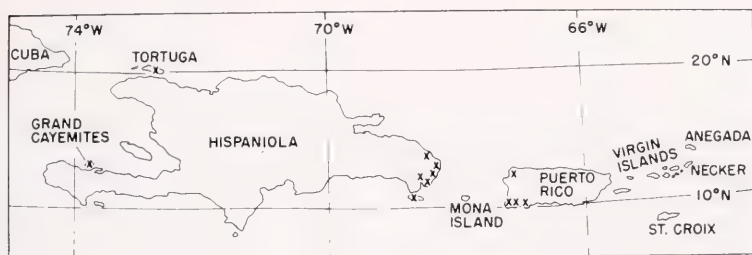

Fig. 1. The distribution of eastern cerions. Crosses indicate localities used in this study for the large islands only.

Moreover, the linear arrangement of islands leads to simple hypotheses of clinal distribution in our search for coherence, while their geographic range (980 km from Western Haiti to Anegada) permits a truly regional, not merely local, study.

II.   SYSTEMATICS OF EASTERN CERIONS

Collectors of eastern cerions report that these snails share the habitat conventionally assigned to the genus (though our own observations of Bahamian forms demonstrate a much wider range); they live near the coast in limestone regions. Traditional wisdom proclaims that the animals are active on moist evenings, feeding predominantly on fungal mycelia in decaying vegetation; in drier conditions, they secrete an epiphragm and attach to plants, remaining immobile for long periods (several months in dry laboratory conditions). Beyond these basic facts of distribution, we know virtually nothing about the ecology and life history of any *Cerion,* including the eastern forms. (D. S. Woodruff has been studying two populations on Abaco Island, Bahamas during the past three and one-half years; our first adequate data will soon be available.)

Heretofore, the eastern cerions have been defined by conchological characters alone. These snails have a unique and consistent morphology (Fig. 2), rendered in most taxonomic descriptions by two characters:

1) An unusually obtuse apex, giving the entire shell a barrel or egg-shaped appearance (contrasting with the more common cylindrical form of species with pointed apices and rapid attainment in ontogeny of a definitive width; or the triangular form of species with pointed tops and continually increasing width).

2) Fine, abundant and regular ribs, evenly covering the entire surface of the shell.

Fig. 2.   Representative eastern cerions. Top row Hispaniola; second row, Mona Island (left) to Anegada (right). The large specimen at the extreme right is fossil *C. rude* from St. Croix. Note the major clinal trends from coarsely ribbed, apically pointed species in the west (Hispaniola) to copiously and finely ribbed, barrel-shaped forms in the east. Note also, the peculiarities of individual islands as described in the text — i.e., the nearly circular aperture of Puerto Rican specimens. Top row, starting from left: 1) holotype of *"C. tortuga"* (Acad. Nat. Sci. Phil. No. 146701 — locality 22 of this study); 2) holotype of *"C. yumaense ferruginum"* (M.C.Z. No. 76230); 3) paratype of *"C. yumaense"* (M.C.Z. No. 185945 — locality 18 of this study); 4) holotype of *"C. yumaense saona"* (Acad. Nat. Sci. Phil. No. 47200).   Bottom row: 1) holotype of *"C. monaense"* from Mona Island (M.C.Z. No. 171019 — locality 12 of this study); Puerto Rican specimen of *C. striatellum* from locality 7; 3) from Necker Island, Virgin Islands, locality 1; 4) from Anegada, Virgin Islands, locality 2. *C. rude* is from lot No. 60564 Acad. Nat. Sci. Phil. *C. rude* specimen is 34.7 mm in height.

Pilsbry (1902), in the last comprehensive attempt to establish subgroups within *Cerion*, defined the eastern forms as one section among 11 in the subgenus *Strophiops*. He included two extraneous forms within the group:

1. *Cerion antonii* reported by Küster (1847) from the South American coast in Guyana. This species has been dutifully listed by all students of *Cerion;* comments about its anomalous geography abound. But we do not believe that it exists. The shells were described from a collector's cabinet, not from field observations. Mistaken labels in such cabinets once gave other cerions a proud range from India to China. We have no field records of living *Cerion* in South America. Moreover, Küster's shells have not been seen, so far as we can tell, by any subsequent author. All records of *C. antonii* depend upon the single poor figure published by Küster and reproduced by Pilsbry (1902) in making his assignment.

2. *C. caymanense* Pilsbry from Grand Cayman. According to Pilsbry (1902), *C. caymanense* differs from other members of the eastern group by its less obtuse apex and stouter ribs. But these are the very characters that should place it out of the group; for obtuse apices and fine ribs are the defining traits of eastern cerions. We do not understand why Pilsbry didn't include *C. caymanense* with the more similar Cuban group of *C. cyclostomum* (Küster).

The remaining taxa of Pilsbry's eastern group all reside in the geographic area of this study. Current nomenclature divides the eastern cerions according to accepted criteria within the genus: specific names have been awarded to allopatric populations of recognizable morphology. Moving from east to west among living species, cerions of the Virgin Islands (Anegada and Necker) and Puerto Rico belong to the same taxon, *Cerion striatellum* — although the phenetic distance between Puerto Rican and Virgin Island samples is greater than that between most other species in the group (see section VI). Some confusion has surrounded the appropriate name for this taxon. *Pupa striatella*, attributed to Férussac but never described by him, was defined by Guerin-Meneville in the 1829 *Regne Animal* of Cuvier (Mollusca, p. 16, plate 6, fig. 12). But Guerin-Meneville listed only "the Antilles" for a locality, and the task of deciding which cerions merited the designation fell to later authors. Küster (1847) and many others attributed Guerin-Meneville's name to the Puerto Rican specimens, but Poey

and others applied *C. striatellum* to a species from Cabo Cruz, Cuba and used Sowerby's (1875) *C. crassilabre* for Puerto Rico. Pilsbry (1902) followed Poey, but changed his mind later (1943), awarded a new name to the Cuban species (*C. cabocruzense* Pilsbry and de la Torre), and preserved the earlier *C. striatellum* for the Puerto Rican form. We follow Pilsbry's later opinion and consider *C. crassilabre* as a synonym of *C. striatellum*. This is a happy resolution since we will synonymize all living eastern cerions under this name, and since thick lips are decidedly not characteristic of many populations, whereas all are abundantly ribbed.

Moving westward from Puerto Rico, we next encounter *Cerion* on Mona Island. Clench (1951, p. 274) awarded the Mona Island population their own name (*C. monaense*) for their coarser costae and smaller size compared with Puerto Rican relatives.

Taxonomy of the Hispaniolan forms is more exuberant, but the defining criteria — size, ribbing, relative width, and shape of apex — have not been enlarged. Küster's name (1847), *Pupa striatella minor* from Haiti, is the earliest available, but all subsequent authors have ignored Küster's inadequate description, and we will not challenge this tradition. Pilsbry and Vanatta described the first full species in 1895 (p. 210): *Cerion yumaense* from the Dominican Republic — not so wide, more pointed apically, and more coarsely ribbed than the Puerto Rican populations. Maynard (1896) followed soon afterwards with *Strophia ferruginea* from Haiti, generally ranked as a subspecies of *C. yumaense* by later authors (e.g., by Pilsbry, 1902). Two additional subspecies accrued in later years: *C. yumaense sallei* (Pilsbry and Vanatta, 1896, p. 325; first attributed to *C. striatellum,* but later, and more appropriately, switched to *C. yumaense* by Pilsbry, 1902), and *C. yumaense saona* (Vanatta, 1923). Definitions involve little more than size: *sallei* is quite small, while *saona* is larger, with coarser costae than either *sallei* or the nominate subspecies. Finally, Pilsbry and Vanatta (1928) erected *Cerion tortuga* for more strongly colored, thicker lipped specimens from the nearby island of Tortuga.

In summary, living eastern cerions are generally ranked in seven taxa: *C. striatellum* ("Férussac" Guerin-Meneville) for Puerto Rico and the Virgin Islands, *C. monaense* Clench for Mona Island (between Puerto Rico and Hispaniola), and *C. yumaense* Pilsbry and Vanatta [with subspecies *C. y. yumaense, C. y. ferruginum* (May-

nard), *C. y. sallei* Pilsbry and Vanatta, and *C. y. saona* Vanatta]
and *C. tortuga* Pilsbry and Vanatta for Hispaniola and associated
islands. They are distinguished by little more than variation in the
key characters used to define the entire eastern group: coarseness
of ribbing, obtusity of the apex, and width of the shell.

A somewhat different fossil form has long been known from St.
Croix — *Cerion rude* (Pfeiffer). [Pfeiffer's (1855) second taxon, *C.
latilabre*, has been properly synonymized by all later authors as
nothing more than a short specimen of *C. rude*.] *C. rude* is consid-
erably larger than other eastern forms. It also departs from its near-
est neighbors in the very characters distinguishing them from other
Cerion — *C. rude* has a more pointed apex and fewer, coarser ribs
than most living eastern *Cerion*. Yet its general appearance is still
closer to the living eastern cerions than to any other group within
the genus. Jacobson (1968) states that the fossil shells are buried
in soils and often appear at the surface after preparation of the
land for cultivation of cane. He attributes their extinction to cul-
tivation and burning (itself, primarily, for cultivation), but we have
no firmly documented record of St. Croix *Cerion* living in historic
times.

III.   MATERIALS, METHODS, AND INTENTIONS

Following the protocol of Gould, Woodruff, and Martin (1974),
we made 19 measurements on 20 specimens (when available) for 23
samples of eastern cerions. All taxa but *C. yumaense sallei* are
represented in our samples. Our measures attempt to capture the
standard taxonomic characters of adult size, whorl sizes and num-
bers, size and shape of the aperture, shape of the spire, and pat-
terns of ribbing. With the exception of one sample personally col-
lected on Anegada (by C.P.), all shells come from museum collec-
tions (see Table 1). In all but two cases (Maynard's paratypes of
C. yumaense ferruginum, and fossil *C. rude* — where we amalga-
mated whatever we could find from the collections of four museums
to form an adequate sample), we restricted ourselves to large, recent
samples collected *en masse* without obvious preference for large,
unusual or attractive specimens. We gathered these data for a mul-
tivariate study of geographic variation in eastern cerions. We
wished to address the following issues of distinction (at several
levels) and coherence.

Table 1.   Samples used in this study.*

1. Necker Island, 220391
2. Anegada, 229017
3. Anegada, collected C. Paull
4. Anegada, 203778
5. Near Tower Guanica Insular Forest, Puerto Rico, 212303
6. Tamarindo Beach, Puerto Rico, 212302
7. Guanica Insular Forest, Tower Road, Puerto Rico, 212293
8. Cabo Rojo Colony No. 2, Puerto Rico, 212298
9. Pt. Criollo, Guanica, Puerto Rico, 216702
10. Cayo Maguey, La Paruera, 212292
11. Cabo Rojo Colony No. 1, 212297
12. Mona Island paratypes, 171020
13. Mona Island, 190144
14. Mona Island, Isabella Anchorage paratypes, 184052
15. N.W. Saona Is., Hispaniola, 98829
16. Lighthouse Cabo Engaño, Altagracia, Hispaniola, 251314
17. North Shore Bahia de Yuma, Hispaniola, 251313
18. Yuma River, paratypes, Hispaniola, 181967
19. Romana Prov. 0.7 mi. east of Macao, Hispaniola, 250638
20. N.E. Grande Cayemites Is., Hispaniola, 251161
21. Juanilo, Altagracia, Hispaniola, 25132
22. Tortuga Island ANSP 146701 and 146702
23. St. Croix [composite sample: MCZ, Harvard; ANSP, AMNH (N.Y.) and Field
    Museum (Chicago)].

*Samples 1–21 (with the exception of sample 3 collected by C. Paull) are from the
Dept. of Molluscs, Museum of Comparative Zoology (lot number indicated). Sam-
ple 22 is from the Academy of Natural Sciences, Philadelphia. Conventional iden-
tifications follow: samples 1–11, *C. striatellum;* 12–14, *C. monaense;* 15, *C. yumaense
saona;* 16–19, and 21, *C. yumaense;* 20, *C. ferruginum;* 22, *C. tortuga;* 23, *C. rude.*

1. Distinction of eastern cerions from other sections of the
genus: Are evident differences in morphology matched by pat-
terns of covariation not encountered in other cerions?

2. Distinction among islands: Do the morphologies of eastern
cerions record unambiguously the island of their occurrence? If
so, we may identify isolation by geography as the primary corre-
late of morphological variation in these animals.

3. Distinction among samples: A long tradition in *Cerion* studies
(amply affirmed by all our qualitative observations) holds that
nearly every local population has developed its own recognizable
morphology. (The older conchologists chose to recognize this pri-

mary observation by granting each form its own specific name.) Does such local differentiation exist among the eastern cerions?

4. Coherence: If cerions are distinct by island (issue 2 above), can we detect any interisland pattern (clinal or otherwise) that might suggest a common control correlated with geography (selection along climatic gradients, gene flow, or isolation by distance, for example)? The discovery of such a pattern will not permit us to distinguish among these potential explanations, for a pattern of coherence does not specify its cause, and museum specimens will not settle the issue. If we find no such pattern, current taxonomy granting autonomy to each major island must be maintained. If overall patterns exist, some consolidation may be in order, since hypotheses of direct interaction or similar responses of a single system to common factors would gain strong support from such patterns.

The subsequent definition of our measures follows Gould et al. (1974, pp. 522–524) except for 6 and 11. *Cerion* is a biometrician's delight for three reasons:

1) It preserves its entire ontogeny on fully exposed whorls.

2) It ceases growth with a definitive adult aperture. Thus we measure patterns of covariation among truly standardized adults.

3) We can specify comparable stages of ontogeny among specimens because the boundary between protoconch and accretionary shell provides an unambiguous, biological criterion for numbering whorls. Our characters can record both terminal sizes (for reason 2 above) and standardized traits of intermediate growth stages.

Our measures include:

1. Width of protoconch.
2. Width at the end of the fourth whorl.
3. Total number of whorls of the adult shell (with the termination of the protoconch taken as the 0th whorl).
4. Number of ribs on the fourth whorl.
5. Number of ribs on the sixth whorl.
6. Number of ribs in 40 micrometer units (2.22 mm) at the end of the first whorl.
7. Length of the adult shell, apex to lower apertural tip.
8. Maximum width of the adult shell.
9. Height of the protoconch.
10. Total height of the shell at the end of the fourth whorl.

11. Height from the end of whorl 4 to the end of whorl 6.
12. Width of the umbilicus.
13. Width of the apertural lip at its widest point (measured parallel to the plane of the aperture).
14. Thickness of the apertural lip at its thickest point (measured perpendicular to the plane of the aperture).
15. Height of the aperture.
16. Width of the aperture.
17. Protrusion of the aperture beyond the junction of aperture and terminal whorl (see fig. 5 of Gould et al., 1974) — a measure of both adult size and intensity in change of adult coiling.
18. Tilt of the aperture — a "pure" (ratio) measure of change in coiling to produce the adult aperture.
19. Weight of the shell.

IV. DISTINCTION OF EASTERN FORMS FROM OTHER CERIONS: PATTERNS OF COVARIATION

The distinction of eastern cerions on traditional criteria of static adult morphology has long been recognized (Pilsbry, 1902). We have been experimenting with the promising, but rarely-used criteria of "dynamic morphology," or differences in the structure of covariation among variables (Gould, 1969; Gould et al., 1974). We have, so far, studied in detail only the *C. bendalli* Pilsbry and Vanatta group of Abaco cerions (Gould et al., 1974). We wish to report some interesting differences between these and the eastern cerions.

For seven samples of *C. bendalli* from Abaco we studied factor loadings on oblique axes (following varimax rotation) in separate R-mode analyses of each sample. We found that five axis solutions (recovering 70 to 75 per cent of the total information) yielded consistent and sensible interpretations with sufficient reduction of dimensions to form interesting clusters. We grouped each variable with the axis of its highest loading. In all seven samples, we obtained the same five groups, each defined by the unvarying association of two measures (see previous list of measures), and the more variable inclusion of others:

1. Adult size with whorl number (3) and shell height (7) as its focus.

2. Ribbing, with ribs on the fourth (4) and ribs on the sixth (5) whorl. This group is by far the most distinct among Abaco shells. It always occupies the second or third axis and never includes other measures (except, in two cases, the anomalous ratio measure of apertural tilt, where there can be no consistency, for measure 18 loads once positively, once negatively, and both times weakly).

3. Early whorl heights, with protoconch height (9) and height at the fourth whorl (10).

4. Later whorl sizes, with height of the middle whorls (11) and width at the fourth whorl (2).

5. Apertural lip, with lip width (13) and thickness (14).

We performed similar R-mode oblique factor analyses for 21 eastern samples with sufficient specimens, using the DUVAP program (with provision for missing data) as in Gould et al., 1974. Five axes encompass 71 to 90 per cent of all information in these samples. No new groupings appear with any consistency or frequency. Associations three through five occur with less regularity but similar composition (in 14, 10, and 11 samples respectively). We note two outstanding differences between eastern and Abaco cerions:

1. In Abaco samples, whorl number and shell height are invariably associated as the focus of a group representing adult size. We find this association in only 9 samples of eastern cerions. In 16 samples (including some of these 9), whorl number appears in *negative* association with one or more measures of shell size at standardized early whorls (measures 1, 2, 9, 10, and 11). Such a negative association appears in no sample of Abaco *C. bendalli.* We assume that this disparity reflects a difference in the control exerted via growth over final adult size. A shell may reach large size either by growing more whorls or by growing larger whorls. If final size is strictly controlled, we anticipate a negative interaction of whorl number and whorl size — as in the eastern cerions (and in our one sample of a second Abaconian species, Gould et al., 1974, p. 528). In a jigsaw puzzle with rigid borders, increase in the size of one piece must be matched by decreasing size in others. But if size is not so strictly controlled, and if all factors that increase it work in concert (or at least independently), then we expect no negative interaction — as in the seven samples of Abaconian *C. bendalli.* If the borders of the jigsaw puzzle can expand, then all pieces might increase together.

We do not know which of our characters best measures the elusive property of overall "size," but let us consider shell weight as a possible surrogate: For all nine samples of Abaconian *C. bendalli* (only seven were factor analyzed), the mean coefficient of variation for shell weight is 21.00 (range from 15.51 to 25.85). Twenty-one eastern samples yield a mean C.V. of 16.82 (range from 9.9 to 30.2, with only three samples above 20.0). This difference is significant at the 5 per cent level (t = 2.33 at 28 d.f.). Adult weight within samples is less variable for eastern than for Abaco cerions. Final size may be more strictly controlled in the eastern cerions.

C.V.'s for weight exhibit an interesting heterogeneity among eastern cerions. Hispaniolan samples have a mean C.V. of only 12.41 (range from 9.9 to 14.3), while all other samples average 19.02 (range from 15.0 to 30.2, no overlap with Hispaniola). The lower value for Hispaniola is correlated with stronger negative interaction between whorl number and whorl size. In factor analyses of all seven Hispaniolan samples, for example, whorl number (3) always sorts in negative association with shell height from the fourth through sixth whorls (11). We find this negative interaction in only 5 of the remaining 14 groups.

2. In Abaco *Cerion*, the ribbing measures always form a tight cluster, completely distinct from all other variables. Their association in eastern cerions is equally strong, but their group often includes other measures, almost invariably of adult size. In 18 of 21 samples, other measures group with rib numbers. Shell width (8) and umbilical width (12) join in four samples, width at the fourth whorl (2) and lip width (13) in three (but never lip thickness), apertural width (16) and apertural height (15) in two. This discovery supports our intuition that the "ribs" of eastern cerions — with their even spacing, complete coverage of the shell, and regularity of form — are not controlled in the same manner as the stronger, more irregular, and more widely spaced ribs of most other cerions. The more common pattern of other species may record environmental fluctuations and the pauses in growth that accommodate to them. Perhaps the ribbing in eastern cerions reflects a more regular, internal metabolic pattern correlated with general growth (and final size) of the animal.

We gain some support for this speculation from coefficients of variation. In Abaco *C. bendalli,* mean C.V. for ribs on the fourth whorl is 14.75 (range from 12.27 to 20.94), and for ribs on the sixth whorl, 14.83 (range from 11.93 to 17.00). Comparable figures for the same measures in eastern cerions are 8.57 (range from 3.67 to 13.59) and 8.68 (range from 3.42 to 11.27). This distinction cannot be explained by differences in absolute numbers of ribs, for the ranges are comparable in both groups (mean rib number varies from 33 to 80 in Abaco samples and from 25 to 78 in eastern samples).

V. DISTINCTIONS AMONG ISLANDS FOR EASTERN CERIONS

The traditional taxonomy of eastern cerions records primarily a distinction among islands (though we note with some surprise that no one ever split the Virgin Island from the Puerto Rican cerions). We have already reported an interesting difference in variability of shell weight between Hispaniola and other areas. Differences in variation and covariation should be pursued more vigorously (if only because they are so widely neglected); but for now we proceed along traditional lines and examine differences in form.

We performed a canonical analysis on all 23 samples (373 specimens) using D/DA, a program written by John Rhoads, Department of Anthropology, Yale University (see Gould et al., 1974). We treated each sample separately, without any prior identification of its island. Table 2 records the order of discriminating power for variables expressed in univariate ANOVA. We find a perfect correspondence between this order and the traditional criteria of taxonomic distinction: strength of ribbing (variables 4, 5), width of the shell (8, 13, and 16), and obtusity of the apex (10). (Shells bearing obtuse apices are high at the end of the fourth whorl; whorls enlarge quickly and begin their rapid translation down the axis of coiling early in ontogeny. Triangular apices are lower at the end of the fourth whorl; the "triangle" records a slower increase in whorl size and a later incidence of the strong allometry that gives *Cerion* its characteristic shape by increasing height relative to width during post-juvenile to pre-adult growth.) The matrix of means for islands also records the rough order of discrimination. (Table 3 —

Table 2.   Univariate ANOVA: discriminatory power of individual variables for all 23 samples F-ratios with 22 and 350 degrees of freedom. All are significant.

Name	Number	F-ratio
4th ribs	4	208.5
6th ribs	5	157.0
aperture width	16	102.9
width	8	102.9
4th height	10	101.8
lip width	13	67.2
aperture height	15	54.1
height	7	53.0
1st ribs	6	52.4
4–6th height	11	52.1
umbilicus	12	45.2
4th width	2	40.4
whorls	3	33.6
lip thickness	14	25.2
protrusion	17	22.7
protoconch width	1	19.5
protoconch height	9	18.8
tilt	18	3.3

not the mean of sample means, but the mean of ungrouped shells for each island.)

The first three canonical axes account for 87 per cent of the variance among sample means (45.1, 29.6 and 12.3 per cent respectively; the fourth axis falls below 5 per cent). Figure 3 displays the projection of sample centroids upon the first two axes. Samples clearly group by islands; all islands are widely separated with the exception of Hispaniola and Mona. The introduction of axis three completes the pattern; Mona and Hispaniola are now distinct (Fig. 4). We need only three components of variation to sort 23 samples unambiguously into five larger groups. The strength of determination by island is well recorded in the classification matrix: 309 of 373 specimens are correctly classified, and every misclassified specimen sorts with another sample of its island. If we redo the analysis with islands rather than samples, as groups, not a single specimen is misclassified. Each lies closest to the centroid of its own island. Geographic isolation seems to be the primary correlate of morphological variation in eastern cerions.

Table 3.   Matrix of mean values for islands. Weight in grams. Linear measures in mm.

		Necker	Anegada	Puerto Rico	Mona	His-paniola	St. Croix
	Number of specimens	6	59	140	40	110	19
1.	protoconch width	3.35	3.01	3.12	3.41	2.96	3.52
2.	4th whorl width	9.48	8.70	8.96	9.48	8.18	10.44
3.	total whorls	7.58	6.95	7.26	6.42	6.80	8.41
4.	4th ribs	74.33	68.78	56.67	30.47	33.05	36.47
5.	6th ribs	60.50	53.78	51.09	26.02	29.70	34.68
6.	1st ribs	13.92	16.97	15.85	11.94	9.23	12.03
7.	height	24.70	20.03	22.29	22.32	20.17	28.60
8.	width	10.82	9.34	10.25	9.93	8.85	12.40
9.	protoconch height	1.96	1.96	2.08	2.64	2.53	2.71
10.	4th height	6.63	6.48	4.10	5.32	4.51	4.61
11.	4th-6th height	7.56	7.01	5.19	7.34	5.72	4.69
12.	umbilical width	4.19	4.05	4.16	4.33	3.83	6.23
13.	lip width	.66	.48	1.02	1.02	.63	1.22
14.	lip thickness	.99	.55	.92	1.08	.59	.87
15.	aperture height	9.58	7.89	8.99	8.59	7.82	10.59
16.	aperture width	7.63	6.59	8.10	7.23	6.40	9.87
17.	protrusion	2.45	2.01	2.78	2.21	2.04	3.35
18.	tilt	2.10	1.95	2.07	1.85	2.12	2.08
19.	weight	1.20	.55	.77	.80	.56	

The matrix of factor pattern for the analysis by samples (Table 4) defines the uniqueness of each island and exhibits the morphological bases of separations in Figures 3 and 4. (The factor pattern matrix of standardized partial regression coefficients permits us to discern how the original measures vary together in distinguishing samples along the canonical axes.) We did not include shell weight (variable 19) in this analysis because we could not weigh the St. Croix fossils with their permineralized shells and filled interiors.
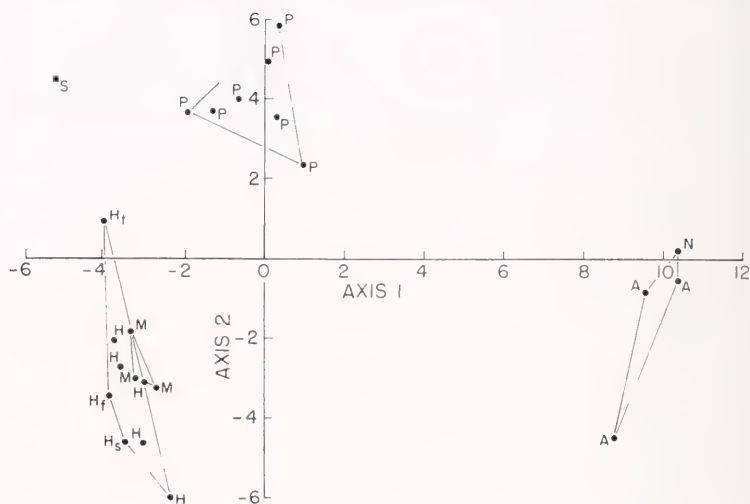
Fig. 3.   Plots of centroids for all samples on first two axes of a canonical analysis (74.7 per cent of all information) to show distinction of islands and coherence within an island. Islands are circumscribed by minimum convex polygons. A–Anegada, N–Necker, P–Puerto Rico, M–Mona, S–St. Croix, and H–Hispaniola. H_t–*Cerion tortuga* (locality 23), H_f–*C. yumaense ferruginum* (locality 20), H_s–*C. yumaense saona* (locality 15).
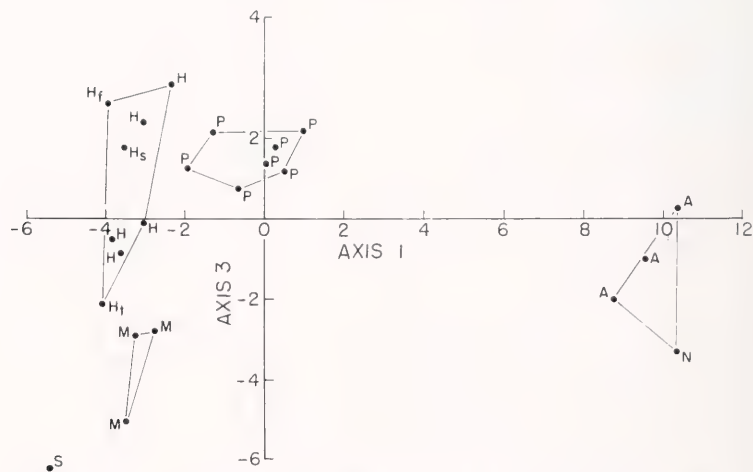

Fig. 4.   Axis 1 vs. axis 3 for the same canonical analysis depicted in Figure 3. Code letters same as in Figure 3. Note that Mona and Hispaniola (overlapping in Fig. 3) are distinguished by the third axis.

Table 4. Factor pattern (structure of covariance) for original variables on first five canonical axes for all 23 samples.

No.	Name	1	2	3	4	5
1	protoconch width	−0.0430	0.1082	−0.3254	0.2116	−0.0632
2	4th width	−0.0239	0.2443	−0.4745	0.1357	−0.1085
3	whorls	−0.0047	0.2851	−0.1552	−0.4931	−0.1116
4	4th ribs	0.6196	0.4860	0.2486	−0.0291	−0.1228
5	6th ribs	0.4526	0.5397	0.2748	−0.0553	−0.2221
6	1st ribs	0.2427	0.3124	0.0459	0.2449	0.4016
7	height	−0.0968	0.3027	−0.4599	−0.1611	−0.4270
8	width	−0.0607	0.5167	−0.5713	−0.1082	−0.2853
9	protoconch height	−0.1590	−0.1151	−0.1863	−0.0339	−0.0540
10	4th height	0.3893	−0.2690	−0.4891	0.1371	0.1004
11	4–6th height	0.1832	−0.2792	−0.2773	0.4856	−0.2967
12	umbilicus	−0.0624	0.2278	−0.4813	−0.3020	0.2144
13	lip width	−0.2000	0.4035	−0.2115	0.3895	0.1607
14	lip thickness	−0.0726	0.2054	−0.1453	0.4387	−0.1463
15	aperture height	−0.0788	0.3720	−0.3568	−0.0482	−0.4348
16	aperture width	−0.1126	0.5692	−0.3769	−0.0336	−0.1512
17	protrusion	−0.0602	0.2759	−0.0882	−0.0274	−0.0037
18	tilt	−0.0180	0.0311	0.0417	−0.1369	−0.1053

The first axis separates Virgin Island samples from all others (see Figs. 3, 4). Its factor pattern records high values for measures of ribbing and whorl heights (10 and 11). Indeed, the Virgin Island samples exceed all others in their number of ribs and the obtuseness of their apices (Fig. 2). The negative loading of protoconch height (9) also reflects the obtuse apex of Virgin Island cerions (see mean values in Table 3). High protoconchs are followed by slowly expanding whorls that join the embryonic shell to produce a pointed apex with modest whorl heights; low protoconchs precede rapid expansion (high values of 10–11) and build more obtuse apices.

The second axis separates Puerto Rican samples (positive projections) from Mona Island and Hispaniola (negative projections). The factor pattern contains high positive loadings for two groups of variables: measures of ribbing (4 and 5) and shell widths, particularly aperture width (8 and 16). Whorl heights (10 and 11) load negatively. The cerions of Puerto Rico can be distinguished visually by their more circular apertures; this feature translates to high values for aperture width in our quantitative analysis. The St. Croix specimens (which also project strongly and positively on

axis two) are wide as a simple function of their large size. The ribbing measures set the major contrast between Puerto Rican samples and Mona and Hispaniolan samples. Puerto Rican cerions are abundantly ribbed (though not so abundantly as Virgin Island samples), while Mona and Hispaniolan cerions have the fewest (though strongest) ribs among eastern cerions. Puerto Rican specimens also have fairly triangular apices. This feature translates as low whorl height (10 and 11) in our measures; the negative loading of measures 10 and 11 assures the high positive projection of Puerto Rican samples on the second axis.

The third axis separates Mona and Hispaniola to complete the distinction among islands. Mona and Hispaniolan samples fell together with negative projections on the first two axes for essentially the same reason — their small number of ribs. Several measures of size — particularly of widths (2, 8, 12, and 16 — load strongly and negatively upon the third axis. Hispaniolan shells are small and especially narrow (note low mean values of 2 and 8 in Table 3); they project positively upon an axis with negative loadings for these measures. Mona samples are large and wide; since measures for size and width have negative loadings, these samples project negatively upon the axis.

Subsequent axes continue the patterns of distinction by island. The fourth axis, for example, separates Mona, having high projections, from St. Croix, having low projections. Highest loadings are for height from whorl 4 through 6 (positive) and number of whorls (negative). St. Croix specimens with their maximal number of whorls and minimal fourth to sixth whorl heights project negatively. Mona samples with their distinctively low number of whorls project positively. The fifth axis separates Virgin Island samples into their two areas of Necker and Anegada. The Necker Island sample projects strongly and negatively upon an axis with positive loadings for its low number of ribs on the first whorl (relative to Anegada), and high negative loadings for various measures of shell size.

VI. DISTINCTION AMONG SAMPLES

A persistent tradition of *Cerion* studies holds that virtually every local population bears its own distinctive morphology. This remarkable phenomenon has inspired the burden of an exuberant

specific nomenclature for these animals. Nothing we have seen in several years of study contradicts this conventional observation. We therefore predicted that samples within islands should be distinct in separate canonical analyses for each island. Our results confirm this prediction with great accuracy. The classification matrix for four Virgin Island samples correctly assigns 63 of 65 specimens to their correct sample (96.9 per cent). Only 3 of 40 specimens from Mona Island lie closest to the centroid of a sample not their own (92.5 per cent are correctly classified). Of specimens from Hispaniola, 101 of 110 are correctly allocated among eight samples (91.8 per cent). Only Puerto Rico falls below 90 per cent success — 116 of 139 specimens in seven samples (83.5 per cent).

We have, in summary, established a hierarchy of distinction among the eastern cerions. Their basic design is strikingly different — both in form and in pattern of covariance — from other cerions. Islands are distinct. Samples within islands can also be separated with little overlap.

VII. A UNIFYING THEME AND A TAXONOMIC PROPOSAL

The distinction of islands does not preclude the existence of pattern among them. We concluded that geographic separation serves as the primary correlate of morphological distinction among the eastern cerions. But does the degree of morphological separation reflect geographic distance? If so, we might expect a clinal distribution of morphology, since the islands form an essentially linear array. If we find no coherent pattern, taxonomic distinction by island should be maintained (with, God forbid, a new taxon for the Virgin Islands).

The output of our canonical analysis for islands includes a matrix of Mahalanobis distances (D^2) — a measure of separation between centroids with adjustments for variance and covariance (Table 5). Each entry is a measure of morphological distinctness (based on all variables) between shells of two islands. If we plot D^2 (see Sneath and Sokal, 1973, pp. 127, 128) against geographic separation (defined, for any island pair, as the distance between our two closest sample localities), we obtain a remarkably tight and linear relationship ($r = .96$). This calculation (Fig. 5) excludes the St. Croix fossils as representatives of another time with no expected relationship to current trends. When we plot the St. Croix

Table 5.   Matrix of Mahalanobis distances (D^2) for analysis using all specimens grouped by islands.

	N	A	P	M	H	S
Necker	0					
Anegada	18.87	0				
Puerto Rico	125.33	102.90	0			
Mona	155.33	134.73	54.66	0		
Hispaniola	164.32	131.32	38.00	31.23	0	
St. Croix	214.23	187.83	65.86	65.29	57.11	0
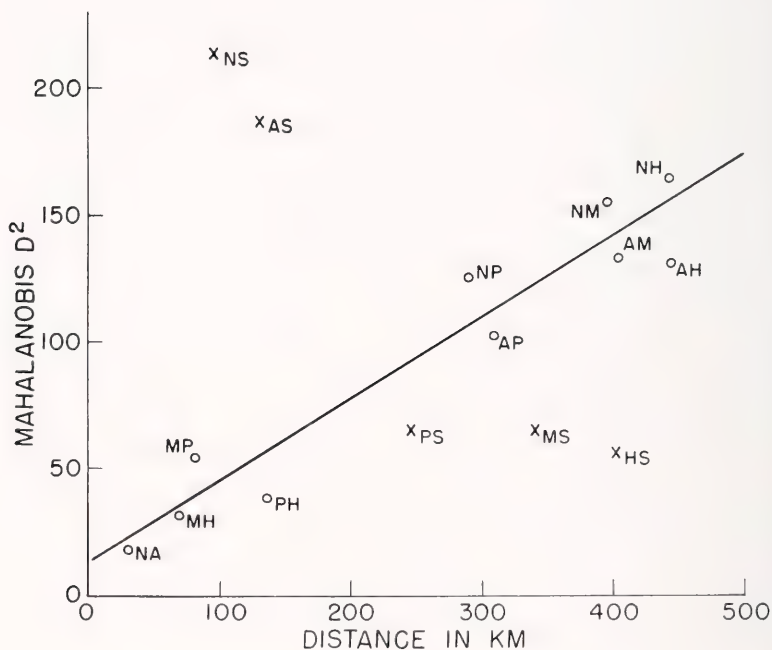
Fig. 5.   Mahalanobis distance (morphological) vs. geographic separation for eastern cerions. Note the tight correlation and the departure of St. Croix fossils from the trend. A–Anegada, N–Necker, P–Puerto Rico, M–Mona, H–Hispaniola, and S–St. Croix.
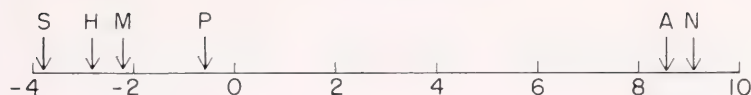
Fig. 6. Projections on the first canonical axis for a discriminant analysis by islands. This axis explains more than half (58.8 per cent) of all information. Note the perfect correspondence of morphological gradation and geographic position for the modern samples. Only the St. Croix fossils depart from the trend. Code letters as in Figure 5.

distances on Figure 5, they depart markedly from the regression line of modern samples. Geographic and morphological distance are closely correlated in living eastern cerions. But this relationship does not guarantee any graded trend of morphology along the linear array of islands. In fact, we already have a test for clines in the results of our canonical analysis.

In our canonical analysis for islands, the most significant discriminator (the first axis) explains 58.8 per cent of all information. Figure 6 shows the array of projections. Living cerions are arranged in perfect geographic order; only the fossils of St. Croix depart from the pattern. The morphological gradation runs from egg-shaped, finely and copiously ribbed shells with very obtuse apices (Virgin Islands) to more cylindrical, apically pointed shells with fewer, stronger ribs (Hispaniola) — see the discussion of factor patterns in Section V. The direction of the cline also meets our expectations. Virgin Island shells represent the extreme expression of morphological features that characterize eastern cerions; they are also geographically furthest from any contact with non-eastern congeners. The Hispaniolan specimens, situated in closest proximity to non-eastern cerions, depart most strongly from modal eastern morphology towards the more "normal" form of the genus.

We are not addicted to speculative biogeography, and we offer no preferred hypothesis for this pattern; we do not see how museum specimens can distinguish among such alternatives as selective gradients and gene flow, and we know virtually nothing about the history of colonization. We only note that the strikingly discordant position of the St. Croix fossils may indicate a fairly recent origin for the graded series of modern forms. (The St. Croix fossils are morphologically furthest from their nearest modern relatives on Necker and Anegada.)

In the light of this pattern, we see no reason to maintain the taxonomic distinction among living eastern forms. Some common factor accounts for most of the morphological variabiity among these populations. We therefore consider all of the following names as synonyms of the first-named form, *Cerion striatellum* ("Férrusac" Guerin-Meneville), 1829: *C. monaense* Clench, 1951; *C. yumaense* Pilsbry and Vanatta, 1895 (with its four subspecies); *C. ferruginum* (Maynard, 1896 — ranked as a subspecies of *C. yumaense* by most later authors); and *C. tortuga* Pilsbry and Vanatta, 1928. We maintain, for now, *Cerion rude* (Pfeiffer), 1855 for the St. Croix fossils. The St. Croix shells depart completely from modern trends in geographic variation. Indeed, this departure serves as a strong support for taxonomic identity of recent populations — for it argues against any appreciable antiquity for the modern pattern. Moreover, the St. Croix shells, while closer to the eastern mode than to any other morphotype of *Cerion,* vary from this mode in the direction of more conventional Bahamian and Cuban forms — shells are larger, more cylindrical, and more sparsely and strongly ribbed. As another argument for the taxonomic unity of modern forms, we note that the morphological distances among islands are trifling compared with the distinction of several forms that interbreed freely throughout the Bahamas. In fact, and incredible as it may seem in the light of *Cerion*'s fantastic morphological variety, we have located no unambiguous case of sympatry without interbreeding for the entire genus (two of nine reported cases have a fair chance of validation in our opinion).

VIII. CONCLUSION

Studies of *Cerion* have been dominated by the conviction that no regular patterns of geographic variation exist. All leading students have invoked haphazard transport by hurricanes to support a notion of "crazy-quilt" distributions (Mayr and Rosen, 1956). We now present the first evidence for simple, graded, coherent variation over a large part of *Cerion*'s range. Moreover, S. J. Gould and D. S. Woodruff, working in the northern Bahamas during the past four years, have found strikingly consistent patterns of within-island variation on all islands visited (Abaco, Grand Bahama, New Providence, Great Exuma, and Long). The "ribby" morphotype, for example (called *C. glans* (Küster) and

about 50 synonyms on New Providence, *C. abacoense* Pilsbry and Vanatta and 3 synonyms on Abaco and Grand Bahama, etc.), always inhabits coastal areas at the edges of the Pleistocene banks; while the mottled morphotype inhabits interior coasts (with respect to the banks) and interior areas. The two morphotypes intergrade in a variety of interesting ways at their contacts. The discovery of simple and coherent patterns, both within and between islands, leads to a hope — even an expectation — that some sense will yet be made of *Cerion*.

IX. ACKNOWLEDGMENT

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BREVIORA

Museum of Comparative Zoology

A NEW INTERPRETATION OF THE MAMMALIAN TEETH OF TRIBOSPHENIC PATTERN FROM THE ALBIAN OF TEXAS

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ABSTRACT. A reappraisal has been made of tribosphenic teeth from the Albian of Texas, previously described by Patterson, Slaughter and Turnbull. At least six genera are represented. *Pappotherium* and *Holoclemensia,* the most common genera, are sufficiently alike to be placed in the same family, Pappotheriidae. They have four molars as in marsupials and complex premolars as in placentals. They cannot be classified either as marsupials or placentals but are considered to belong to a separate evolutionary line (Pappotherida, new order). Two forms of smaller size, *Kermackia texana* and *Trinititherium slaughteri* gen. et sp. nov., whose lower molars are at a more primitive stage of evolution than the Pappotheriidae, are placed in a new family Kermackiidae (Aegialodontia, new order). *Slaughteria eruptens* gen. et sp. nov., the only species for which there is evidence of tooth-replacement, is placed provisionally in the same family. A new infraclass, Tribotheria, is proposed to include mammals with tribosphenic molars that are not classifiable as marsupials or placentals.

INTRODUCTION

Patterson (1956) reported on a collection of teeth found in the Greenwood Canyon, near Forestburg in eastern Texas. Many of the molar teeth are of tribosphenic pattern. They are mid-Creta-ceous (Albian), the oldest tribosphenic molars known at that time. The Greenwood Canyon fauna is intermediate in age between the late Jurassic Purbeck and Morrison faunas and the late Cretaceous Djadokhta fauna of Mongolia. During this long interval of about 50 million years, the Jurassic mammal orders were largely replaced

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by marsupials and placentals. Only the multituberculates survived
into the late Cretaceous in more than small numbers.

The differentiation between marsupials and placentals is believed
to have taken place during the earlier part of the Cretaceous. Both
marsupials and placentals share the tribosphenic molar pattern.
With only the evidence of isolated teeth, Patterson was unable to
decide in which infraclass his specimens belonged or whether they
represented a group from which both marsupials and placentals
would arise. Accordingly, he classified them as "Therian mammals
of uncertain infraclass affinities but of Metatherian-Eutherian
grade."

Between 1965 and 1971, Slaughter published descriptions of im-
portant additional material. He obtained it from Butler Farm, a
locality of similar age to the Greenwood Canyon locality. He
named two species based on upper molars: *Pappotherium patter-
soni* and *Holoclemensia texana*. The holotype of *P. pattersoni* is
a fragment containing the last two molars. The holotype of *H.
texana* is a penultimate molar of which the protocone shelf is lack-
ing; Slaughter used a complete last molar as a paratype and re-
ferred a lower molar to this species. He named a third species,
Kermackia texana from another isolated lower molar.

Holoclemensia differs from *Pappotherium* in the arrangement of
the buccal stylar cusps of its upper molars (Fig. 1). In *Pappother-
ium* there is a large stylocone (Style B), about as high as the meta-
cone. In *Holoclemensia,* the stylocone is much smaller, but there
is a large conical cusp (Style C) opposite the notch between the
paracone and the metacone. In the incomplete material at his dis-
posal Patterson (1956) mistook Style C for the stylocone. Style C
occurs in many late Cretaceous marsupials; it is higher than the
stylocone in *Albertatherium* and *Aquiladelphis* (Fox, 1971).

Slaughter (1968b) regarded *Holoclemensia* as a marsupial, not
only because of the presence of Style C, but also because the meta-
cone is less reduced than in *Pappotherium.* In 1968a he described
some partly molariform premolars, unlike those of any marsupial.
In 1971, he referred to *Pappotherium* a mandible that contained a
newly erupted and a partially erupted premolar together with worn
molars. This specimen indicates diphyodonty of the anterior den-
tition, characteristic of placentals. He therefore regarded *Pappo-
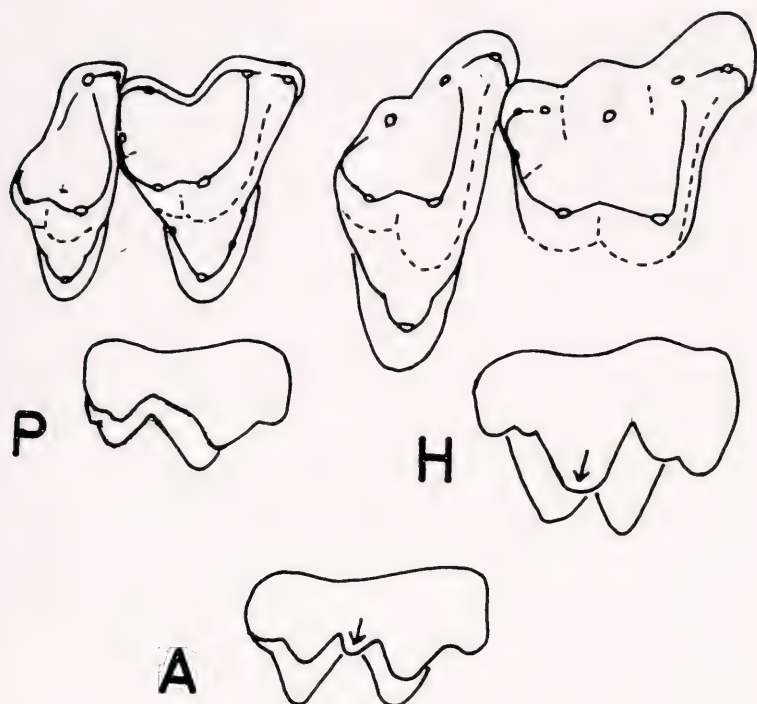therium* as a placental. Subsequently Fox (1975) deduced from the

Figure 1. P, last two upper molars of *Pappotherium pattersoni*, SMP-SMU 61725, and buccal view of penultimate molar. H, the same, *Holoclemensia texana*, SMP-SMU 62099 and 62147. A, buccal view of upper molar of *Alphadon marshi*. Stylar cusp C is indicated by an arrow.

shapes of the last two teeth that *Pappotherium* had only three molars.

Lillegraven (1969, 1974) and Hoffstetter (1970, 1972) believe that the marsupial-placental differentiation was due to isolation on different continents. Placentals in Asia and marsupials in North America suggest that the placentals that appear in North America towards the end of the Cretaceous are immigrants from Asia. This opinion does not accord with Slaughter's view that both infraclasses were present on the continent as early as the Albian. It seemed desirable to reexamine the evidence provided by the Texas Albian fauna that affects a crucial stage of mammalian evolution.

During visits to the United States in 1966 and 1974 I studied specimens from Greenwood Canyon that Patterson described (1956) as well as additional material that Turnbull (1971) described. The latter was subsequently collected from the same locality. The Greenwood Canyon material is housed in the Field Museum of Natural History, Chicago (registration numbers PM —). Of the Butler Farm collection, I saw the specimens described by Slaughter (1965, 1968a) and the jaw containing premolars with molars (Slaughter, 1971). I studied other Butler Farm specimens from casts. The material from Butler Farm is housed in the Shuler Museum of Paleontology, Southern Methodist University, Dallas, Texas (registration numbers SMP-SMU —). I used a Wild M5 microscope to make camera lucida drawings, at known magnifications, of all the specimens studied.

Nearly all the specimens consist of isolated teeth. A primary aim of the investigation was to find the most probable way in which they could be combined into dentitions. The relationships of the species believed to be present in the fauna could then be considered.

UPPER MOLARS

All the upper molars that I have seen are drawn in crown view in Fig. 2. Except in the holotype of *Pappotherium,* all are isolated, and their position in the series must be judged from their shape alone. Last molars, whether M^3 or M^4, are easily recognizable. Reduction of the metacone and loss of the metastyle accompany a reduction of the posterobuccal lobe of the outline. These features are widespread and almost certainly primitive among mammals with tribosphenic molars. On passing forward along the molar series, both in marsupials and placentals, the posterobuccal lobe becomes relatively larger, so that eventually it projects buccally beyond the level of the parastyle; the metacone also enlarges and the metastylar crest becomes longer. The degree of difference between adjacent molars varies considerably between genera and families and to some extent individually. The penultimate molar is preserved in the holotypes of *Pappotherium* and *Holoclemensia* (Fig. 2, d, 1). In both, the posterobuccal lobe is less prominent than the parastylar region, though both possess the metastylar crest.

When measured by the relative distances of the metacone and par-
acone from the buccal edge, *Holoclemensia* has a rather less prom-
inent posterobuccal lobe, but the difference between the two genera
is not great. *Holoclemensia* also has a higher metacone than *Pap-
potherium,* a difference that is repeated on the last molar.

Of the isolated last molars, PM 1075 (Fig. 2, c), though smaller
than the holotype of *Pappotherium,* agrees with that specimen in
structure; PM 1015 (Fig. 2, b) has a less reduced posterobuccal
lobe and a larger metacone; PM 1287 (Fig. 2, p) has a smaller pro-
tocone shelf than *Pappotherium.* The posterior surface of the stylo-
cone of PM 1015 has a small cusp, indistinctly indicated on PM
1075. Whether this cusp is the equivalent of Style C is uncertain.
Style C is comparatively well developed on the last molar of *Holo-
clemensia,* but Turnbull (1971, Fig. 1) misidentified it as the meta-
style. PM 1015 and PM 1075 both differ from *Holoclemensia* and
resemble *Pappotherium* in having a concavity of the anterior out-
line lingually to the parastyle. PM 1287, with its small protocone,
is clearly distinct from both *Holoclemensia* and *Pappotherium.*

Several upper molars have the posterobuccal region less reduced
than on the penultimate molars of *Holoclemensia* and *Pappothe-
rium,* and they must be considered as examples of more anterior
molars. PM 1000 (Fig. 2, o) has a well preserved buccal stylar shelf
on which Style C is the highest cusp. This identifies the tooth as
Holoclemensia, but the metacone is farther from the buccal edge
than the paracone is. PM 886 (Fig. 2, m) has lost the parastylar
region, but Style C, which is preserved, is as high as the metacone.
This tooth is larger than PM 1000 and differs from it in that the
paracone and metacone are nearly equidistant from the buccal
edge. PM 1004 (Fig. 2, n), poorly preserved, agrees with PM 886
in comparable parts. There is evidence that *Holoclemensia* had two
molars anterior to the penultimate tooth and four molars with all
included (Fig. 5, H).

PM 999 (Fig. 2, h) resembles the penultimate molar of *Pap-
potherium* in the enlarged stylocone and in the metacone, which
is less high than the paracone; however, the posterobuccal lobe of
PM 999 is prominent and bears a strong metastylar crest. PM 1238
(Fig. 2, i), of which the anterior part of the stylar shelf is missing,
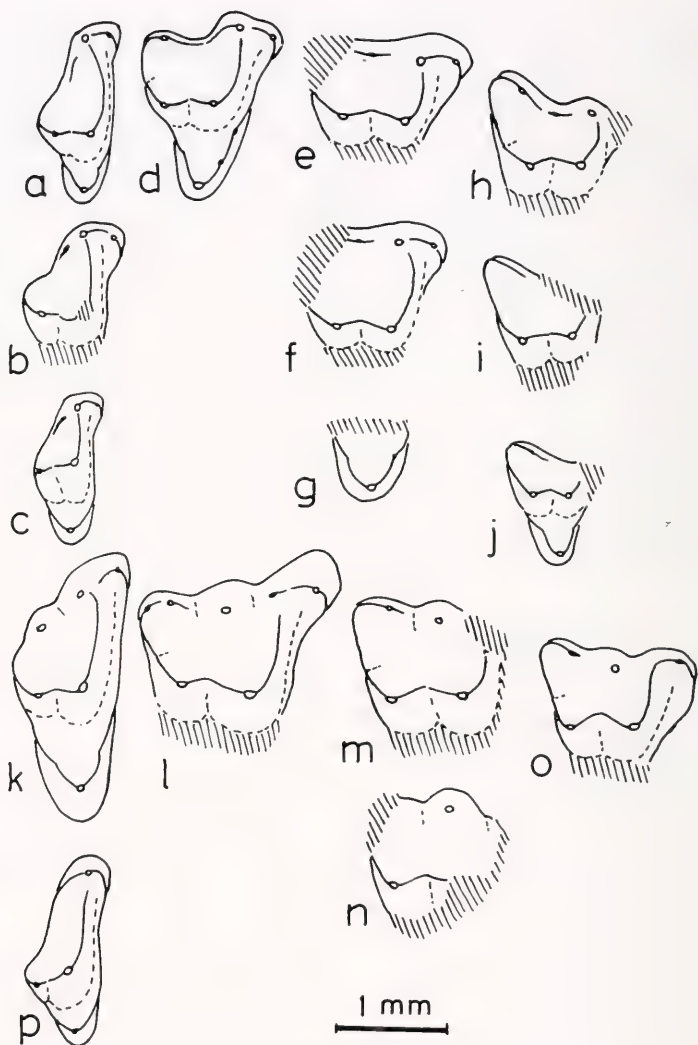agrees with PM 999 in the metacone and metastyle and is almost

Figure 2.   Crown views of upper molars. a, SMP-SMU 61725 (holotype of
Pappotherium pattersoni); b, PM 1015; c, PM 1075; d, SMP-SMU 61725 (holotype
of *P. pattersoni*); e, PM 884; f, PM 1749; g, PM 1325; h, PM 999; i, PM 1238;
j, SMP-SMU 62402; k, SMP-SMU 62099 (paratype of *Holoclemensia texana*); l,
SMP-SMU 61947 (holotype of *H. texana*); m, PM 886; n, PM 1004; o, PM 1000;
p, PM 1287. All drawn as right teeth: b, c, e, f, i, o, p have been reversed.

certainly another example of the same tooth. PM 884 and PM 1749 (Fig. 2, e, f) represent a different type of molar. The metastylar region has broken off in both specimens. As in *Pappotherium,* the stylocone is high and the metacone is lower than the paracone. These teeth are larger than PM 999 and PM 1238 (Fig. 2, h, i), and based on the incomplete crowns, the metacone and paracone were nearly equidistant from the buccal margin. On PM 999, PM 884 and PM 1749 there is a slight elevation of the marginal ridge in the region corresponding to Style C, but this elevation is very different from the enlarged Style C of *Holoclemensia.*

There are therefore two types of upper molar, with a pattern similar to *Pappotherium,* that correspond to the supposed first two molars of *Holoclemensia* — a larger, more symmetrical M^2 and a smaller M^1 with a more prominent metastylar corner. The evidence suggests that *Pappotherium* has four molars like *Holoclemensia* (Fig. 5, P).

PM 1325 (Fig. 2, g) is the lingual part of an upper molar which seems from its size to be more probably referable to *Pappotherium* than to *Holoclemensia.*

SMP-SMU 62402 (Fig. 2, j) resembles PM 999 and PM 1238 in pattern but differs from them in its smaller size. This tooth may be M^1 of a smaller species, of which PM 1075 might be the last molar.

LOWER MOLARS

The allocation of lower to upper molars is particularly difficult in the case of the therians from the Albian of Texas. This difficulty arises because *Pappotherium* and *Holoclemensia* have been distinguished mainly by the buccal stylar shelf, which does not occlude with the lower teeth. The protocone, which does occlude, is missing from most upper molars.

Patterson and Slaughter have distinguished six types of lower molars, Types 1, 2, and 3 by Patterson (unworn examples illustrated in Fig. 3), Types 4, 5 and 6 by Slaughter. Combinations of some of these types seem probable.

Teeth of Type 1 are characterized by the anteroposteriorly short trigonid, in which the paraconid is lower than the metaconid, and a comparatively wide talonid on which the hypoconid is elevated and placed nearly in line with the protoconid. In Type 1 Patterson

placed PM 1005 (Fig. 3, H) and the trigonid PM 887; to these may
be added the trigonid PM 3877. Slaughter (1965) classified three
teeth from Butler Farm as Type 5 (SMP-SMU 62131, 61727, and
61735). These differ from Type 1 in the less elevated trigonid,
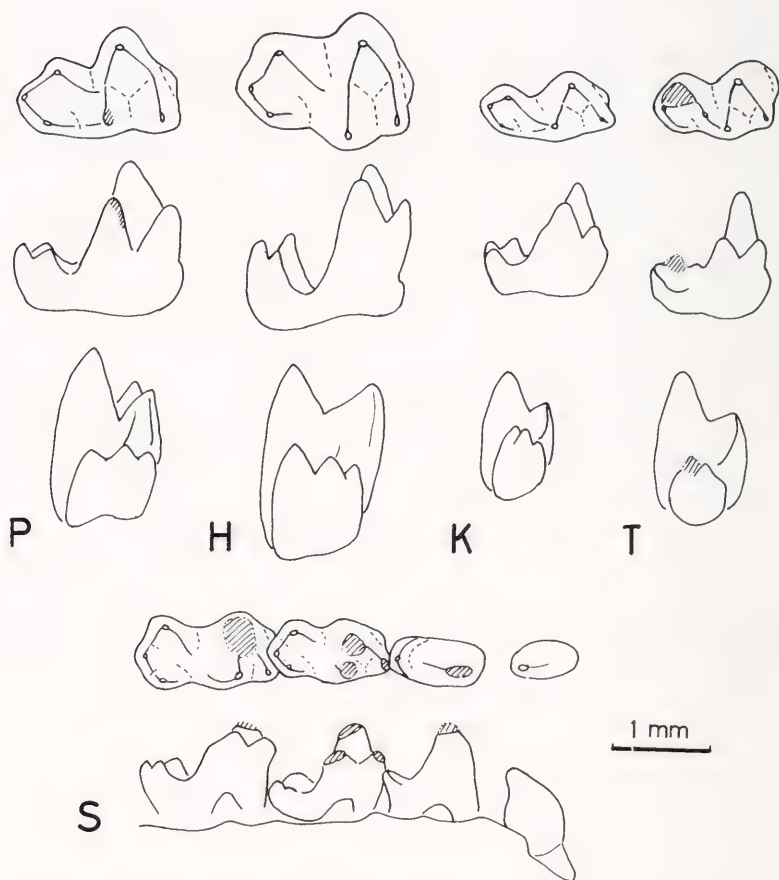which has a greater anterior tilt, and in the narrower talonid. Teeth

Figure 3.   P, H, K, and T, left lower molars drawn in crown, lingual and pos-
terior views. P, Type 2 (PM 965, reversed), referred to *Pappotherium;* H, Type 1
(PM 1005, reversed), referred to *Holoclemensia;* K, Type 3 (PM 1245, reversed),
Kermackia; T, Type 6 (SMP-SMU 61728), holotype of *Trinititherium slaughteri.*
S, SMP-SMU 61992, holotype of *Slaughteria eruptens,* crown and lingual views.

of Type 5 were referred by Slaughter (1968b) to *Holoclemensia.*
SMP-SMU 61726, belonging to Slaughter's Type 4, has a relatively
long and narrow talonid with a less elevated hypoconid; it has lost
the tops of the trigonid cusps.

The differences between Types 1, 4, and 5 could be due to serial
position in a single species — Type 4 being the last molar, Type 5
the penultimate, and Type 1 the most anterior molar of the three.
A trigonid, PM 966, agrees with Type 1 in the relative height of the
paraconid and metaconid, but the trigonid is narrower transversely
and less compressed anteroposteriorly. Probably because of its
more open trigonid, Patterson included this specimen with Type 2,
but it could be a first molar standing in the same dentition as Type
1 and bringing the number of molars to four (Fig. 5, H).

Teeth of Patterson's Type 2 have a more open trigonid than those
of Type 1. The metaconid is smaller; it is similar in height to the
paraconid. The talonid is narrower than in Type 1. The hypoconid
is comparatively low, and it is not placed so far buccally in relation
to the protoconid. The talonid is preserved completely only in PM
965 (Fig. 3, P); in PM 948 the hypoconulid has been broken off.
PM 930, PM 660, PM 1249, and PM 1119 are isolated trigonids.
A feature of Type 2 teeth, not noted by Patterson, is the oblique
crest that continues along up the posterior wall of the trigonid al-
most to the top; it ends in an intermediate position between the tip
of the metaconid and the notch dividing that cusp from the proto-
conid. In teeth of Types 1 and 5, and also in PM 966, the oblique
crest is confined to the lower part of the trigonid wall. Type 2 teeth
are smaller than those of Types 1, 4 and 5: their trigonid widths
range from 0.91 to 1.16 mm compared with 1.26 to 1.46 mm in the
other types (measurements from Turnbull, 1971). No teeth of Type
2 have been reported from Butler Farm.

It is probable that Types 1, 4, and 5 are referable to *Holocle-
mensia* and Type 2 to *Pappotherium.* The upper molars of *Holo-
clemensia* are larger, and they have larger metacones which might
correlate with large and buccally situated hypoconids on the lower
molars. The upper molars referred to *Pappotherium* are too small
to fit lower molars of Types 1, 4, and 5, but their occlusion with
Type 2 lower molars is feasible. PM 930, the Type 2 tooth with
the smallest and most open trigonid, would be a first molar. The
largest examples of Type 2, PM 965 and PM 660, would be second

molars, corresponding to the largest upper molars. The smaller PM 948 and PM 1249 would be third or perhaps fourth molars (Fig. 5, P). It is to be noted that Crompton (1971) used a Type 4 tooth to illustrate the occlusion of *Pappotherium.*

Patterson's Type 3 was represented by only one damaged tooth (PM 922), but an unworn specimen (PM 1245; Fig. 3, K) has been recovered subsequently. It is very similar to the holotype of *Kermackia texana,* from which it differs by its higher and more pointed protoconid and metaconid. This difference is due to loss of enamel from the trigonid of the holotype. The trigonid is widely open, and the paraconid points anteriorly. The protoconid is the highest trigonid cusp, the paraconid the lowest. From the metaconid arises a strong posterior crest (named *Distal Metacristid* by Fox, 1975), continuous with the crista obliqua. The talonid is narrower than the trigonid. The hypoconid stands only slightly more buccally than the hypoconulid. The entoconid is small, and the talonid basin is open on the lingual side between the entoconid and the metaconid.

Slaughter's Type 6 is based on the jaw fragment SMP-SMU 61728. This contains a molar (Fig. 3, T), apparently the last, and the alveoli of the next anterior tooth. Type 6 resembles *Kermackia texana* in size and general proportions, but the metaconid of Type 6 is much smaller, no higher than the paraconid. As in *Kermackia,* the crista obliqua runs to the metaconid. As the crest continues up the posterior surface of the metaconid, it is much weaker and nearly vertical. The talonid basin is widely open on the lingual side as in *Kermackia,* but the entoconid is almost absent, and an additional cusp is present on the crista obliqua. The top of the hypoconid has been broken off. Two trigonids from Greenwood Canyon, PM 1065 and PM 1045, have the same structure. This form is sufficiently distinctive to deserve a name, which I propose formally as follows:

Trinititherium, gen. nov.

Diagnosis. The lower molars differ from those of *Kermackia* as follows: (1) metaconid and paraconid subequal; (2) an accessory cusp present on the crista obliqua; (3) the crest on the posterior surface of the metaconid weaker and more vertical; (4) entoconid rudimentary. Type species:

Trinititherium slaughteri, sp. nov.

Diagnosis. This is the only known species of *Trinititherium.*

Holotype, SMP-SMU 61728, from Butler Farm. Illustrated by Slaughter (1965, Fig. 4, and 1971, Pl. 1).

W. A. Clemens (personal communication) has raised the question whether *Trinititherium* might represent the posterior molar of *Kermackia.* This would imply a reduction of the metaconid towards the posterior end of the series. Such a process occurs as an aspect of carnassial specialization in Cenozoic carnivorous mammals (Butler 1947). The metaconid is also reduced in Deltatheridiidae and Stagodontidae in the late Cretaceous. In all these, there is evidence of a sectorial specialization of the paraconid which is not shown by *Trinititherium.* The metaconid is similar in height to the paraconid in *Kielantherium* and probably in *Aegialodon.* In these genera, however, the talonid is shorter and narrower than in *Trinititherium* and *Kermackia.*

Turnbull (1971) grouped together Types 1, 2, and 5 as *Holoclemensia* and Types 3, 4, and 6 as *Pappotherium.* He included in *Holoclemensia* the specimens of Type 2 that are here regarded as *Pappotherium.* He did not consider in detail the morphological features that distinguish Type 2 from Types 1 and 5. He ascribed the differences to individual variation, to position in the series, and possibly to the presence of more than one species of *Holoclemensia.* The teeth that Turnbull identified as *Pappotherium* include those of *Kermackia* and *Trinititherium,* together with Type 4, regarded here as the last molar of *Holoclemensia.* The criteria by which he distinguished *Pappotherium* from *Holoclemensia* are those which in the present paper are used to distinguish *Kermackia* and *Trinititherium* from *Pappotherium* and *Holoclemensia.* *Kermackia* had not been described when Turnbull wrote his paper, and his supposition, that all the tribosphenic molars in the collection could be referred to *Pappotherium* or *Holoclemensia,* was not unreasonable.

There remains to be considered the lower jaw with four teeth (SMP-SMU 61992; Fig. 3, S), referred by Slaughter (1971) to *Pappotherium.* Two teeth are simple, and two are molariform. The first molariform tooth is narrower than the second and has less elevated cusps. Slaughter says the first is less worn than the second molariform tooth and identifies it as a premolar. The existence of a molariform premolar at such an early date seems very unlikely. Both molariform teeth are much more worn than the two premo-

lariform teeth, one of which is in process of eruption. Slaughter's statement (1971: 137) that X-rays showed no unerupted teeth excludes the possibility that the first molariform tooth is a milk molar. The molariform teeth must be regarded as permanent molars.

M_1 is similar in size to that of *Kermackia;* M_2 is larger than M_1, though it is smaller than the smallest specimen of Type 2 (PM 930). On both teeth, the tops of the trigonid cusps are broken off or worn, but the metaconid was evidently higher than the forwardly projecting paraconid. On both molars the talonid is as wide as the trigonid, and the hypoconid is buccally situated in relation to the hypoconulid. The entoconid is as high as the hypoconulid on M_2, but lower on M_1. On both molars the anterior end of the crista obliqua has been obliterated through wear, and its relations to the trigonid are uncertain. However, the metaconid of M_2 carries a strong posterior ridge that resembles *Kermackia* and differs from Type 2. This specimen cannot be placed in any of the species so far described, and because of its importance I propose a name for it as follows:

<div align="center">

Slaughteria, gen. nov.

</div>

Diagnosis. M_2 differs from lower molars of Type 2, referred to *Pappotherium,* in that (1) the metaconid is higher than the paraconid, and (2) the metaconid has a posterior ridge, probably continuous with the crista obliqua. M_2 differs from lower molars of *Kermackia* in that (1) the talonid is equal in width to the trigonid, and (2) the entoconid is larger than that of *Kermackia.* There is no metaconid on the lower premolars. Type species:

<div align="center">

Slaughteria eruptens, spec. nov.

</div>

Diagnosis. This is the only known species of *Slaughteria.*

Holotype, SMP-SMU 61992, from Butler Farm. Illustrated by Slaughter, 1971, Pl. 9. It is a mandibular fragment with two molars and two premolars, the anterior premolar in process of eruption.

<div align="center">

PREMOLARS

</div>

The last premolar of *Slaughteria* is a two-rooted tooth with a well developed, one-cusped heel but no anterior cusp. The anterior premolar is smaller and seemingly has a single root. There are some isolated two-rooted premolars from Greenwood Canyon. PM 1247 (Fig. 4, a) is larger than the last premolar of *Slaughteria.* It has a

small posterior heel and an anterior basal cusp which is displaced towards the lingual side, indicating that the tooth is from the lower jaw. PM 1098 (Fig. 4, b) is the posterior part of a lower premolar, probably a little larger than PM 1247 and with a larger, two-cusped heel. PM 1136 (Fig. 4, c) is a much smaller tooth with no anterior
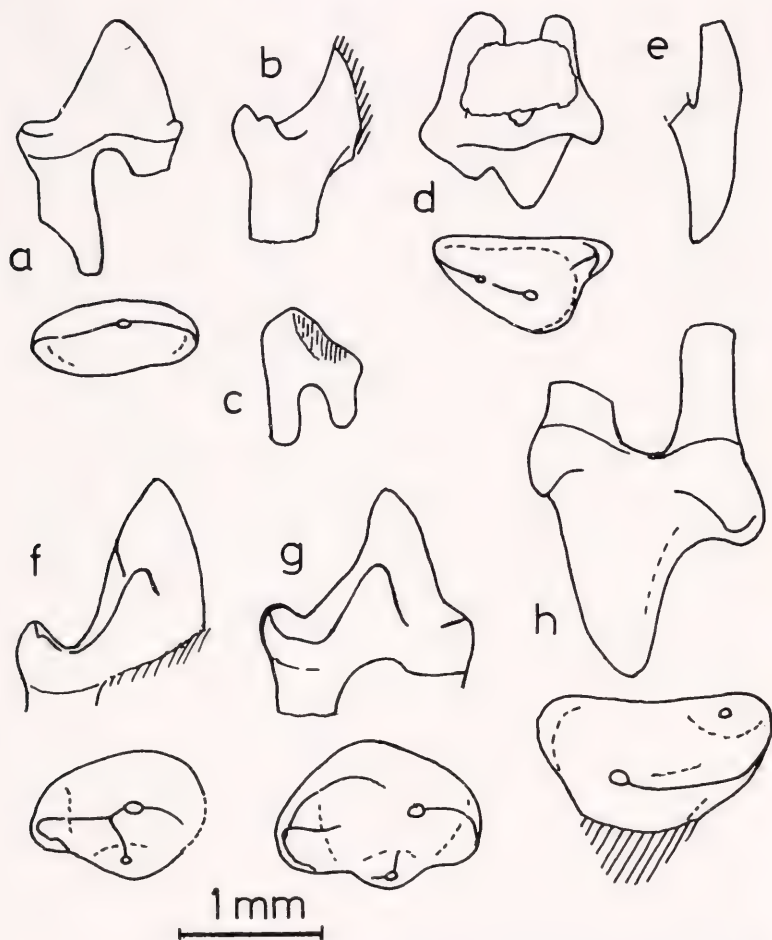

Figure 4.   Premolars and canine. a, PM 1247, lingual and crown views; b, PM 1098, lingual view; c, PM 1136, ? buccal view; d, PM 931, buccal and crown views; e, PM 1124; f, SMP-SMU 62399, lingual and crown views (from a cast); g, SMP-SMU 61947, lingual and crown views; h, SMP-SMU 61948, buccal and crown views.

cusp or posterior heel. Its anterior profile is strongly convex, and there is a posterior crest which shows wear. None of the Texas specimens resembles the Wealden specimen that Clemens (1963, Fig. 10) described. The latter is a narrow tooth with divergent roots and a low crown, having the appearance of a milk molar. SMP-SMU 61730 and 61731 (Slaughter 1965, Fig. 5) are triconodont.

The submolariform premolars that Slaughter (1968a, 1971) described are of greater interest. SMP-SMU 61947 (Fig. 4, g) is a lower premolar with a small talonid, a low, lingually placed paraconid, and a low metaconid. A crest on the buccal side from the talonid cusp continues up the posterobuccal surface of the protoconid. In addition, there is a median talonid crest (=crista obliqua) which terminates at the base of the trigonid. SMP-SMU 62399 (Fig. 4, f) resembles SMP-SMU 61947 in having a small metaconid, but it differs from that specimen in a number of details. The tooth is narrower and the protoconid is taller. The crista obliqua continues up the posterior surface of the protoconid to meet the crest that connects the protoconid with the metaconid. As the paraconid of SMP-SMU 62399 has broken off, the length of the tooth can only be estimated, but it was probably a little shorter than SMP-SMU 61947 (length about 1.4 mm, compared with 1.55 mm).

It is unlikely that either of these teeth is a penultimate premolar (conventionally called P_3). Among late Cretaceous mammals a metaconid is known on P_3 only in *Gypsonictops*. In that genus P_3 also has a partly molariform talonid, and its possession of a metaconid can be ascribed to the unusually high level of molarization of the tooth. Such molarization is almost certainly a specialization of *Gypsonictops*, unlikely to be present in ancestral placentals (Butler 1977). A metaconid occurs on the last premolar (P_4) in several late Cretaceous genera: *Zalambdalestes, Protungulatum, Procerberus* and *Batodon*. Both the Albian specimens are interpreted as P_4. The differences between them show that they belong to different species.

SMP-SMU 61948 (Fig. 4, h) is a triangular upper premolar which Slaughter (1968a) compared with a placental P^3. The lingual lobe was broken off, but a small protocone must have been present originally. The paracone is a tall cusp, similar in height to the protoconid of SMP-SMU 62399. There is no metacone. This tooth resembles P^3 of *Asioryctes*, but whether it is a P^3 or a P^4 is uncer-

tain. In *Asioryctes*, as in *Kennalestes* and *Zalambdalestes*, the paracone of P^3 is higher than that of P^4 and subequal to the protoconid of P_4. However, P^3 may have been secondarily enlarged (Butler 1977). There is no metaconid on the lower premolars of *Kennalestes* and *Asioryctes*, and comparison with these genera may be misleading. In Cretaceous marsupials, such as *Alphadon*, the last upper premolar is the largest, and this is true also of *Deltatheridium*.

PM 931 (Fig. 4, d) is an upper premolar which differs greatly from SMP-SMU 61948. It has a metacone on the shearing crest, but no protocone. This last cusp is represented only by an indistinct cingulum. The strongly developed shearing crest suggests that PM 931 is a last premolar that functioned against the trigonid of M_1. The absence of the protocone suggests that the corresponding lower premolar lacked a metaconid, and therefore that PM 931 did not occlude with either of the known complex lower premolars. It is too large to fit the lower dentition of *Slaughteria*. There are only two roots. The posterior one is flattened in cross section and arranged obliquely, to support the lingual as well as the posterior apex of the crown. A similar arrangement is known in symmetrodont molars, but PM 931 is much too large to be referred to *Spalacotheroides*.

Probably some of the submolariform premolars belong to species of which the molars are already known. Only in *Slaughteria* have premolars been found in association with molars, and there the last premolar has no metaconid. In *Slaughteria*, the length of the last premolar is 65 per cent of that of M_2. The two lower premolars with metaconids are as long as or longer than the molars of *Kermackia* and *Trinititherium*, and they are therefore probably too large to belong to these forms. Moreover in *Kermackia* and *Trinititherium* the crista obliqua on the molars runs directly to the metaconid. The possibility that the submolariform premolars belong to *Pappotherium* or *Holoclemensia* must therefore be considered.

The crista obliqua of SMP-SMU 62399 resembles that of Type 2 (supposedly *Pappotherium*) molars in meeting the protoconid-metaconid crest, whereas that of SMP-SMU 61947 fades out near the base of the trigonid as on *Holoclemensia* molars. In the late Cretaceous marsupials, *Alphadon* and *Pediomys*, the last lower

premolar is about three-quarters as long as the longest molar, and in the placental *Kennalestes* the proportion is about 80 per cent. SMP-SMU 61947 is 80 per cent as long as PM 1005, interpreted as M_2 of *Holoclemensia;* the somewhat shorter SMP-SMU 62399 would bear about the same proportion to PM 965, the largest supposed *Pappotherium* molar. Size as well as structure is therefore consistent with the reference of SMP-SMU 61947 to *Holoclemensia* and SMP-SMU 62399 to *Pappotherium.*

The upper premolar SMP-SMU 61948 would fit either of the two complex lower premolars. It possesses a strongly developed stylar cusp on the buccal edge, anterior to the metastyle. This cusp might be considered serially homologous with Style C of the molars. For this reason I refer SMP-SMU 61948, tentatively, to *Holoclemensia* as a P^4 or P^3.

PM 931 (Fig. 4, d) is too small and its shearing crest too longitudinal to have functioned against the trigonid of PM 966, the supposed M_1 of *Holoclemensia.* The absence of the protocone on the premolar suggests that this cusp was relatively small on the molars. Perhaps this tooth belongs to the same species as the last molar PM 1287 (Fig. 2, p) in which the protocone is small.

The mandible PM 583 (Patterson 1956, Figs. 10, 11) contains alveoli for four two-rooted premolars. The posterior alveoli are of a size to fit *Kermackia* molars and are probably too large for premolars of that genus. The last pair of alveoli, however, could have held either of the premolars with metaconids, and the simple premolar PM 1247 would fit the alveoli for P_3. There is a possibility that this mandible belongs to either *Holoclemensia* or *Pappotheium.* The remarkably large canine alveolus differentiates this specimen from SMP-SMU 62400 (Slaughter 1971, Pl. 10), a fragment containing a small, procumbent canine. PM 1124 (Fig. 4, e) is an upright two-rooted canine of small size, probably from the upper jaw. The mandible PM 583 contains alveoli for four lower incisors. Slaughter (1971, Pl. 10) described a rather large, spatulate upper incisor.

DISCUSSION

Number of Genera Represented

The material from the Albian of Texas consists almost entirely of isolated teeth. Until more complete specimens are discovered,

any interpretations or conclusions must remain highly speculative. Differences in the molars, premolars, canines and incisors indicate that a number of distinct taxa are present, at least on the generic level. In attempting to allocate the various sorts of teeth, I have avoided the introduction of additional taxa as far as possible. The minimum number of taxa necessary to include the known molars seems to be the following six:

1. *Holoclemensia,* the largest form, is represented by several upper and lower molars; complex upper and lower premolars are allocated to this form.

2. *Pappotherium,* a somewhat smaller form, is represented again by several upper and lower (Type 2) molars; a complex lower premolar is referred to it.

Holoclemensia and *Pappotherium* are the most common members of the fauna, but *Pappotherium* seems to be relatively more common at Greenwood Canyon than at Butler Farm. The toothless mandible may belong to either genus.

3. *Slaughteria* is represented by a single mandibular specimen, which is the only one to show associated molar and premolar teeth; it is smaller than *Pappotherium.*

4. *Kermackia* is a small form known only by three lower molars.

5. *Trinititherium,* similar in size to *Kermackia,* is known by one complete lower molar and two trigonids. The small upper molar SMP-SMU 62402, and the last molar PM 1075 may belong to either *Kermackia* or *Trinititherium.*

6. The last upper molar PM 1287 and the upper premolar PM 931 do not appear to belong to any of the foregoing and probably represent one or two additional species.

The Family **Pappotheriidae**

As interpreted here, *Pappotherium* and *Holoclemensia* are much alike in the organization of their molar series. Both have four molars, of which the second is the largest, and in the upper jaw, M^3 is reduced posterobuccally. M^1 of *Holoclemensia* is more symmetrical than in *Pappotherium,* and M^3 less so, but such differences are to be found frequently in closely related genera of mammals.

There is a wide stylar shelf in both genera. The trigonid is elevated, and it has a well developed, trenchant paraconid. The talonid is narrower than the trigonid. The lower molars have no cingu-

lum except on the anterior surface of the protoconid. The last lower premolar has a metaconid and, at least in *Holoclemensia*, the last upper premolar has a protocone.

The large Style C of *Holoclemensia* is represented in some specimens of *Pappotherium* by a minor elevation of the buccal marginal ridge. The metacone of *Holoclemensia* is larger in comparison with the paracone than in *Pappotherium*. The lower molars of *Holoclemensia* have a more compressed trigonid, a higher metaconid, and a more buccally situated hypoconid. The crista obliqua in *Holoclemensia* fades out at the base of the trigonid, whereas in *Pappotherium* it continues up the trigonid wall. These differences seem insufficient to place the two genera in separate families, and I propose to include them both in the Pappotheriidae Slaughter 1965.

Relationship of Pappotheriidae to Marsupials and Placentals

The Pappotheriidae agree with the primitive marsupial *Alphadon* in the possession of four molars and in the wide stylar shelf of the upper molars. *Holoclemensia* resembles *Alphadon* in having a distinct Style C, but in *Alphadon* this is smaller than the stylocone (Style B), and it varies in size between the species. In *Alphadon* M^3 is the largest molar, and its posterobuccal apex and metastylar blade are not reduced. A further difference appears to be that the protocone shelf of *Alphadon* is better differentiated with more strongly developed conules. In *Alphadon* the metacone is as tall or taller than the paracone; *Holoclemensia*, with its larger metacone, approaches *Alphadon* in this respect more closely than *Pappotherium* does.

The lower molars of Pappotheriidae resemble *Alphadon* in the trenchant paraconid and in the connection of the crista obliqua to the middle of the posterior trigonid wall. However, in the marsupials the talonid is as wide as the trigonid, sometimes wider. The hypoconulid is in a lingual position, close to the entoconid, and a cingulum, arising from the hypoconulid, passes behind the hypoconid. In pappotheriids the trigonid, especially in *Holoclemensia*, is more elevated. *Holoclemensia* also differs from *Alphadon* in that the trigonid is more compressed on M_2-M_4. The metaconid is higher than the paraconid, and the hypoconid is higher in comparison with the entoconid on M_2 and M_3. *Pappotherium* (i.e. Type 2)
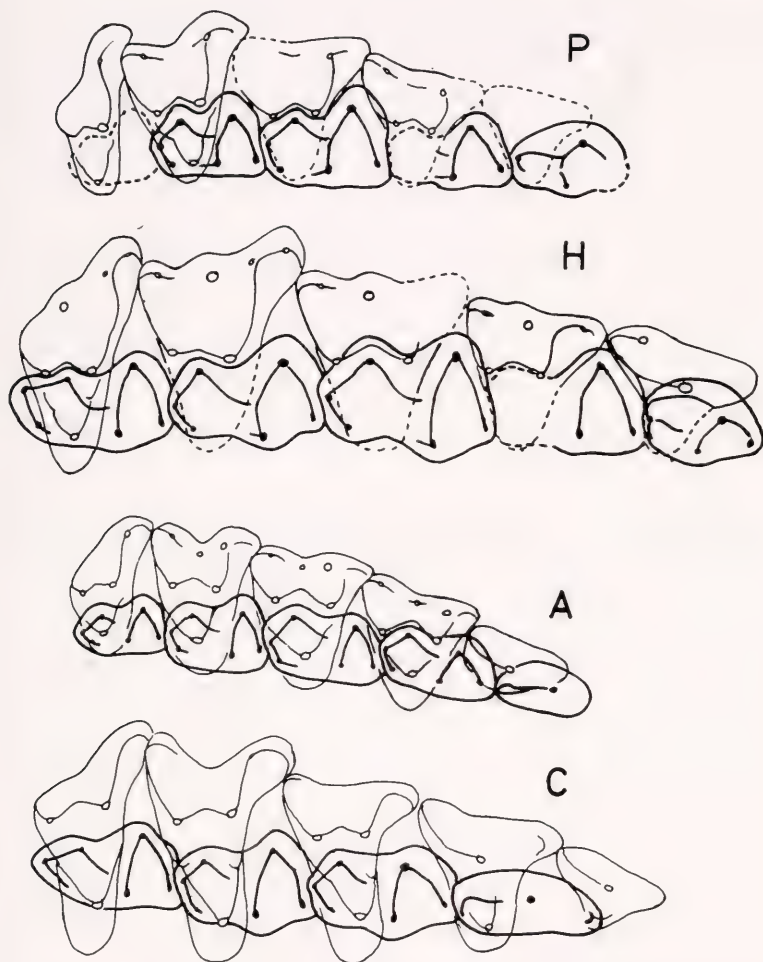
Figure 5. Reconstructions of cheek teeth in occlusion. P. *Pappotherium patter-soni;* H, *Holoclemensia texana;* A, *Alphadon marshi* (a marsupial); C, *Cimolestes incisus* (a placental).

Specimens used in the reconstruction of *Pappotherium:* M^1, PM 999; M^2, PM 894; M^3 and M^4, the holotype; P_4, SMP-SMU 62399; M_1, PM 930; M_2, PM 965; M_3, PM 948.

Specimens used in the reconstruction of *Holoclemensia:* P^4, SMP-SMU 61948; M^1, PM 1000; M^2, PM 886; M^3, the holotype; M^4, the paratype; P_4, SMP-SMU 61947; M_1, PM 966; M_2, PM 1005; M_3, SMP-SMU 61727; M_4, SMP-SMU 61726.

agrees more with *Alphadon* in these characters, as was noted by Clemens (1966:16–17).

Albertatherium (Fox 1971), from the early Campanian, approaches *Holoclemensia* in that Style C is higher than the stylocone, and the metaconid is somewhat higher than the paraconid. However, the stylar shelf of *Albertatherium* is narrower than in *Holoclemensia*. The metacone and metastyle of M³ are larger, and the conules are better developed. On the lower molars, the trigonid is less compressed; the talonid wider; and the hypoconulid is lingual in position, and the entoconid is higher. As Fox (1971) noted, *Albertatherium* does not link *Alphadon* with *Holoclemensia*. Style C is also enlarged in *Aquiladelphis,* an early Campanian pediomyid in which the stylocone is reduced to two small cusps. In other respects this form resembles *Holoclemensia* even less than *Albertatherium;* for example, the crista obliqua meets the posterior wall of the protoconid.

The primitive eutherian molar pattern is believed to be preserved best in the late Cretaceous *Cimolestes* and *Kennalestes* (Butler, 1977). *Holoclemensia* and *Pappotherium* differ from these in the retention of the fourth molar, in the wide stylar shelf with better developed styles posterior to the stylocone, and in the correspondingly weaker development of the protocone shelf. Lower molars of Pappotheriidae agree with those of primitive placentals in the high trigonid and comparatively narrow talonid, in the connection of the crista obliqua to the middle of the trigonid wall, and in the absence of the posterior cingulum. *Holoclemensia,* not *Pappotherium,* agrees with *Cimolestes* and *Kennalestes* in that the metaconid is higher than the paraconid. If the tooth has been correctly referred, the possession of a premolar protocone would constitute another resemblance of *Holoclemensia* to placentals. However, there is no metaconid on P₄ in *Cimolestes* or *Kennalestes*.

Fox (1975) noted a resemblance in the outlines of the last two upper molars between *Holoclemensia* and the late Cretaceous *Deltatheroides,* which has four molars. He concluded that *Holoclemensia* must have four molars. Because the penultimate molar of *Pappotherium* shows less reduction in the metastyle, Fox inferred that only three molars were present in that genus. I find his argument unconvincing; the relationship between the shapes of teeth and their numerical position is too inconstant for such deductions

to be made. Late Cretaceous didelphids have four molars, and yet the metastyle of their penultimate molar is more developed than in *Pappotherium*. *Deltatheroides,* in which the metastyle of M³ is reduced, can be regarded as being in the process of losing its M⁴, which is absent in *Deltatheridium* (Kielan-Jaworowska 1975); *Holoclemensia* might by analogy be considered to be evolving towards the three-molar state characteristic of placentals.

It seems impossible to fit *Holoclemensia* and *Pappotherium* into a simple metatherian-eutherian framework. They have a mixture of characters which indicate that they belong to neither infraclass. Though *Holoclemensia* approaches primitive marsupials in some ways, *Pappotherium* is more like them in others; *Holoclemensia* also shows some resemblances to primitive placentals. No doubt some of the characters that pappotheriids share with marsupials or placentals are plesiomorphs inherited from a common ancestor, which may include the wide stylar shelf of primitive marsupials and the narrow talonid of primitive placentals. The fourth molar is probably another plesiomorphous character lost in placentals but retained in Deltatheridiidae (Butler & Kielan-Jaworowska, 1973; Kielan-Jaworowska, 1975) as well as in marsupials. Other shared characters may be due to parallel evolution, such as the enlarged Style C. The metaconid of P_4 may also have evolved independently, for it occurs in some placentals but not in others.

Placentals have been reported from Khovboor in Mongolia (Beliajeva et al., 1974; Dashzeveg, 1975) in a deposit that is believed to be of Aptian age. The fauna, still undescribed, is said to contain forerunners of the much later Djadokhta fauna. If the Aptian age of these specimens is correct, the divergence of placentals and marsupials must already have taken place at that time. The Albian Pappotheriidae would in that case be too late to be the common ancestors of the two infraclasses. Clemens (1971: 174) states that "The evidence . . . does not exclude the possibility that when the tribosphenic grade of dental evolution was attained an adaptive radiation occurred producing lineages in addition to those ancestral to marsupials and placentals." The Pappotheriidae may well have belonged to one such lineage.

During much of the Cretaceous the land surface was more than usually fragmented by epicontinental seas (Lillegraven, 1974; Telford, 1974). North America was divided, from middle Albian time

onwards, into eastern and western land-masses by the Interior Sea-way. The northern part of the Atlantic was closed: the seaway between Greenland and Canada developed only in the Campanian (Martin, 1973). Europe was separated from Asia by the Turgai Strait. In mid-Cretaceous time, eastern North America and Europe thus formed a single continent from which the mammals from Texas are the only known representatives of their class. Following Lille-graven (1974) one may imagine a wide dispersal, in the early Cre-taceous, of an ancestral group with tribosphenic molars, of which *Aegialodon,* from the English Wealden, is the only known example. Subsequently isolated on different land-masses, the ancestral group gave rise to the placentals in Asia and the marsupials in western North America (or as Telford (1974) suggests, in South America). Possibly the Pappotheriidae represent another lineage that evolved on the Euramerican continent, but subsequently became extinct. A molar from the Campanian of Champ-Garimond, France (Le-doux et al., 1966; Butler, 1977) might conceivably be a pappotheriid derivative, but it is more advanced, and it might equally well be a placental immigrant from Asia.

Kermackiidae, *Fam. nov.*

Kermackia and *Trinititherium* are distinguished from *Pappo-therium* and *Holoclemensia* by the continuation of the crista ob-liqua to the tip of the metaconid, so that on the posterior surface of that cusp it forms a ridge (the distal metacristid of Fox, 1975). The talonid is narrow, its basin is widely open lingually, and the entoconid is small or rudimentary. These genera are at a lower level of molar evolution than the Pappotheriidae. In the latter the con-nection of the crista obliqua to the trigonid has shifted to a more buccal position, the talonid is wider, and the entoconid is larger. Dashzeveg (1975) noted the resemblance of *Kermackia* to *Aegialo-don* and *Kielantherium,* which belong to the family Aegialodonti-dae Kermack (1957). However, these differ from *Kermackia* in having the talonid reduced in length as well as in width. Because of this difference I propose the family Kermackiidae to include *Kermackia* and *Trinititherium.* The Kermackiidae resemble the Aegialodontidae in retaining the distal metacristid but differ from them in that the talonid is equal in length to the trigonid. The

Aegialodontidae, Kermackiidae and Pappotheriidae represent three stages in the evolution of the talonid (Fig. 6).

Slaughteria, which probably possesses a distal metacristid, has a wide talonid, and (on M_2, but not on M_1) a fully developed entoconid like the Pappotheriidae. It may represent another family, but, as some doubt remains over the details of the molar pattern, I prefer to place *Slaughteria* provisionally in the Kermackiidae. To judge from the relative size of the penultimate premolar, the number of premolars may bave been reduced. *Slaughteria* is the only Albian therian for which there is evidence of tooth replacement, and on this character, Slaughter (1971) placed it in the Eutheria. However, diphyodonty occurs in pantotheres (Butler & Krebs, 1973), and it must be considered a plesiomorphous character, re-
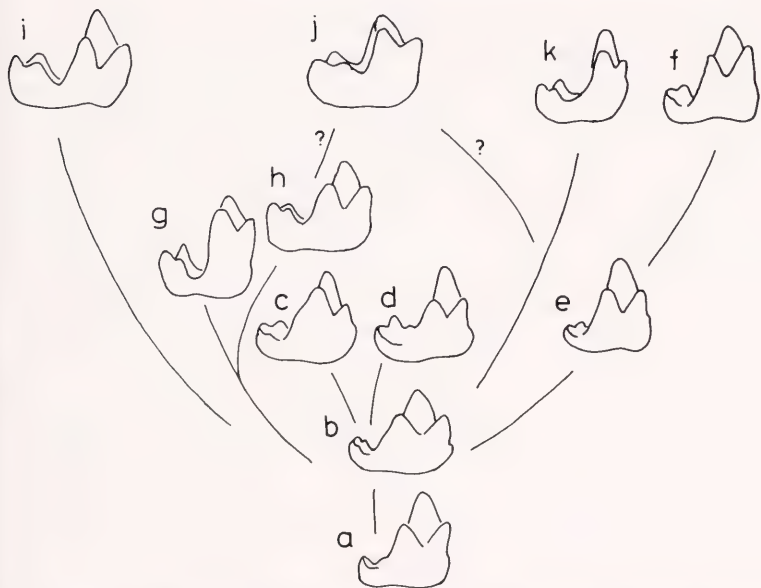
Figure 6.   Left lower molars in lingual view, to illustrate possible evolutionary radiation in the early Cretaceous. a, *Peramus* (Pantotheria); b, *Aegialodon;* e,*Kielantherium* (Aegialodontidae); c, *Kermackia;* d, *Trinititherium* (Kermackiidae); f, *Deltatheridium* (Deltatheridiidae); g, *Holoclemensia;* h, *Pappotherium* (Pappotheriidae); i, *Alphadon* (Metatheria); j, Champ-Garimond molar; k, *Kennalestes* (Eutheria).

tained in placentals and lost (except for the last premolar) in marsupials.

CLASSIFICATION ABOVE THE FAMILY LEVEL

A name is required for an infraclass to include those therians that have a functional protocone and have advanced beyond the pantotherian stage, but nevertheless cannot be regarded either as marsupials or placentals. Turnbull (1971) proposed a cohort Tribosphenata, equal in rank with his Marsupiata and Placentata, including all within the infraclass Eutheria. The Tribosphenata comprised two orders: (1) Tribosphena, containing *Pappotherium, Holoclemensia, Aegialodon* and *Peramus,* and (2) Zalambdodonta, consisting of a number of placentals and marsupials with zalambdodont molar teeth. Since zalambdodont molar patterns have been derived, more than once, from dilambdodont ("euthemorphic") patterns (Butler 1972), I consider the order Zalambdodonta to be artificial.

I propose the name Tribotheria for an infraclass standing between the Pantotheria, on the one hand, and the Metatheria and Eutheria on the other. The Tribotheria differ from the Pantotheria in having reached the tribosphenic stage of molar evolution by the acquisition of a protocone that functioned against the talonid. The infraclasses Metatheria and Eutheria originated from members of the Tribotheria, but there were other, less diversified lineages, such as the Deltatheridiidae and Pappotheriidae, which may be left in the Tribotheria. Turnbull's order Tribosphena was similar in conception, but it included *Peramus,* which lacks a functional protocone.

For Tribotheria with a distal metacristid I propose an order Aegialodontia. This corresponds to stage IIA in the scheme of molar evolution tabulated by Fox (1975, Table 1). The Aegialodontia includes the families Aegialodontidae and Kermackiidae. The late Cretaceous Deltatheridiidae may also be placed here. Their lower molars show a considerable resemblance to *Kielantherium,* and it seems likely that they have an aegialodontid ancestry, from which they have retained the small talonid. *Potamotelses* (Fox 1975) may represent another family in the Aegialodontia. For the Pappotheriidae, which have lost the distal metacristid, and are at a stage of evolution comparable to the primitive marsupials and placentals, I propose a new order Pappotherida.

The classification proposed may be tabulated:

Subclass Theria
  Infraclass Pantotheria
  Infraclass Tribotheria
    Order Aegialodontia
      Family Aegialodontidae (*Aegialodon, Kielantherium*)
      Family Kermackiidae (*Kermackia, Trinititherium,* ? *Slaughteria*)
      Family Deltatheridiidae (*Deltatheroides, Deltatheridium*)
      Family ? (*Potamotelses*)
    Order Pappotherida
      Family Pappotheriidae (*Pappotherium, Holoclemensia*)
  Infraclass Metatheria
  Infraclass Eutheria

SUMMARY

1. At least six genera of mammals with tribosphenic molars are represented in the collection, but most specimens can be referred to *Pappotherium* and *Holoclemensia.*

2. There are four types of upper molar of *Holoclemensia* pattern, and four of *Pappotherium* pattern, showing that both these genera had four molars.

3. Of the six types of lower molar distinguished by Patterson and Slaughter, Types 1, 4, and 5 are referred to *Holoclemensia* and Type 2 (except for PM 966) to *Pappotherium.*

4. Lower molars of Type 3 are *Kermackia,* and those of Type 6 are named *Trinititherium slaughteri* gen. et sp. nov.

5. The two lower premolars with metaconids are referred to *Holoclemensia* and *Pappotherium* respectively, and the upper premolar with a protocone is referred to *Holoclemensia.*

6. The mandible SMP-SMU 61992, which Slaughter (1971) referred to *Pappotherium,* has two molars and two premolars. It is named *Slaughteria eruptens* gen. et sp. nov. It is the only specimen that provides evidence of tooth replacement.

7. *Pappotherium* and *Holoclemensia* are united in the family Pappotheriidae. They are neither marsupials nor placentals, but represent a separate line of evolution.

8. *Kermackia* and *Trinititherium* are placed in a new family Kermackiidae. They are at a more primitive stage of molar evo-

lution than the Pappotheriidae. *Slaughteria* is provisionally placed in the Kermackiidae.

9. A new infraclass Tribotheria is proposed to include mammals with tribosphenic molars that are not classifiable as marsupials or placentals. This infraclass includes two new orders, Aegialodontia and Pappotheria.

ACKNOWLEDGMENTS

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BREVIORA

Museum of Comparative Zoology

FOOD SELECTION BY BEAVERS: SAMPLING BEHAVIOR

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ABSTRACT. Beavers in central Massachusetts frequently remove small pieces of bark (less than 25 cm^2) from standing trees. After removing a sample, the beavers may abandon these trees. At two ponds studied by the author in fall 1973, there were significant differences in species composition of trees sampled, felled, and available near the ponds. If beavers are physiologically capable of measuring the nutritional value of small pieces of bark, then sampling may be an economical way for them to assess spatial and temporal variation in relative nutritional value of different tree species.

INTRODUCTION

During a recent study of food selection by beavers (*Castor can-adensis*) at two ponds in central Massachusetts (Jenkins, 1974), I observed numerous trees from which the beavers had removed small patches of bark (often less than 25 cm^2). Without using them further, the beavers then abandoned these trees. During September and October 1973, beavers at Blue Heron Cove cut into or partially stripped the bark from the lower trunks of 46 trees without com-pletely felling them. At Tamplin Road Pond, there were 36 such trees. The beavers removed less than 25 cm^2 of bark from 25 of the 46 trees at Blue Heron Cove and the same amount from 17 of the 36 trees at Tamplin Road Pond.

Chabreck (1958) reported that beavers in Louisiana stripped the bark from the lower trunks of many trees without felling them. Aldous (1938) and many others have noted that beavers may not use all the bark of the trees they fell. The present study is the first to describe and to consider the possible adaptive significance in the beavers' pattern of removing small pieces of bark (less than 25 cm^2)

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from standing trees. Secondly, the study compares the beavers' patterns of selection of species for sampling with their patterns of selection of species for more complete utilization.

For economy of expression, I will call the beavers' incomplete use of trees (described above) *sampling*. I define light sampling as use of less than 25 cm^2 of bark near the base of a tree without felling it and heavy sampling as cutting into the wood of a tree and/or stripping more than 25 cm^2 of bark near its base without felling it. Several authors (Rozin, 1969; Freeland and Janzen, 1974; Westoby, 1974) have attached functional connotations to the word *sampling* in their discussions of optimal foraging. I wish to avoid a specific functional connotation in using the word. Instead, I present six alternative hypotheses which could account for beavers' incomplete use of trees. The first of these hypotheses argues that beavers' sampling might not be of direct adaptive value but is rather an incidental byproduct of the foraging process. The remaining five suggest five different ways in which sampling might function as an adaptive component of a beaver's foraging strategy. My data are insufficient to discriminate completely among these hypotheses; I present them to establish that sampling by beavers is a phenomenon worth further study, especially in the context of recent developments in optimal foraging theory (Krebs et al., 1977; Pyke et al., 1977).

RESULTS AND DISCUSSION

Table 1 shows the generic distributions of trees sampled, felled, and available at the major tree cutting sites of Blue Heron Cove and Tamplin Road Pond between 1 September 1973 and 6 November 1973 (Blue Heron Cove) or 2 November 1973 (Tamplin Road Pond). The following hypotheses might explain beavers' tree sampling behavior.

(1) A beaver may be interrupted while starting to fell a tree. Sampled trees simply represent those abandoned because of such interruption. If the probability of interruption is independent of tree genus, and if the time to remove less than 25 cm^2 of bark from a tree is less than the time to fell even a small tree (but one more than 2.5 cm diameter, the lower size limit considered in this study), then this hypothesis predicts that the generic distributions of lightly sampled and felled trees should be the same. (Heavily sampled

Generic Distributions of Trees Sampled, Felled, and Available at
Blue Heron Cove and Tamplin Road Pond, Fall 1973

	Lightly Sampled*	Heavily Sampled**	Felled	Available†
		Blue Heron Cove		
Oak (*Quercus* spp.)	11 (44%)	16 (76%)	31 (51%)	63 (25%)
Maple (*Acer* spp.)	4 (16%)	1 (5%)	14 (23%)	97 (38%)
Birch (*Betula* spp.)	9 (36%)	3 (14%)	1 (2%)	41 (16%)
Others	1 (4%)	1 (5%)	15 (25%)	53 (21%)
Totals	25	21	61	254
		Tamplin Road Pond		
Oak (*Quercus* spp.)	6 (35%)	7 (37%)	2 (6%)	15 (12%)
Maple (*Acer* spp.)	4 (24%)	9 (47%)	12 (34%)	59 (45%)
Cherry (*Prunus* spp.)	5 (29%)	3 (16%)	15 (43%)	18 (14%)
Others	2 (12%)	0 (0%)	6 (17%)	38 (29%)
Totals	17	19	35	130

*Less than 25 cm² of bark removed.
**Wood cut and/or more than 25 cm² of bark removed.
†Based on randomly placed, 78.5 m², circular quadrats. See Jenkins (1975) for
details.

trees are excluded because it may take less time to fell a small tree
than to sample heavily a large tree, and a difference in the generic
distributions of sampled and felled trees might arise from differ-
ences in the available diameter distributions of various genera.) At
Blue Heron Cove, generic distributions of lightly sampled and felled
trees are significantly different ($\chi^2 = 15.0$, 2 df, $p < 0.001$, only oak,
maple, and birch considered because few trees of other genera were
sampled). At Tamplin Road Pond, these distributions are not quite
significantly different ($\chi^2 = 5.2$, 2 df, $0.05 < p < 0.10$, only oak,
maple, and cherry considered). This hypothesis may account for
the existence of some sampled trees. However, it does not explain
the marked difference in generic distributions of felled and sampled
trees at Blue Heron Cove (Table 1).

(2)   Beavers cannot identify trees taxonomically without tasting their bark, so sampling is necessary for selection of preferred tree genera. If this is true, the generic distribution of trees felled or sampled (the sum of columns 1, 2, and 3 in Table 1) should match that of trees available. The significant differences between these distributions at both ponds (Blue Heron Cove: $\chi^2 = 50.4$, 3 df, p < 0.001; Tamplin Road Pond: $\chi^2 = 31.3$, 3 df, p < 0.001) cast doubt on this hypothesis.

(3)   Sampling is used to avoid ingestion of potential toxins and demonstrates cautiousness with novel food items (Freeland and Janzen, 1974). This hypothesis suggests that unfamiliar food types will be sampled more than familiar ones. Comparison of lightly sampled and felled trees at both Blue Heron Cove and Tamplin Road Pond refutes this hypothesis. In particular, oak is the genus most often sampled as well as felled at Blue Heron Cove, and cherry is most often felled and also frequently sampled at Tamplin Road Pond. Cautiousness in using new, potentially toxic foods may lead to sampling behavior in some species, but it does not explain these instances of sampling behavior by beavers.

(4)   Sampling satisfies a requirement for certain vitamins or minerals, needed in small quantities and available only in some tree species. This hypothesis fails to explain the extensive sampling of maples and oaks at Blue Heron Cove and maples and cherries at Tamplin Road Pond. Many trees of these species are felled. The felled trees should supply any micronutrients which may be uniquely available in these species, unless the felled trees have concentrations of particular micronutrients several hundredfold less than sampled trees of the same species.

(5)   Sampling represents practice at tree selection by young animals. I have no data on the amount of sampling done by individual members of the two colonies. However, young animals could practice tree selection on branches and logs brought to the edge of the pond by adults with less risk of predation than if the young animals sampled standing trees at distances as great as 50 m from shore. Therefore, it is unlikely that sampling would evolve solely to serve this function.

(6)   Sampling is used by beavers to assess possible spatial and temporal variation in the nutritional quality of alternative foods. Unlike some of the others, this hypothesis cannot be tested by

comparing generic distributions of trees sampled, felled, and available. I present evidence elsewhere that beavers select different genera of trees for cutting at different sites around a pond (Jenkins, 1975), and different genera in different years at the same site (Jenkins, in preparation). There is evidence of spatial (Cowan et al., 1950) and temporal (Kramer and Koslowski, 1960) variation in nutritional value of some tree species. It seems reasonable to suggest that the spatial and temporal variation in beavers' tree selection is related to spatial and temporal variation in relative nutritional value of different tree species. Sampling may be a mechanism for achieving an optimal diet in the face of such variation.

CONCLUSIONS

Two kinds of data, both difficult to collect, are needed to prove more conclusively which of the above hypotheses are incorrect. First, direct observations of beavers in the act of sampling would help decide the validity of hypotheses 1 and 5. Unfortunately, beavers are primarily nocturnal, so special methods (e.g., radio telemetry, use of night vision instruments) would be needed to assist in making such observations. Data might be obtained on sampling during twilight hours without such assistance. However, such data probably would be inconclusive. For example, failure to observe sampling by young animals during twilight would certainly not prove that young animals don't sample; they might in fact be active samplers, but only at night. Second, data on toxin and nutrient content of bark of individual trees would help decide the validity of hypotheses 3, 4, and 6. To get adequate data of this sort would require analyzing a large number of samples for numerous nutrients and possible toxins (since both intraspecific and interspecific, as well as spatial and temporal variations in these attributes of tree bark are important components of these hypotheses). In addition, some of the toxins probably are unidentified or incompletely characterized at the present time.

In this note, I show that beavers are highly selective in sampling trees, but that they choose genera in different proportions than in felling trees. I suggest that sampling may be an economical way for beavers to assess spatial and temporal variation in relative nutritional value of different tree species, assuming they are capable of measuring the nutritional value of small pieces of bark. The

physiological and behavioral mechanisms by which sampling functions are important subjects for future research.

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SYSTEMATIC NOTES ON THE LOONS (GAVIIDAE: AVES)

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ABSTRACT.   The following discussion documents the treatment of the loons for the revision of Volume 1 of Peters' *Check-list of Birds of the World*. The family is thought to be most closely related to the Charadriiformes. The Cretaceous genera *Enaliornis* and *Lonchodytes* are thought to be convergent with rather than related to the loons (*contra* Brodkorb). *Gavia immer* and *G. adamsii* are considered full species but members of the same superspecies, while *pacifica* is considered conspecific with *arctica*. The subspecies *Gavia stellata squamata*, *G. arctica suschkini*, and *G. immer elasson* are not recognized. The sequence of forms followed is: *stellata, arctica pacifica, a. arctica, a. viridigularis, immer, adamsii.*

I. INTRODUCTION

The purposes of this paper are to present reasons for decisions made in preparing the section on the Gaviidae for the revision of Volume 1 of Peters' *Check-list of Birds of the World* and to present some preliminary information gained while examining and measuring specimens of loons preparatory to making an analysis of geographic variation within the family. To date, I have examined over 2200 study skins of loons but still need to study material in several important collections before the final analysis can be made.

For a group of only four species, there have been many divergences of opinion on such matters as the systematic position of the family, the sequence of species within the genus, the specific status of some of the forms, and the validity of several of the subspecies.

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II. SYSTEMATIC POSITION OF THE LOONS

There is general agreement that the living loons belong to the single genus *Gavia*. This, with one or two genera known only as fossils, constitutes the family Gaviidae. Several fossil genera referred to families of uncertain systematic position have also been included in the order Gaviiformes, which otherwise contains only the Gaviidae. These fossils are discussed below.

The varied opinions on the systematic position of the living loons within the class Aves have been well summarized by Sibley and Ahlquist (1972: 53–58). On the basis of fossil evidence (Storer, 1956) and studies of egg-white proteins (Sibley and Ahlquist, *loc. cit.*), loons are believed most closely related to the gulls, auks, and shorebirds. Ideally, they should be placed next to or near the Charadriiformes, but this is impractical as only the first volume of Peters' check-list is being revised at present.

III. SEQUENCE OF SPECIES

In presenting a linear sequence of species, it is customary to start with the most primitive and end with the most advanced. In the case of the loons, there is fossil evidence bearing on the matter of primitiveness.

The known fossil record of these foot-propelled diving birds goes back to the Upper Eocene of England (*Colymboides anglicus*) and the Aquitanian deposits (late Oligocene or early Miocene) of France (*C. minutus*) and probably the Oligocene of North America (*Gaviella pusilla*). The Lower Cretaceous genus *Enaliornis* and the Upper Cretaceous genus *Lonchodytes* have been considered as families of the same order (Gaviiformes) as the loons by Brodkorb (1963a: 220–221; 1963b: 56–60). However, the material of these genera is fragmentary, and the pieces of leg bones resemble those of loons in showing adaptations for swimming and diving but in other respects are quite different from them. The distal end of the carpometacarpus of *Lonchodytes pterygius,* as shown in Brodkorb's figure (1963b: 59), differs so markedly in the relative sizes, angles, and positions of the distal articulations from those of the loons as to cast considerable doubt in my mind on the alleged phylogenetic relationship between *Lonchodytes* and *Gavia*.

If, as I am convinced, these Cretaceous genera are convergent with the loons and if we accept Brodkorb's comment that the position of the little-known Upper Paleocene genus *Eupterornis* is "tentative," the earliest known loons (*Colymboides* and *Gaviella*) were smaller than later ones. The best-known species (*C. minutus*) was about the size of a teal, and, judging from the size of its wings, a strong flier (Storer, 1956: 423). The earlier species (*C. anglicus*) is poorly known but was somewhat larger and apparently had relatively shorter wings than *C. minutus*. It may have "represented a specialised offshoot from a more generalised gaviid stem, rather than a direct ancestral form of either the later *Gavia* species or *C. minutus*" (Harrison, 1976: 66). The Oligocene species, *Gaviella pusilla*, was also smaller than the species of *Gavia*. Known only from the proximal end of a carpometacarpus, *Gaviella* differs from other loons in several respects and is probably not closely related to them (Wetmore, 1940: 30). Thus the limited evidence from fossils indicates that *Gavia* evolved from smaller birds which were less well adapted for diving and had relatively larger wings. While the modern genus *Gavia* contains several Pliocene species, studies of these species have not as yet provided information regarding the relative antiquity or phylogenetic relationships among the Recent species.

The Red-throated Loon, *Gavia stellata,* is the most distinct species in both its winter and nuptial plumages, and for this reason it should be placed at one end of the sequence. The square white spots on the upperparts and the well-developed stripes and iridescence on the head and neck of the other three species can be considered advanced characters. *G. stellata* is the smallest of the living loons and also has the lowest wing loading. To estimate this, I divided the weight of the bird by the square of the length (arc) of the folded wing. The means of this index for ten specimens of each of the species are as follows: *stellata* 2.00, *a. pacifica* 2.25, *immer* 3.03, and *adamsii* 3.17 grams/cm^2. Although detailed comparative studies have not been made, *stellata* is said to be able to take off from water more easily than the other loons and alone among them can take off from land (Palmer, 1962: 59). As pointed out above, small size and greater flying ability may be considered primitive characters in loons, so I have placed *stellata* first on the basis of its relatively simple nuptial plumage, small size and good flying ability.

As members of a superspecies, *adamsii* and *immer* should be placed next to each other. *Arctica* has been known to hybridize with *immer* (Hunter and Dennis, 1972; Robertson and Fraker, 1974) and therefore these two species should be adjacent on the list. Assuming the largest species to be the most advanced and lacking other strong evidence to the contrary, I prefer the sequence *arctica, immer, adamsii* to the reverse for these three species. If one considers the forms of *arctica* to represent a broken rassenkreis, as I do, the sequence should be either *pacifica, arctica, viridigularis* or the reverse. I prefer starting with the smaller, better-known form, and thus the sequence I have adopted is: *stellata, arctica pacifica, a. arctica, a. viridigularis, immer, adamsii.*

IV. SPECIES PROBLEMS

THE COMMON AND YELLOW-BILLED LOONS, *G. immer* and *G. adamsii.* — The breeding ranges of these forms were presumably separated during the last glaciation — that of *immer* lying south of the glaciers and that of *adamsii* in Yukon-Bering Sea refugia to the north (Rand, 1948: 317–318). Of the principal differences between the species, the color of the bill and of the iridescence on the head and the head patterns may have been selected for as reproductive isolating mechanisms; all are located where major specific differences among other groups of diving birds such as penguins and grebes are found. On the other hand, evolution in bill shape in *adamsii* was presumably related to feeding. The upturned mandibles of this species and of *stellata* appear to be adaptations for bottom foraging. When birds are moving close over the bottom, the bill must be held below the body to catch bottom-living prey. In this position of the head, the lower part of the upturned mandible would lie nearly parallel to the bottom, making capture of prey in this situation easier than if the bill were shaped like those of *immer* and *arctica*. The upturned bills of *adamsii* and *stellata* are probably an example of convergence, because there is no other reason to consider the former more like *stellata* than it is like either of the other two species. The difference in size between *immer* and *adamsii* might be accounted for by Bergman's rule, and like bill form, is probably not primarily related to reproductive isolating mechanisms.

The effectiveness of the isolating mechanisms mentioned above is evident in the paucity or lack of known hybrids between the two

species. There is an adult "female" in the Royal Ontario Museum (No. 76,360) found dead at Pt. Credit, Ontario on December 7, 1957, which has been thought to be a hybrid between *immer* and *adamsii* (Godfrey, 1966: 11). In the recurved lower outline of the proximal segment of the mandibular rami (character 6 of Binford and Remsen, 1974: 115) this specimen resembles *adamsii*. The size of the remaining white squares on the back are within the range of those of *adamsii* and of males of *immer*, but not of females of *immer*. In size of wing, tarsus, and bill, the bird is well within the range of males of *immer*. In the other bill characters described by Binford and Remsen, the specimen is within the range of *immer*. While the possibility that this bird is an *immer* — *adamsii* hybrid cannot be completely discounted, I think it is more probably a male *immer* which was mis-sexed by the collector, who recorded nothing concerning the size or condition of the gonads.

THE STATUS OF *pacifica*. — The three forms of the Arctic or Black-throated Loon (*arctica*) complex (*arctica*, *viridigularis*, and *pacifica*) replace one another around the arctic except in Iceland and Greenland, where none occurs. Thus they might be thought of as forming a broken rassenkreis. The nominate form, *arctica*, ranges from the British Isles eastward across the northern parts of Eurasia and intergrades with *viridigularis* in Siberia. The latter form is found in western Siberia, largely south of the range of *pacifica*, and in parts of western Alaska. The widespread North American form, *pacifica*, also breeds in northeastern Siberia. Portenko (1939) and Bailey (1948) have shown that the breeding ranges of *pacifica* and *viridigularis* overlap in Anadyrland and western Alaska and reported no interbreeding. They concluded that the two were, therefore distinct species, an opinion followed by Vaurie (1965).

There are several reasons for doubting the specific status of *pacifica*. In the first place, those who have discussed the problem in the past have ignored one pertinent question: would *arctica* and *pacifica* interbreed if their ranges were to expand and meet? I think it likely that they would because the throat color is the same and the difference in size is less than that between *pacifica* and *viridigularis*. Secondly, there has been no thorough, detailed field study of *pacifica* and *viridigularis* in the area of overlap, and thirdly, there is evidence of interbreeding between the two forms.

Of the two forms, *viridigularis* is larger in all measurements, has a green (not purple) sheen on the throat, and a darker gray nape.

Green- or blue-throated individuals, otherwise indistinguishable from typically purple-throated individuals of *pacifica* are known to occur (Bailey, 1948: 140; Palmer, 1962: 45; Vaurie, 1965: 5), but whether this is a result of introgression with *viridigularis* or part of the normal range of variation of *pacifica* is unclear. To date, I have measured and examined 12 examples of *viridigularis* and approximately 270 of *pacifica* in breeding plummage. Of the latter, at least nine, or 3.3 percent have green or blue-green throats. All nine have measurements well within the range of *pacifica*. In addition, a male from Savoonga, St. Lawrence Island, Alaska (Colo. Mus. Nat. Hist. No. 26,769) labelled *"viridigularis"* has measurements well within the range of *pacifica,* although all above the means for males of that form. The nape is dark, like that of *viridigularis,* and it is either a very small example of that form or an intergrade. Two other green-throated birds may be intergrades: a male (Nat. Mus. Canada No. 8,816) from Barter Island, Alaska, has a nape intermediate in color between those of the two forms, a long wing (318 mm. or nearly 1.5 standard deviations above the mean for *pacifica*), a long tarsus (near the maximum for *pacifica*), but a small bill (below the mean for males of *pacifica*); and an unsexed bird (Amer. Mus. Nat. Hist. No. 348,959) from SE Victoria Island, Canada, has a light nape, long wing (321 mm.), a short tarsus (between the means for males and females of *pacifica*), a long bill (above the mean for males of *pacifica*) and a deeper bill than that of any *pacifica* I have measured. Two purple-throated males with long wings (323 and 325 mm.), long tarsi, and bills somewhat above the mean for males of *pacifica,* are also within the range of *viridigularis* in all these measurements and may be intergrades. While the sample of *viridigularis* which I have seen to date is too small to permit an accurate analysis of variation within that form, the presence of several probable intergrades suggests that interbreeding occurs between it and *pacifica.*

V. SUBSPECIES PROBLEMS

Gavia stellata squamata Portenko. — Vaurie (1965: 4) lists this subspecies as not well differentiated but warranting nomenclatural recognition, while Dement'ev and Gladkov (1968: 291) question its validity. I have examined 12 breeding adults from the range of this form from Franz Josef Land (3), Spitsbergen (7), and Bear Island (2), and I find that the plumage characters used to

differentiate this form from nominate *stellata* (Vaurie, *loc. cit.*) are not consistent within the population, and as Dement'ev and Glad-kov (*loc. cit.*) pointed out, are found in some specimens from outside the range. On the evidence now available, I see no value in recognizing this subspecies.

Gavia arctica suschkini Zarudny. — Although this race, based on migrant individuals from Russian Turkestan, was recognized by Peters (1931: 34), it is generally considered a synonym of the nominate race by recent authors (e.g. Dement'ev and Gladkov, 1968: 297; Vaurie, 1965: 5). I have not seen the material on which this race was based and follow the above authors in not recognizing *suschkini*.

Gavia immer elasson Bishop. — This subspecies was also recog-nized by Peters (1931: 35), but not by Vaurie (1965: 7) and many other recent authors. This species varies greatly in size, wing lengths of adults ranging at least from 287 to 411 mm., but I have not collected sufficient data to work out the pattern of geographic variation, which appears to be largely clinal. While realizing the possibility that there may be recognizable subspecies within this species, I prefer to consider *immer* monotypic at least until a thorough revision can be made.

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B R E V I O R A

Museum of Comparative Zoology

SOUTH AMERICAN ANOLES: THE SPECIES GROUPS. 2. THE PROBOSCIS ANOLES (*ANOLIS LAEVIS GROUP*).

ERNEST E. WILLIAMS[1]

ABSTRACT. The *Anolis laevis* group is known from three species represented by only nine specimens, all males, from four localities. All are distinguished by a soft multi-scaled proboscis and form a graded series from Peruvian *A. laevis* (proboscis minimally developed) through Brazilian *A. phyllorhinus* (proboscis of moderate size) to Ecuadorian *A. proboscis* (proboscis very long). Color in life and habitat are known only for *A. phyllorhinus*. The proboscis is interpreted as primarily an intraspecific social signal increasing the virtual size of the animals.

The most readily recognizable — at least in males — of all South American *Anolis* are the three species that have a nasal appendage or proboscis. The group may be described as follows:

Anolis laevis species group

Type species: A. *laevis* Cope 1876.

Definition: (Many possibly useful details are not determinable in *A. laevis* and hence are not mentioned here.) Alpha anoles of moderate size (60–97 mm snout-vent length) distinguished by a soft multi-scaled nasal appendage projecting forward *above* the rostral scale. Four to 10 scales across the snout between the second canthals. Supraorbital semicircles in contact or separated by as many as three scales. Loreal rows two to five. Interparietal of moderate to large size in contact with the surpaorbital semicircles or separated by as many as three scales. Supralabials in contact with suboculars. Middorsal scales uniform or the median row raised into a crest of triangular scales. Tail crest single or double. Lamellae

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under fourth toes ranging between at least 17 and 26. Dewlap and postanals large in males. Females unknown.

Distribution: Widely disjunct: (1) trans-Andean Ecuador; (2) southern tributaries of the Amazon in central Amazonia; (3) western Amazonia.

INCLUDED SPECIES

Anolis laevis Cope 1876
(Fig. 1)

Scytomycterus laevis Cope, Jour. Acad. Nat. Sci. Phila., NS **8**: 165.

Holotype. ANSP 11368, collected by Prof. James Orton.

Type locality. "Between Moyabamba and Balsa Puerto on the river Huallaga in eastern Peru."

Additional references: Boulenger, 1885: 56 (referred to the genus *Anolis* and placed between *A. tigrinus* and *A. punctatus*); Burt and Burt, 1933: 17 (listing only); Barbour, 1934; 154 (placed along with *A. tigrinus* as synonym of *A. transversalis*; both synonymies quite mistaken); Williams, 1965: 6–13 (discussed as member of the *punctatus* group *sensu lato*); Peters and Donoso-Barros, 1970. 57 (citation only); Malnate, 1971: 358 (listing of type in the Philadelphia Academy).

Anolis phyllorhinus Myers and Carvalho 1945
(Figs. 2 and 3)

Anolis phyllorhinus Myers and Carvalho, Bull. Mus. Nac. NS No. **43**: 2.

Holotype. MN (Rio de Janeiro) 1864, adult male collected by Alexandre Parko on June 14, 1943.

Type locality. "Borba, lower Rio Madeira, State of Amazonas, Brasil."

Additional references: Williams, 1965. 8–13 (discussed as member of the *punctatus* group *sensu lato,* first mention of the second known specimen MZUSP 7118, Jacareacanga, Rio Tapajoz, Pará, Brasil[1]); Peters and Donoso Barros, 1970. 63 (citation only).

Anolis proboscis Peters and Orcés 1956
(Figs. 4, 5, and 6)

Anolis proboscis Peters and Orcés, Breviora No. **62**: 2.

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[1]Note that the region between the Madeira and Tapajoz is one of Haffer's (1974, p. 70) "distribution centers" for endemic Cis-Andean birds.
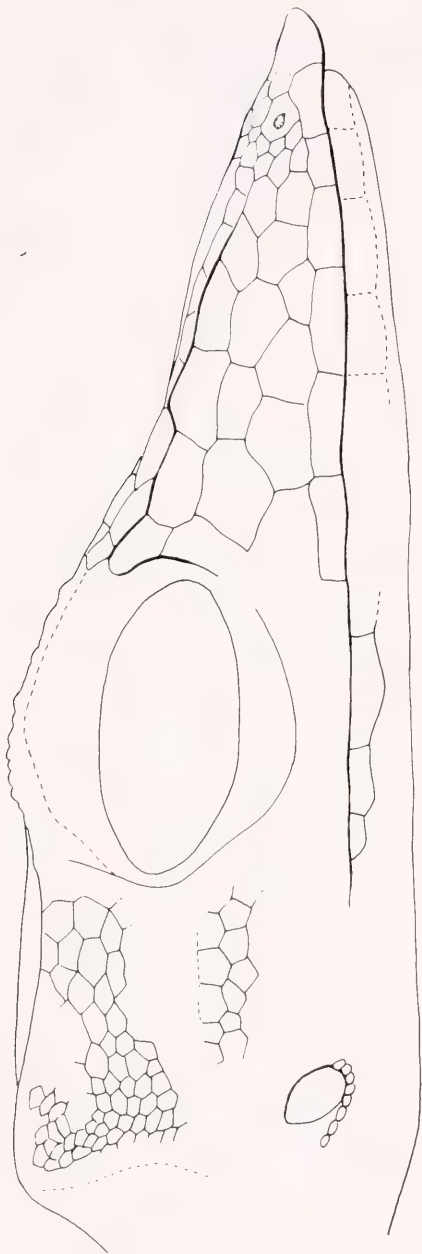
Figure 1. *Anolis laevis*, ANSP 11368. Lateral view of head of type.

Holotype. MCZ (Cambridge) 54300, a mature male collected by Antonio Proano during April 27–29, 1953.

Type locality. "Neighborhood of Cunuco, a small town at 1200 meters elevation, five kilometers northwest of Mindo, on the south bank of the Rio Mindo, a northern tributary of the upper Rio Blanco, in Pichincha Province, Ecuador." (The five additional specimens — USNM 207671–73, in the National Museum of Natural History, Washington, D.C.; IPN 7611, 7612, in the collection of Gustavo Orcés V in Quito, Ecuador — are from Mindo or "region of Mindo.")

Additional references: Williams, 1965: 8 13 (discussed as member of the *punctatus* group *sensu lato*); Peters, 1967: 13, 17 (key and citation); Peters and Donoso Barros, 1970: 63 (citation only).

Ecological information. None except for *A. phyllorhinus* Myers and Carvalho: "Mr. Parko collected the holotype of *Anolis phyllorhinus* in the capoeira (second growth or low jungle) that surrounds the town of Borba. This locality is in the Amazonian lowlands on the lower Rio Madeira, about 90 miles (airline) south-southeast of the city of Manaus. The lizard was caught on a low tree while Mr. Parko was collecting butterflies. . . ."

Distinguishing characters of the species. A. laevis differs from the two other species in the small number of scales between the second canthals (4, rather than 9 or 10), the low number of loreal rows (2, rather than 3 to 5) and in having a very rudimentary proboscis. *A. proboscis* has a crested dorsum and tail and a very long proboscis, while *A. phyllorhinus* lacks such crests and in fact has two rows of scales dorsally on the tail and a shorter proboscis. Table 1 lists the standard scale characters for each species.

Size. Snout-vent length: *laevis* 60 mm, *phyllorhinus* 73 mm, *proboscis* 74 mm. Tail: *laevis* 79 mm, *phyllorhinus* 153 mm, *proboscis* 97 mm. Hind limb length: *laevis* 39 mm, *phyllorhinus* 49 mm, *proboscis* 42 mm.

Color. Laevis: Cope reported the preserved specimen as follows: "Color above dark gray, below pigmented white (in spirits). The two colors are abruptly defined between the orbit and there are brown spots behind the axilla. Tail distinctly annulate."

Phyllorhinus — Myers and Carvalho: "Color in alcohol (formalin-fixed) plain, dull, bluish gray above, lighter beneath, with no sign of a color pattern anywhere save on the toes and undersides of the legs.
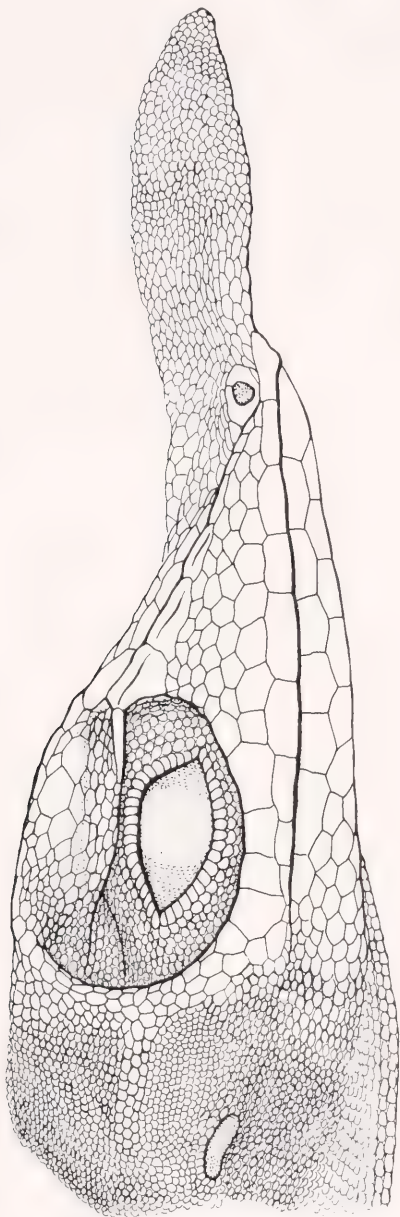
Figure 2. *Anolis phyllorhinus*, MZUSP 7118. Lateral view of head of São Paulo specimen.

Table 1. Scale counts and characters.

	laevis	*phyllorhinus*	*proboscis*
	soft protuberance covered with ? small scales	leaf-like laterally compressed with granular scales	leaf-like laterally compressed with elongate scales
	N = 1	N = 2	N = 6
scales between second canthals	4 (Cope)	10	9–10
scales between semicircles	0	0	1–3
scales between interparietal and semicircles	0	1–2	1–3
loreal rows	2	4–5	3–5
rows between suboculars and supralabials	0	0	0
labials to center of eye	?	6–7	9–12
sublabials in contact with infralabials	?	5–6	2–3
median gular scales in contact with mental between sublabials	?	4	2
middorsal rows enlarged	0	0	1 (crest of triangular scales)
tail crest	double row, no crest	double row, no crest	crest present
lamellae 4th toe	?	25–26	17–21
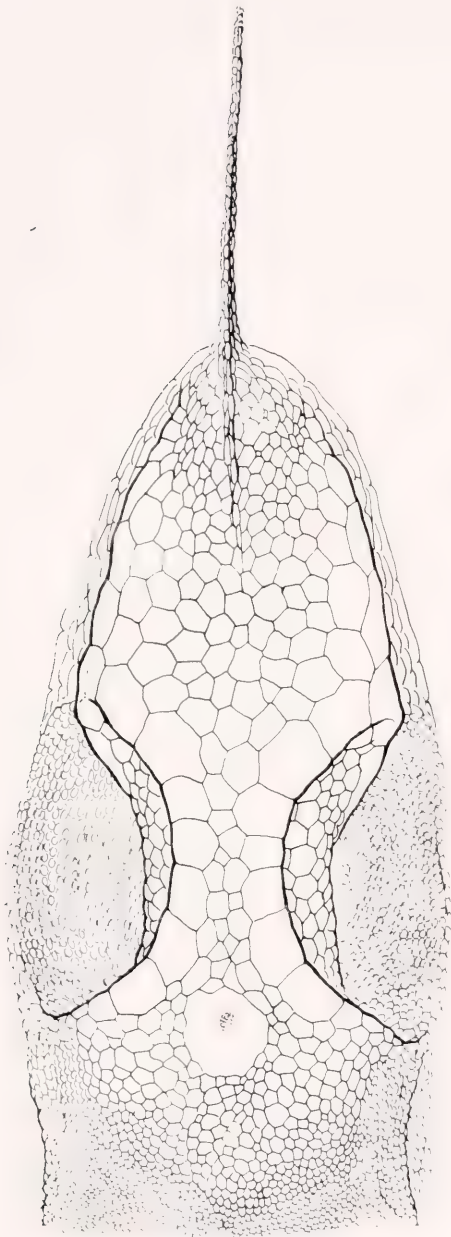
Figure 3. *Anolis phyllorhinus*, MZUSP 7118. Dorsal view of São Paulo specimen.

The undersurfaces of the legs and arms bear a fine, light mottling, perhaps better described as a bluish reticulation on a yellowish ground color. The undersurfaces of the digital expansions are dark. The superior surfaces of the toes and fingers (but not of the feet and hands) are light, with bold, blackish crossbands. The tail gradually becomes brownish toward the end. A color sketch made by Mr. Parko from life shows the creature bright blue-green, the dewlap yellowish, with traces of pink or red on the toes, the top of the snout, and the end of the rostral appendage." Mr. Parko's notes say the beast immediately changed from bright blue-green to brown when captured, but changed back to green on preservation.

Proboscis — Peters and Orcés: "Dorsal ground color (in alcohol) a dull gunmetal blue, with irregular, parallel, horizontal black streaks along vertebral margin. These streaks vaguely line up and form a pair of lateral bands between the limbs. Dark brownish-black spot at shoulder. Limbs and lateral surfaces spotted with light yellowish white; limbs vaguely barred with darker blue; skin in interstices between scales of dorsum of digits light, giving appearance of banding on fingers and toes. Dorsum of head unicolor, as back; temporal region and lips lighter, with faint reddish or purplish tinge and a marked light spot over ear opening. Ventral surfaces generally lighter, with vague reddish tints on chest and chin; belly stippled with light spots. Venter of limbs heavily spotted with white proximally, becoming totally white on the foot. Tail alternately barred with gunmetal blue and blackish bands approximately equal in width."

TAXONOMY AND NOMENCLATURE

The single recognition character — the proboscis — differs considerably in the three known species, which are abundantly distinct. The extent of the differences might reasonably raise the issue of parallel evolution, but the proboscis is so singular a feature that it seems subjectively more probable that the known species are the relicts of a once much larger radiation. It is also very possible that there are more species still to be discovered, perhaps with quite restricted distributions.

It is clear that the first adumbrations of a proboscis are found in *A. punctatus* and some of its relatives. In these the rostral scale and rostral area are produced to overhang the lower jaw. In *laevis* there
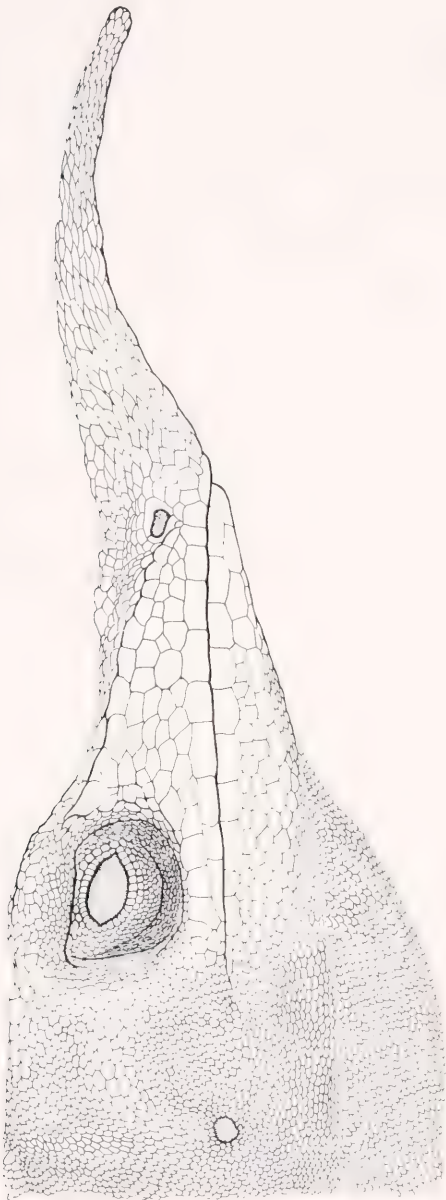
Figure 4. *Anolis proboscis*, USNM 207672. Lateral view of head.

appears to be a soft protuberance which involves the smaller post-rostral scales. In *A. phyllorhinus* and *A. proboscis* the rostral remains at the same level of development as in *laevis* but the area above the rostral is expanded into an impressive nose leaf, longest in *A. proboscis.*

The distinction between the *proboscis* and *punctatus* group is thus perhaps somewhat artificial. The morphological sequence is, however, clear and leads from *proboscis* at one extreme back to *punctatus* at the other. I find it convenient to make the distinction at the point at which the scales and tissues above the rostral are involved in the swelling. Since the relation of this area to the rostral is very similar in the three species, it provides greater plausibility for the contention that this is a single lineage. It is not, on the other hand, clear that *A. punctatus* is directly related to the species that mimic it by means of the presence of a projecting rostral in the male. However, any decision on this point is necessarily tentative, and I emphasize convenience rather than certainty of phyletic affinity as a basis for recognition of this group.

Nothing is known of the function of the proboscis (see below) and all nine specimens of this group thus far collected have been males. This has raised (e.g. Peters and Orcés, 1956) the issue that the proboscis anoles might be the males of species already described on the basis of females. However, there are few described species still known only from females. Also the other external characters of each of the proboscis anoles are such that it would require a degree of sexual dimorphism beyond anything known in lizards to make any of the three proboscis species possibly conspecific with any other described anoles. In the case of *A. punctatus* and the other species with projecting rostrals, this and the presence of a dewlap, enlarged postanal scales and sometimes minor differences in color distinguish the males. Scale counts and other aspects of morphology do *not* significantly differ between the sexes.

Only *A. proboscis* is known from series (the type, three newly collected specimens given to the United States National Museum by Orcés, and two in the Orcés collection in Quito). *A. phyllorhinus* is represented by only two specimens, the type and a badly preserved second specimen. *A. laevis* is still known only from the type, which is now in extremely poor condition.
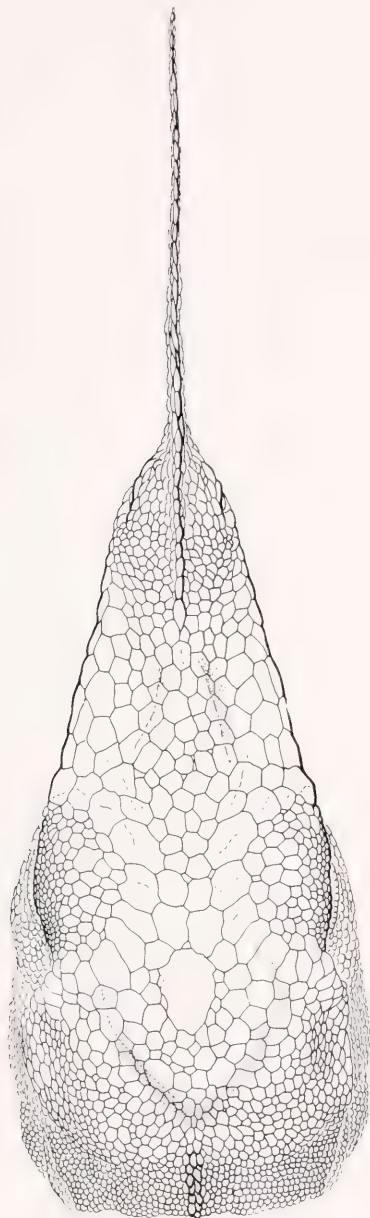
Figure 5. *Anolis proboscis*, USNM 207672. Dorsal view of head.

EVOLUTIONARY ASPECTS

Three species, nine specimens, four localities and one note on habitat are the sum of our objective data on the proboscis anoles. They provide little opening for discussion or for evolutionary speculation.

It is possible, however, to place this minimal amount of data against a background of the much greater knowledge of anoles as a whole. It is a peculiarity of the proboscis anoles that in no other way are they known to be different or indeed especially interesting. The single aspect that appears striking is the proboscis itself.

Other bizarre structures are known in anoles. The dewlap would be bizarre were it less common and less familiar. High tail fins supported by heightened caudal neural spines occur in a number of distantly related species. Casque heads — heads enlarged by crests and ridges — occur in several *Anolis* and in the related anole genera *Phenacosaurus* and *Chamaeleolis.* All these structures — dewlap, tail fin, casque head *and* proboscis – have the effect of increasing the apparent size of the animals that bear them. In the case of the dewlap, there is evidence of use in agonistic encounters, and evidence (Rand 1967) that larger animals usually win in such encounters.

Trivers (1976) has shown the importance of sexual selection for size in one species of *Anolis;* he has inferred the generality of the rule. There are, however, aspects of increase in real size that make the course of evolution complex. A real increase in size with its implied increase in weight can carry with it functional restrictions that compel changes in the life style of the species that exercises this option. Sometimes such changes are realized within the ontogeny of a single species. Sometimes we see them as the alternative strategies utilized by sympatric species (Schoener, 1970; Williams, 1972). Virtual changes in size — unreal but visually effective — are still another alternative. Virtual size has the advantage of introducing few if any functional problems.

I have called attention to elongation of the head in many crown anoles (Williams, 1965). It is probable that this initially has a (still undefined) functional explanation. However, there are side effects: the change of head shape probably has its species-recognition aspects and the size of the head has its agonistic advantage aspects. Yet if these latter aspects have too much effect, the bony structure of

Figure 6. *Anolis proboscis*, USNM 207672. Lateral view.

the head is elongated beyond its functional optimum. There will therefore again be a premium on virtual rather than real change of head shape. We see the beginning of such a phenomenon in *Anolis punctatus* and in some related species where (in males) only the rostral scale is enlarged. *A. laevis* carries this process a slight step further. *A. phyllorhinus* and *A. proboscis* have gone much further.

It is significant that the proposces in *A. phyllorhinus* and *A. proboscis* are not similar in detail. One would expect this if there were functional aspects to the structure *per se*. On the contrary, it appears a similar visual effect may readily be achieved by only broadly comparable means. This corresponds with species recognition devices and intra-species display where there is no requirement that structures be similar; rather the requirement is that they be different. (In view of the wide allopatry of the known proboscis anoles, there could be no selection for striking difference *now*, but perhaps it has existed in the past.)

Within the Iguanidae, the basiliscines would seem to be quite parallel cases. Head casques — very different in structure — are present in all three genera; in *Basiliscus*, dorsal and tail fins are present, different and wonderfully conspicuous in three species, very reduced in a fourth. (Once a bizarre structure has been adopted as an intra- and interspecies signal, an option open to a new member of a group is to abandon the structure: absence of a signal is itself a signal.) The absence of a dewlap is a strategy adopted by two species in the very complex anole fauna of Cuba; the dewlap is consistently retained in the simplest faunas and is reduced only in the fauna almost as locally complex as Cuba, that of Hispaniola (Williams and Rand, 1977).

Outside the Iguanidae, a number of species in the closely related family Agamidae show parallels to the proboscis anoles: *Ceratophora* (Ceylon, three species, see M. Smith, 1935 and Taylor, 1953); *Harpesaurus* (Java, Sumatra, Nias, five species *fide* Wermuth, 1967); *Lyriocephalus* (Ceylon, one species, Taylor, 1953) and *Cophotis* (Ceylon and Sumatra, De Roois, 1915). The proposces in these are all soft structures but considerably more variable in shape, number and squamation than those of the proboscis anoles. (Figs. 7–9 show the differences within the genus *Ceratophora*.) For chameleons Rand (1961) has already discussed the function of the ornamentation that is so remarkably developed in the montane
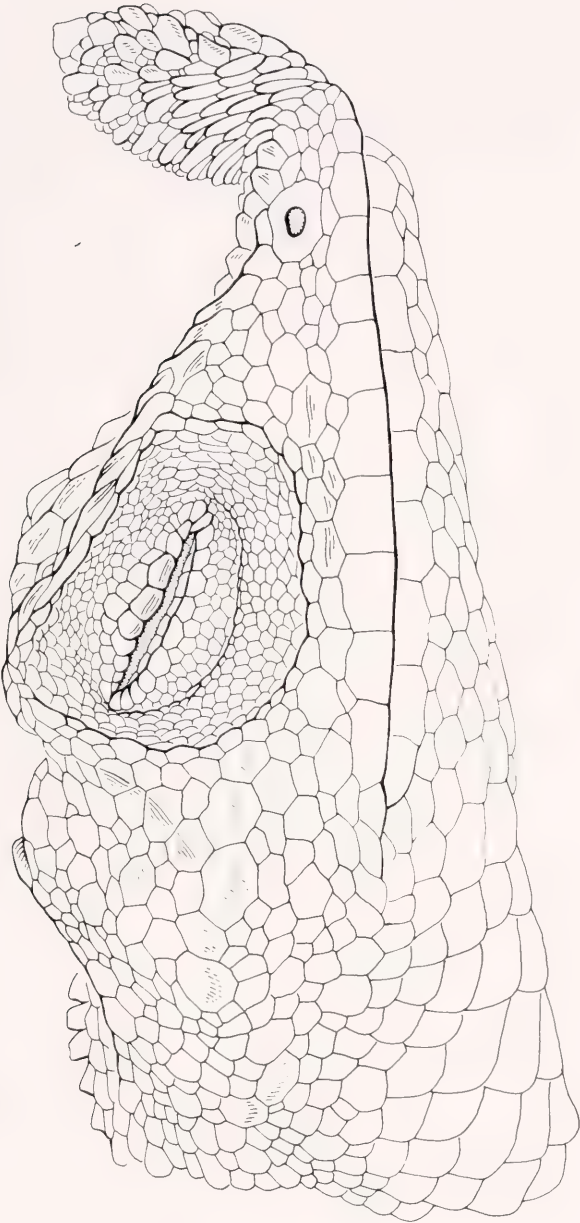
Figure 7. *Ceratophora tennenti*, MCZ 136187. Side view of head.

species of Africa. In the horned chameleons, however, the ornament is a solid structure. In this case, the ornament may serve a physical function in aggression, as the horns do.

Still further afield, Hopson (1975) has discussed the singular crests of hadrosaurian dinosaurs as cranial display structures. His paper (see also Molnar, 1977) also cites the parallels with mammalian horns and has references to the extensive literature.

Of course, alternative explanations are available for structures such as probosces in *Anolis,* e.g. camouflage. However, such other functions, if they exist, do not disprove the display function of *Anolis* probosces or basiliscine crests. The value of a structure for more than one function is a familiar phenomenon and will, not surprisingly, be sustained by natural selection.

ACKNOWLEDGMENTS

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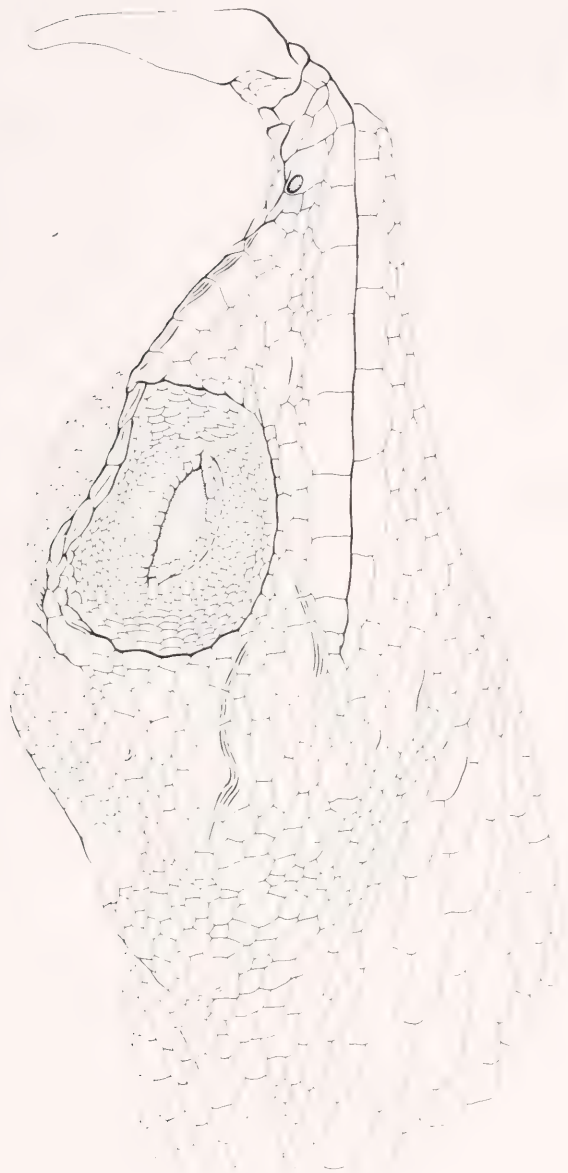Figure 9. *Ceratophora stoddaerti*, MCZ 116378.

B R E V I O R A

A NEW SPECIES OF *MOENKHAUSIA* FROM THE MATO GROSSO REGION OF BRAZIL (PISCES: CHARACIDAE)

WILLIAM L. FINK[1]

ABSTRACT. A new species of the characid fish genus *Moenkhausia* is described from the Arinos River of the Mato Grosso region of Brazil. A brief discussion of some of the characters used in analyses of characid relationships is included.

INTRODUCTION

The fish described here as new presents some interesting problems regarding current classification criteria for characids. These problems arise primarily because the system now in use, which dates from the work of Eigenmann (1917), is obsolescent and no longer able to incorporate the diversity of the fishes it was intended to classify. Most of the characters which are used to "define" genera and higher categories have been found to be inadequate to express hypotheses about relationships within the family. The bases of the subfamilies Cheirodontinae and Tetragonopterinae have been recently reviewed by several authors (see Fink and Weitzman, 1974) and this critical reappraisal is being carried on in other areas within the Characidae.

The characters which cause problems in hypothesizing the relations of the fish herein described are lateral line length and color pattern. The former character is of major importance in the "Eigenmann" system while the latter has been virtually ignored by characid systematists. Both of these characters are discussed below after the description.

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The methods of taking morphometric and meristic data used in this analysis are described in Fink and Weitzman (1974). Proportions are given as percent of standard length (SL). Paratypes have been deposited in the following institutions: Academy of Natural Sciences of Philadelphia (ANSP), British Museum of Natural History (BMNH), California Academy of Sciences, San Francisco (CAS), National Museum of Natural History, Washington, D.C. (USNM), Museum of Comparative Zoology, Cambridge, Mass. (MCZ), Museu de Zoologia, Universidade de São Paulo (MZUSP), and the Zoologisch Museum, Universiteit van Amsterdam (ZMA).

Moenkhausia phaeonota, new species
Figures 1, 2

Holotype: MZUSP 13793; Brazil, Mato Grosso, from the shores of an island "below Rio dos Peixes," Rio Arinos, Jurena-Tapajós drainage; collected by Harald Schultz, 16 June 1962; 32.6 mm SL.

Paratypes: ANSP 135924, same data as holotype, one specimen 26.7 mm SL.
BMNH 1978.9.12.1, same data as holotype, one specimen 28.8 mm SL.
CAS 41707, same data as holotype, one specimen 29.1 mm S.L.
FMNH 83856, same data as holotype, one specimen 25.6 mm SL.
MCZ 54087, same data as holotype, three specimens 27.5 29.9 mm SL.
MZUSP 13794, same data as holotype, one specimen 19.5 mm SL.
MZUSP 13795, same data as holotype, one specimen 20.6 mm SL.
USNM 218798, same data as holotype, twenty specimens 16.1–36.4 mm SL.
ZMA 115.273, same data as holotype, one specimen 24.1 mm SL.

Description

See Tables 1 and 2 for variable meristic and morphometric data. Body elongate, compressed laterally. Predorsal body profile slightly

Figure 1. *Moenkhausia phaeonota*, paratype, USNM 218798, 31.4 mm SL.

convex with a slight concavity at nape. Dorsal body profile abruptly angles ventrally along dorsal-fin base, then becomes straight or slightly convex to adipose fin where profile dips ventrally a small amount, then continues as a nearly straight line to dorsal procurrent caudal-fin rays. Ventral profile gently rounded to anus; steepest inclination ventral to jaws. Ventral profile protrudes ventrally its greatest distance just anterior to pelvic-fin insertions. Body profile along anal fin-base nearly straight, or slightly convex; at anal-fin termination, profile nearly straight or slightly concave to procurrent caudal-fin rays.

Maxillary with 3–7 teeth; in specimens below 21–25 mm SL, teeth mostly conical; specimens in that size range usually with dorsalmost tooth tricuspid (rarely with 4 cusps); specimens above that range usually with tricuspid maxillary teeth.

Premaxillary outer row teeth, 2–5, larger fish usually with larger tooth number; in smaller specimens teeth usually conical; in specimens above about 24 mm SL, teeth usually tricuspid.

Premaxillary inner row teeth, 5–6, each tooth usually smaller than tooth medial to it. Ontogenetic changes include replacement of earlier teeth by teeth with a greater number of cusps until adult condition reached. Smaller specimens (about 16–19 mm SL) usually have medial three teeth with 3 cusps, with lateral teeth having 1 or 2 cusps, giving a tooth cusp formula of 33311 or 33321. In the size range 22–25 mm SL there is a variable pattern: medial tooth 3–4 cusped, second tooth 3–5 cusped, third tooth 3–5 cusped, fourth tooth with 3 cusps, teeth lateral to those with 1–2 cusps. In adults, inner row premaxillary tooth formula usually 45533 or 45433.

Dentary teeth show ontogenetic trends similar to those exhibited by inner row premaxillary teeth, replacement teeth usually with more cusps. Small specimens usually have a formula 3331 +(6–10 very small conical teeth); adults usually have tooth formulae ranging from 4333 +(6–10) to 5353 +(6–10); second tooth from symphysis is offset anteriorly in adults and rarely has more than 3 cusps.

Fontanels moderate, that part anterior to the epiphyseal bar slightly more than two-thirds as long as that part posterior to bar. Gill rakers moderate. Infraorbital bones well ossified, infraorbital 3 wide, with a narrow naked area behind and below.
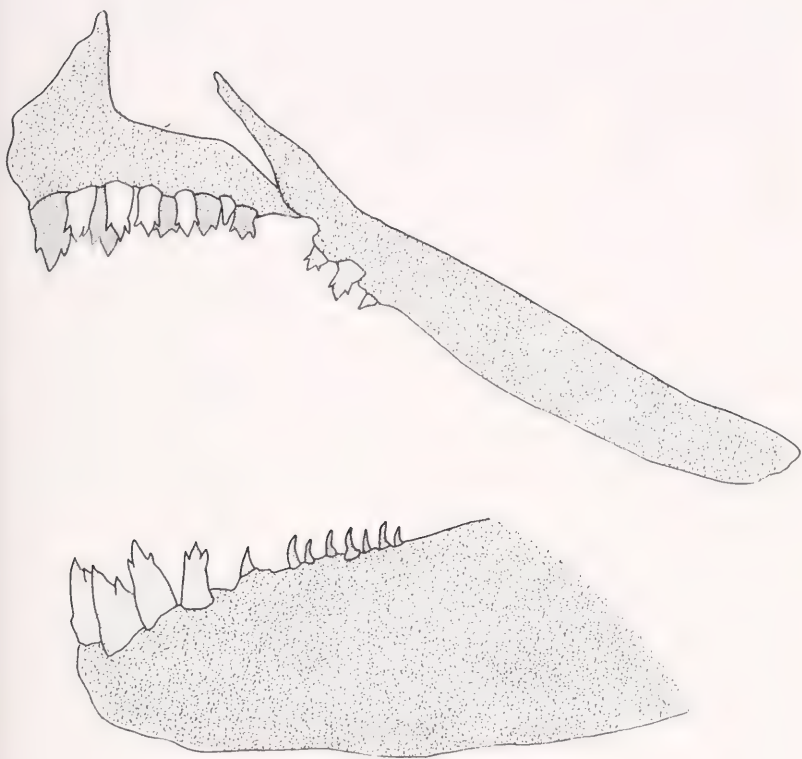
Figure 2. Dentition of *Moenkhausia phaeonota*, paratype, USNM 218798, 28.2 mm SL.

Scales moderately large, thin, cycloid with concentric circuli and about 2–7 radii on the exposed posterior field. Lateral line with a slight ventral curve along body, complete, with scales perforated to end of caudal base. Scales above lateral line 5; scales below lateral line 4. Scale sheath of about 4–7 scales along anterior anal-fin base. Scales extend over about 1/5 to 1/4 of caudal-fin rays. Small accessory scales present ventral to pelvic-fin insertion.

Dorsal-fin origin anterior to anal-fin origin, posterior to pelvic fin insertion, nearer eye than caudal-fin base. Third or fourth ray of dorsal fin longest with posterior rays shorter, forming a straight or slightly convex posterior margin to fin. First unbranched ray of anal fin usually not visible externally; last unbranched anal-fin ray and first through fourth or fifth branched rays longer than posterior rays, forming a slightly concave fin margin. Pectoral fin low on body, pointed or slightly rounded, reaching to or beyond pelvic-fin insertion. Pelvic fin with distal tip reaching from just anterior to just posterior to anal-fin origin; i 7 rays. Caudal fin with 10/9 principal caudal-fin rays; fin forked, not split to base. Dorsal and ventral caudal-fin lobes equal in size. Dorsal and ventral procurrent caudal-fin rays are equal in size and extend cephalad same distance. All fin rays without hooks.

Color in alcohol. — Ground color light brown. Nape, top of head, and jaws covered with numerous small brown melanophores. Back with a reticulate pattern of dark brown melanophores. A broad stripe almost devoid of melanophores extends from just above and behind eye along side of body, terminating ventral to dorsal procurrent caudal-fin rays. Below pale stripe is a broad dark stripe consisting of numerous melanophores extending from cheek and opercle behind eye, across body side and onto caudal peduncle and posteriorly onto about six of middle caudal-fin rays. Immediately posterior to opercle on second through fourth lateral scales, melanophores are extremely dense, forming a large humeral spot about two-thirds diameter of eye. Posteriorly, above anal fin and on caudal peduncle, melanophores very dense and tend to concentrate along junctions of myomeres. Immediately dorsal to anal fin, melanophores abruptly become less dense, leaving a pale stripe at anal-fin base which is continuous with pale color of belly. Dorsal fin with melanophores concentrated on interradial membrane between first and fifth branched rays. Pectoral and pelvic fins with a few

Table 1. Measurements of *Moenkhausia phaeonota*

Character	N	Range	x̄	s	Holotype
Standard Length (SL)	31	16.1–36.4	25.8	5.670	32.6
% SL					
Greatest Depth	29	25.6–35.5	30.2	2.302	29.1
Eye-Dorsal Fin Origin	31	34.7–38.2	36.7	0.890	36.2
Dorsal-Fin Origin— Base of Caudal Peduncle	31	50.5–56.2	53.3	1.307	52.5
Snout-Dorsal Fin Origin	31	50.3–53.4	51.6	0.737	50.6
Snout-Pectoral Fin Origin	31	24.7–29.8	26.4	1.017	25.5
Snout-Pelvic Fin Origin	31	42.4–47.2	45.3	1.164	44.8
Snout-Anal Fin Origin	31	55.7–60.7	58.8	1.157	59.2
Dorsal Fin Length	25	26.0–31.7	28.1	1.461	30.7
Pectoral Fin Length	30	18.5–24.6	21.9	1.448	19.3
Pelvic Fin Length	31	10.8–16.4	14.6	1.217	14.1
Head Length	31	19.4–28.6	25.2	2.141	24.5
Eye Diameter	31	9.6–13.8	11.3	1.038	10.1
Snout Length	31	6.2– 7.8	6.9	0.384	6.4
Bony Interorbital	31	7.5– 9.0	8.3	0.354	8.0
Caudal Peduncle Depth	31	8.3–10.7	9.5	0.659	9.8
Caudal Peduncle Length	31	10.4–14.3	12.6	1.011	11.3

scattered melanophores on interradial membranes. Caudal fin with melanophores along edges of all rays, in addition to the extremely dark middle caudal rays mentioned above. Anal fin with melanophores loosely scattered on interradial membranes, more concentrated between anterior rays and especially along outer margin of fin. Adipose fin with many small melanophores.

Etymology. — From *phaios*, meaning dusky brown and the suffix — *nota*, meaning having the attribute or quality of. The name refers to the color pattern of the fish.

DISCUSSION

This species, according to Eigenmann (1917), belongs in the genus *Moenkhausia*, which is diagnosed by the following combination of characters: complete lateral line, partially scaled caudal fin, five inner row premaxillary teeth and a naked area between the third infraorbital and the lower limb of the preopercle. However, in color pattern, preserved specimens are extremely similar to several species of *Hyphessobrycon*. A large number of *Moenkhausia* species were examined durng this study in an attempt to find a potential sister group for *M. phaeonota* (see Comparative Material Examined) but no currently recognized species was considered to have any derived characters in common with it. In Eigenmann's (1917) key to the species of *Moenkhausia*, those that are included in the couplet "depth usually more than 2.75 in length" are most similar to *M. phaeonota* in general body shape but they have marked color differences and in most cases meristic count differences. Specimens identified as *M. dichroura* (Kner) by Eigenmann (USNM 86792) approach *M. phaeonota* in both anal-fin ray number and lateral scale number, but are very different in color pattern, in being heavier bodied, and in having a larger third infraorbital. Of the more recently described species, *M. takesi* Géry is phenetically more similar to *M. phaeonota* than other members of the genus. Both are fairly similar in body and head shape, although *M. takesi* is "stouter." *Moenkhausia phaeonota* has more predorsal scales (11-13 versus 9), more lateral scales (36-38, usually 36, versus 33), more anal-fin rays (iii, 22-25, usually 22 or 23, versus iv, 18-19) [The holotype of *M. takesi* has four unbranched anal-fin rays rather than three as reported by Géry (1964)], and fewer gill rakers (17-21, usually 18, versus 20-21). The color pattern of *M. takesi* in life and

Table 2.   Meristic counts of *Moenkhausia phaeonota*

Character	N			Range			$\bar{x}$	s	Holotype
Branched Dorsal Fin Rays	31	$\frac{8}{2}$	$\frac{9}{29}$				8.9	0.250	9
Branched Anal Fin Rays	31	$\frac{22}{7}$	$\frac{23}{18}$	$\frac{24}{3}$	$\frac{25}{3}$		23.1	0.854	23
Branched Pectoral Fin Rays	31	$\frac{9}{1}$	$\frac{10}{9}$	$\frac{11}{20}$	$\frac{12}{1}$		10.7	0.599	11
Branched Pelvic Fin Rays	31	$\frac{7}{31}$					7.0	0.000	7
Lateral Scales	11	$\frac{33}{2}$	$\frac{34}{1}$	$\frac{35}{2}$	$\frac{36}{1}$	$\frac{37}{4}$	35.5	1.635	37
Perforated Lateral Scales	9	$\frac{34}{2}$	$\frac{35}{1}$	$\frac{36}{2}$	$\frac{37}{3}$	$\frac{38}{1}$	36.0	1.414	37
Scales Around Caudal Peduncle	8	$\frac{12}{1}$	$\frac{13}{1}$	$\frac{14}{6}$			13.6	0.744	14
Predorsal Scales	26	$\frac{10}{2}$	$\frac{11}{18}$	$\frac{12}{4}$	$\frac{13}{2}$		11.2	0.710	13
Gill Rakers	13	$\frac{17}{2}$	$\frac{18}{9}$	$\frac{19}{1}$	$\frac{20}{0}$	$\frac{21}{1}$	18.2	0.987	17
Precaudal Vertebrae	31	$\frac{13}{11}$	$\frac{14}{20}$				13.6	0.486	14
Caudal Vertebrae	31	$\frac{23}{18}$	$\frac{24}{12}$	$\frac{25}{1}$			23.5	0.568	23
Total Vertebrae	31	$\frac{37}{28}$	$\frac{38}{3}$				37.1	0.301	37

in preserved specimens consists primarily of dense black melano-
phores dorsal to a light lateral stripe and includes a dark area on the
caudal peduncle and the area dorsal to the anal fin. The black band
in *M. phaeonota* extends from the middle caudal-fin rays onto the
base of the tail and continues to the posterior border of the opercle.

In summary, *M. phaeonota* seems to share no unique characters
with any known species of *Moenkhausia* and is rather different
phenetically from the only *Moenkhausia* species which looks even
slightly similar (*M. takesi*). Inasmuch as there is questionable
phylogenetic reality to *Moenkhausia,* it is useful to look beyond the
bounds of that genus to another group with which *M. phaeonota*
seems to share a number of similarities. This leads us to a group of
species within *Hyphessobrycon,* the members of which share a
specialized color pattern. This group includes *H. metae* Eigenmann
and Henn, *H. loretoensis* Ladiges, *H. peruvianus* Ladiges, and
perhaps *H. agulha* Fowler and *H. herbertaxelrodi* Géry. All of these
species have a color pattern in preserved specimens which includes a
band of dark brown or black chromatophores which generally
extends along the lateral body from the eye to the caudal fin base.
The area of greatest concentration of chromatophores is usually
dorsal to the anal-fin base, and there is often a secondary concentra-
tion in the "humeral" area behind the opercular aperture. In life, the
lateral band is dark brown to black, and dorsal to it is a bright
lateral stripe, usually gold, goldish-red or creamy white. In addition,
in live specimens there is generally some red coloration on the
caudal and dorsal fins, and in some species, dorsally on the eye.
Preserved specimens of *Moenkhausia phaeonota* have a color
pattern nearly indistinguishable from *H. metae* of Colombia, and
differ from that species primarily in meristic counts including:
number of lateral scales (33–37, compared with about 33 in *metae*),
number of branched anal-fin rays (22–25, compared with 17–19 in
metae), and number of vertebrae (37–38, compared with 33 in
metae).

In view of this striking resemblance to these members of *Hyphes-
sobrycon,* I would propose a relationship of *M. phaeonota* with
those species. That group is currently being revised by myself and S.
H. Weitzman and *M. phaeonota* will be considered in that study,
after material available to us has been further examined and
analyzed. In the interim, the species described herein will be referred

to the genus *Moenkhausia,* where it belongs according to the diagnostic characters of that series. A revision of this group of characids must include a redefinition of certain generic limits and a full review of these fishes, something which I am not yet prepared to present.

COMPARATIVE MATERIAL EXAMINED

Hyphessobrycon agulha Fowler, holotype, ANSP 39232, Brazil, Río Madiera, about 200 miles E of Long W62° 20'. Coll. E. A. Smith, 1912.

Hyphessobrycon herbertaxelrodi Géry, holotype, USNM 196089, Brazil, Mato Grosso, Rio Paraguay Basin, Coxim on the Rio Tacquary. Coll. K. H. Stegemann, 1960.

Hyphessobrycon loretoensis Ladiges, MCZ 52154, Colombia, Río Loreto Yacú, in small creeks about 1 km from river mouth (Rio Loreto Yacú is a trib. of Rio Marañon), approx. 03° 30'S, 070° 10'W. Coll. Alfonso Doaz, Dec. 1976.

Hyphessobrycon metae Eigenmann and Henn, holotype, CAS (IU) 13421, Colombia, Barizora, Río Meta, Coll. M. Gonzáles.

Hyphessobrycon metae Eigenmann and Henn, paratypes, CAS (IU) 13422, same data as holotype.

Moenkhausia browni Eigenmann, holotype, FMNH 52733, British Guiana: Arnataima. Coll. C. H. Eigenmann, 1908.

Moenkhausia collettii Steindachner, USNM 66228, British Guiana: Erukin Creek, lower Potaro River. Coll. C. H. Eigenmann, 1908. Identified by Eigenmann.

Moenkhausia copei (Steindachner), USNM 66230, British Guiana: Rockstone, Essequibo River. Coll. C. H. Eigenmann, 1908. Identified by Eigenmann.

Moenkhausia cotinho Eigenmann, USNM 66244, British Guiana: Tukeit, lower Potaro River. Coll. C. H. Eigenmann, 1908.

Moenkhausia dichroura (Kner), USNM 86792, Bolivia: Rurrenabaque. Coll. N. E. Pearson, Oct. 1921.

Moenkhausia eigenmanni Géry, holotype, USNM 198640, Colombia: Rio Marracacias into upper Rió Meta, at Restrepo. Coll. Ross Socolof, June, 1963.

Moenkhausia lepidura gracilima Eigenmann, holotype, USNM 120279, Brazil: Serpa. Coll. Thayer Expd. 1866.

Moenkhausia takesi Géry, holotype, USNM 198136, Brazil: Rio
Guana basin, near Belém do Para. Coll. Takese, 1963.

Moenkhausia robertsi Géry, holotype, USNM 200427, Peru: upper
Amazon, near Iquitos. Coll. J. Roberts, 1963.

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A NEW SPECIES OF CYBOTOID ANOLE
(SAURIA, IGUANIDAE) FROM HISPANIOLA

ALBERT SCHWARTZ[1]

ABSTRACT. *Anolis strahmi,* a new species of clivicolous cybotoid anole from Hispaniola, occurs both north and south of the Sierra de Baoruco, the mountain range associated with the Dominican Península de Barahona. Two subspecies are recognized. Additionally, a new subspecies of *Anolis longitibialis* Noble is named from the Península; nominate *A. l. longitibialis* occurs on Isla Beata off the southern tip of the peninsula. Details of distribution and known ecology of the two species are given, and comparisons of the two species (and their respective subspecies) are made. A hypothetical evolutionary and geographical sequence relating these two species to parent *A. cybotes* has been postulated.

INTRODUCTION

Anolis cybotes Cope is the first-named of a series of related taxa of Hispaniolan anoles. *A. cybotes, sensu stricto,* is a widespread mesophilic species of moderate size that occurs in wooded to rather open situations throughout much of Hispaniola. Although the species prefers mesic habitats, it does not completely shun situations which are xeric. In extremely arid areas, the species is often confined to oases or other shaded enclaves. It reaches elevations in excess of about 1,525 m, depending upon which named upland populations one accepts as subspecies of *A. cybotes* (see Schwartz and Thomas, 1975:77). The species is also known from several of the Hispaniolan satellite islands: Ile de la Gonâve, Isla Catalina, Isla Saona, Ile-à-Vache, Ile de la Tortue, and Ile Grande Cayemite. Only on the first of these has an endemic subspecies been named. The present paper

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does not attempt to deal with those named populations (*armouri* Cochran, *doris* Barbour, *haetianus* Garman) that are or have been associated with *A. cybotes* nomenclaturally.

Three other species form the *cybotes* complex. *A. shrevei* (Cochran, 1939) is restricted to the uplands of the Dominican Cordillera Central; this has been recently affirmed as a distinct species by Williams (1975). A xerophilic ally of *A. cybotes* is *A. whitemani* Williams. This species centers in the Cul de Sac-Valle de Neiba plain, which today encompasses the area between the north and south paleoislands (Williams, 1961), east into the Llanos de Azua. *A. whitemani* and *A. cybotes* occur macrosympatrically in this region; the former occupies xeric situations whereas the latter occupies oases and riverine woods — shaded, mesic situations. There are also records of *A. whitemani* from the northwestern Haitian Presqu'île du Nord Ouest (Môle St. Nicholas) and near Gonaïves. It is likely that these "isolated records" are one end of a linear coastal range from the Cul de Sac Plain along the Golfe de la Gonâve onto the xeric northwestern peninsula, but records are absent to affirm this continuity. *A. whitemani* is also known from the xeric Monte Cristi region in northwestern República Dominicana. Most recently, Williams (1975) named *A. marcanoi* from the southern xeric slopes and associated plains of the Sierra de Ocoa, a southern affiliate of the Cordillera Central. *A. marcanoi* is sympatric (and even rarely syntopic) with *A. cybotes.* Williams has given very pertinent details of this association, and Webster (1975) affirmed species-rank for *A. marcanoi* by electrophoresis. These two species differ slightly meristically, but in living animals the dewlap color and the head and body pattern are distinctive and dichotomous.

Anolis longitibialis was described from Isla Beata, off the southern tip of the Península de Barahona. Cochran (1934) first combined *A. longitibialis* with *A. cybotes;* the species are indeed very similar in general appearance and scutellation. It would seem quite logical that wide-ranging *A. cybotes* would have a local insular population on Isla Beata, despite the absence of *A. cybotes* from the Península de Barahona itself, at least as far as Cochran's data (1941) suggested.

In 1969, Richard Thomas collected a single large female cybotoid on the Península de Barahona. This lizard was so much larger than

female *A. cybotes* from the adjacent foothills of the Sierra de Baoruco that suspicion was aroused that it might represent *A. c. longitibialis.* Comparisons were made, and it was determined this lizard was indeed much more similar in size and ventral scutellation to Beata lizards than to *A. cybotes* from the nearby mountains. In 1971, at a locality 9.6 km N of Pedernales, I collected *cybotes* and *longitibialis* at the same locality; the habitat was grassy and shrubby pasture adjacent to limestone cliffs and their talus. Since Thomas's lizard was secured sleeping adjacent to a cave in limestone cliffs, it seemed a possibility that on the mainland *longitibialis* was limited to this habitat, whereas *cybotes* preferred more shaded and less extreme habitats. There was no doubt, however, that we were dealing with two distinct species, *A. cybotes* and *A. longitibialis,* which have limited sympatry and syntopy on the Península de Barahona, and of which one (*A. longitibialis*) occurs also on Isla Beata.

In June 1974, Fred G. Thompson of the Florida State Museum collected in the República Dominicana on the north face of the Sierra de Baoruco near the Dominico-Haitian border, just northeast of the border post of El Aguacate. He courteously lent me his material from that expedition. Two anoles from 2 km NE of El Aguacate are extremely distinctive; both are males, one is very large, and each has its head more attenuate with a different profile and is much less "jowly" than *A. cybotes.* Most pertinently, the dewlaps were mustard-colored when I examined them 4 months later. Although this is not the dewlap color in life of this population, nevertheless, the retention of such deep and distinctive colors after preservation suggests the dewlaps are differently and brightly colored in life, in contrast to the pale colors of *A. cybotes.*

In December 1974, Michael H. Strahm and I made an attempt to reach Thompson's locality; however, the road to the north face of the Sierra de Baoruco from La Florida was in disrepair and our vehicle was unable to reach the high elevations (900 m) needed to secure the lizards. Dr. Thomson had advised me that the lizards were common on rocky and exposed roadcuts, but we never reached such a situation. In the summer of 1975 we were successful in reaching El Agucate from the north, where the road has high to moderate artificial "cliffs" along its eastern margin as it ascends the mountains. We finally found a population of Thompson's lizards

and secured a series on three visits. My earlier contentions proved correct: 1) the dewlaps are very brightly colored, and 2) the lizards are large and are confined to creviced roadcuts in this area. Their status as a species distinct from *A. cybotes* was confirmed by taking typical *A. cybotes* on fenceposts across the road (5m) from the cliffs which harbored the new lizards. Thus we seemed to have an easily solvable problem: a derivative of *A. cybotes* which is very specialized in habitat (cliff faces) occurring on the north face of the Sierra de Baoruco at elevations of about 900 m. The two species differ grossly in adult size, head shape, and dewlap color as well as in habitat; there was no question that they are distinct and sympatric.

Also during the summer of 1975, Ernest E. Williams and William E. Haas, while collecting in the Península de Barahona lowlands, encountered large cybotoids in a shaded and fairly mesic ravine near sea level at a locality 5 km SE and 2.9–3.0 km N of Pedernales. Superficial examination of their specimens in the field, and subsequent collection of a short series taken there by Thomas Wiewandt and Diderot Gicca, all served to confirm that these lizards were very comparable to the series from high elevations on the north face of this same mountain range. The habitat of the new population near Pedernales is very like that of the El Aguacate specimens — a limestone ravine or wash that is much creviced; however, vegetationally this ravine is much more shaded and mesic than the bare and exposed road cut near El Aguacate.

In 1975 Richard Thomas secured a fine series of *A. longitibialis* at a locality 17 km NW of Oviedo that represents the easternmost record for the species. This locality is a wooded but xeric ravine with creviced limestone walls, that lies on the eastern edge of the north-south limestone ridge which bisects the Península de Barahona. There are specimens of *A. longitibialis* from west (Pedernales) and east (17 km NE of Oviedo) of the ravine which harbors the differently-colored dewlapped population discovered by Williams and Haas. Both species in this region show a predilection for limestone cliffs; they and the north slope lizards show remarkable agility and familiarity with their cliffs and are completely "at home" upon them. Other anoles (*A. cybotes, A. brevirostris* Bocourt) occur on cliffs in this general region but rarely seek refuge in crevices; rather, when pressed, they drop to the ground to hide. This is not true of either the new species or of *A. longitibialis* both of which

almost invariably seek refuge in crevices (see additional comments below). I have never taken the new species at night which suggests that the lizards sleep in crevices. *A. longitibialis,* however, has been secured while asleep on shrubs and low trees adjacent to cliffs. This implies that the two species differ in sleeping sites, although they may forage on the same vertical rocky faces.

Williams (1975:7–8) made the following comment in his "justification" for the naming of *A. marcanoi* despite weak meristic differences between that species and *A. cybotes:* "It becomes more obvious that, in addition to those species in which museum taxonomists rejoice because they are very distinct in terms of the characters conventionally studied, there are in many groups valid biological species only imperfectly separable on museum characters, if at all. This phenomenon is only interesting in terms of the history of museums, not of biology. . . . It will not be necessary in the near future to defend or specially comment on cases like that here described." The same comments, to some extent, apply here. I have no doubt that the peculiarly isolated populations herein described as a new species differ biologically from *A. longitibialis.* Except for some size and modal differences in scale counts, without preknowledge of the dewlap colors as a re-enforcing mechanism, one might be easily led into misinterpreting the situation. Verifying that *A. longitibialis* is distinct from *A. cybotes* required the chance encounter of the two species syntopically after the lapse of two years. *A. longitibialis* geographically surrounds two of the three known populations of the new species. Differences between this new species and *A. longitibialis* are not subtle in life, but assigning long-preserved and discolored museum specimens to one or the other species is and will continue to be difficult. This fact, however, should not be a deterrent from naming a new taxon. Two biological entities (species) exist. It is the duty of the systematist to recognize this fact nomenclaturally and to present whatever data he may have to support his contention.

Before proceeding to the new species, it is pertinent to examine variation in *A. longitibialis.* Noble's (1923) description is detailed but lacks data on some features which are important when comparing the Beata population with the Península de Barahona population. These two samples differ from each other and from the new species about to be named in a number of ways; the differences

in the former case are those which are accepted as being of subspecific rank. Accordingly, I first define *A. longitibialis* in those terms which will differentiate it from the new species, and then name a new mainland subspecies of *A. longitibialis.*

Anolis longitibialis Noble

Anolis longitibialis Noble, 1923, Amer. Mus. Novitates, 64:4.
Type locality: Isla Beata, República Dominicana.
Holotype: AMNH 24329.
Definition. A cybotoid anole characterized by small size (males to 72 mm, females to 59 mm), supraorbital semicircles occasionally not in contact, modally 1/1 scales between the supraorbital semicircles and the interparietal, smaller median dorsal scales (35 to 57 in snout-ear distance), subocular scales often in contact with supralabial scales, usually 4 or 5 postrostral scales, few fourth toe lamellae (15–21), dewlap pale yellow to pale orange, throats of adult males almost always immaculate and rarely streaked.

Anolis longitibialis specuum, new subspecies

Holotype: MCZ 132,370, adult male, 17 km NW of Oviedo Nuevo, Pedernales Province, República, 183 m, 7 8 August 1975, Richard Thomas, coll. Original number RT 3,461.
Paratypes: All paratypes are from República Dominicana, Pedernales Province. ASFS V26,898 901, RT 3,462, LSUMZ 29,541 47, same data as holotype; ASFS V16,728, 6.4 km SE Pedernales, 17 May 1969, J. B. Strong; ASFS V21,531, 8 km N, 2 km E of Cabo Rojo, 1 August 1969, R. Thomas; ASFS V29,766 68, 7 km N, 20.0 km SE of Cabo Rojo, 183 m, 14 August 1971, A. Schwartz; ASFS V30,073–74, 7 km N, 20.0 km SE of Cabo Rojo, 183 m, 22 August 1971, D. C. Fowler; ASFS V42,235, 17 km NE of Oviedo Nuevo, 183 m, 12 August 1975, M. H. Strahm; ASFS V30,086–87, 7 km N, 17.6 km SE of Cabo Rojo, 152 m, 22 August 1971, A. Schwartz, B. R. Sheplan; ASFS V30,114, 9.6 km N of Pedernales, 244 m, 23 August 1971, A. Schwartz; ASFS V41,914, 7 km N, 2 km SE of Cabo Rojo, 29 July 1975, M. H. Strahm; UF FSM 21,567–68, 1 km SW of Las Mercedes, 380 m, 21 March 1974, R. Franz; MCZ 146,848, 1.2 km E of cave near intersection Cabo Rojo-Pedernales roads, 21 July 1975, W. E. Haas; MCZ 146,849, 7 km N, less than

1.2 km E of intersection of Cabo Rojo-Pedernales roads, 21 July 1975, W. E. Haas; MCZ 128,319, MCZ 128,342–43, 2 km E of turn to Cabo Rojo, 16 July 1971, T. P. Webster, R. B. Huey; MCZ 143,483, Cabo Rojo, behind police station, 5 July 1974, P. E. Hertz, R. B. Huey; MCZ 151,864–78, Cabo Rojo, behind laundry, 1–3 October 1976, W. E. Haas; MCZ 132,378–80, 7 km N, 1.2 km SE of Cabo Rojo, 2 October 1976, N. Atkins, W. E. Haas; MCZ 151,902, 7 km N, 1.2 km E of Cabo Rojo, 2 October 1976, W. E. Haas; MCZ 132,381–82, 17.6 km NW of Oviedo Nuevo, 2 October 1976, W. E. Haas; MCZ 151,828–48, 17.6 km NW of Oviedo Nuevo, 2–3 October 1976, W. E. Haas.

Associated specimen. MCZ 58,419, 30 km NW of Oviedo, Pedernales Province, República Dominicana.

Definition. A subspecies characterized by the combination of large size (males to 72 mm, females to 59 mm, snout–vent length), larger dorsal scales (35–52), larger ventral scales (31–52), usually 4 or 5 postrostral scales, dorsum brown with 4 transverse dumbbells and often 1 pair of sacral blotches, throats of females almost always longitudinally streaked with dark brown, very rarely so in adult males; dewlaps very pale orange to very dull yellow or dirty yellow.

Description. An adult male with a snout-vent length of 71 mm and femur length of 23 mm (measured as proposed by Ruibal and Williams, 1961:214); snout scales at second canthal scales 7, vertical loreal rows 4, supraorbital semicircles in contact, scales between semicircles and interparietal 1–1 (counted as proposed by Schwartz, 1968:260); subocular scales in contact with supralabial scales bilaterally; 5 enlarged scales in supraocular discs, 7 postmentals, 4 postrostrals, 3/3 canthals, 19 fourth toe lamellae on phalanges II + III, 49 median dorsal scales and 43 median ventral scales in snout–ear distance. In life, dorsum brown with 4 darker brown dorsal dumbbells (narrow middorsally), the anterior pair the largest and forming a pair of blotches, somewhat faded along their anterior borders, the posterior 3 very fragmented and barely discernible as dumbbells; a dark but centrally very flattened postocular U, the arms very short and touching the upper eyelids; temples, neck, and remainder of dorsum with scattered longitudinal dark dashes or small spots; a pale narrow subocular crescent; lores and infraorbital area pale and without dark mottling; venter white, chin and throat immaculate; upper surfaces of fore- and hindlimbs concolor with

dorsum and with a very few scattered dark brown dots and without defined crossbands; dewlap dull yellow.

Variation. The series of 76 *A. l. specuum* is composed of 38 males and 38 females. MCZ 151,828 is the largest male with a snout vent length of 72 mm; the largest female (ASFS V21,531) has a snout–vent length of 59 mm. The smallest lizard is a female (RT 3,460) with a snout–vent length of 37 mm. Femora measurements (in mm.) of all males are 14.2–24.4 ($\bar{x}$ = 21.1) and are 11.8–19.2 (16.5) in all females. Snout scales between the second canthals vary between 6 and 10 ($\bar{x}$ = 7.4; M_o = 7–44% of the specimens); loreal rows are 4 to 6 (M_o = 5 53%); supraorbital semicircles are in contact in 69 specimens and are separated by one row of small scales in five lizards. Scales between the supraorbital semicircles and the interparietal scale are modally 1 1 (40 specimens); other counts include 0/0 (2), 0/1 (3), 1/2 (12), 2/2 (13). Dorsal scales in snout–ear distance are 35–52 ($\bar{x}$ = 44.3) and ventrals in the same distance are 31–52 ($\bar{x}$ = 38.5). The subocular scales may or may not be in contact with the supralabial scales; bilateral separation between these scales occurs in 44 specimens, unilateral contact occurs in six, and bilateral contact in 16; thus, there is contact at least unilaterally between the suboculars and supralabials in 33% of the lizards. Enlarged scales in the supraocular discs vary between five and 11 ($\bar{x}$ = 7.0; M_o = 7 – 27%); this count is difficult to take since there may be many small (but not granular or tiny) scales along the periphery of the disc that might be counted if one desired. Postmental scales are 2 to 9 ($\bar{x}$ = 6.3; M_o – 41%); postrostral scales are 3 to 5 ($\bar{x}$ = 4.2; M_o = 4 or 5 36% in each category). Canthals are usually 3/3 but three lizards have 4/4 canthal scales and one has 3/4. Fourth toe lamellae on phalanges II + III are 15–21 ($\bar{x}$ = 17.6); femur/snout–vent length ratio × 100 is 28.7–36.3 ($\bar{x}$ = 32.5) in males, 28.8–35.2 (33.2) in females.

Color notes in life on both males and females indicate that the dorsal ground color is brown with darker brown markings. There is often a white subocular semicircle and a gray lateral stripe which may be absent or may be suggested by the remnants of dark dorsal and ventral outlining. In males there are usually four dumbbell-shaped figures with their narrowest portions lying across the midline of the back and followed by a pair of dark sacral blotches; of the dumbbells, the first is the best defined and largest and is less clearly

delimited anteriorly than posteriorly as in the holotype. Occasional adult males (MCZ 128,342) are virtually patternless above, without traces of the dumbbells and with only some longitudinal dashes and dark dots remaining. Another smaller male (ASFS V16,728) has only the finest transverse indications of the dumbbells, whereas in a comparably sized male (ASFS V30,074) the dumbbells are large and form prominent butterfly-shaped markings across the back. The truncate postocular U described for the holotype is present in most males, but may be very reduced, only indicated, or absent. A fine, vertically diagonal dark line often courses across the temporal region toward the dorsal midline and may even occasionally (MCZ 128,342) form a complete nuchal V or vague W. The throats of males are variable; young specimens have them streaked with dark brown while full adults have them most often immaculate. An exceptional male (RT 3,462) has streaking remnants on the throat at a snout–vent length of 71 mm.

Females have the same dorsal pattern variation as do males. The dumbbells are, when present, conspicuous, dark, and well developed. Some females (ASFS V30,086) have the dorsal pattern much reduced or even absent and the postocular truncate U is more often only indicated rather than present and well developed. One female (ASFS V41,914) was described in life as having an orangish middorsal streak with dark brown dorsal flecking between the dumbbells. The throats of females are variable — many are longitudinally streaked with dark brown whereas others have the throats immaculate white. Therefore there seems to be no correlation of size and throat streaking.

Male dewlaps have been described as orange, pale orange, dirty yellow, or dull yellow (the latter two conditions at the type-locality). A male (ASFS V30,074, snout–vent length 54 mm) was recorded as having the dewlap orange (Pl. 9K5; all color designations from Maerz and Paul, 1950); a topotypical male (ASFS V42,235; snout vent length 67 mm) had the dewlap dull yellow (Pl. 12I6) shortly after death. The vestigial dewlaps in females were recorded as pale orange to orange.

Comparisons. A. l. longitibialis from Isla Beata (Schwartz and Thomas, 1975:89, incorrectly assigned *A. longitibialis* to Isla Alto Velo whence the species is unknown) differ from *A. l. specuum* in several ways. The Beata subspecies is smaller (males to 67 mm,

females to 57 mm snout vent lengths), the dorsal scales (39 57) and ventral scales (29–51) are smaller, and there are modally four postrostrals (46%).

The series of *A. l. longitibialis* consists of 30 males and 13 females. The dorsal coloration in life is grayish tan to gray-brown and the color closely matches the cliffs upon which the species lives on Isla Beata. In males, the lower sides are greenish and in this sex the pattern consists of a series of longitudinal fine dark brown lines, dashes, or dots; there is no indication of dark brown dumbbells. The truncate occipital U is barely indicated at best and is usually absent; the fine diagonal temporal line is present but faint or fragmented. All these features, plus dorsal ground color, differentiate *A. l. longitibialis* from *A. l. specuum.* Throats of males are almost always immaculate; seven males show some vague streaking or dark scribbling on the throats. Females are much like the males dorsally, except that there may be a more clear indication of the dumbbells (AMNH 41,431) than in males. Female throats always show some indication of dark streaking or scribbling, but this is seldom bold and prominent. Noble (1923:4) noted that *A. longitibialis* from Isla Beata had the dorsum with "a fine penciling of dark brown." He also commented that the color (in alcohol) was pale chocolate-brown, finely marked with a number of narrow lines of dark brown. Some of the lizards which were available to Noble have been examined by me and they still retain these features.

One peculiarity of Noble's description is his comments on dewlap color. He stated (1923:4) that the dewlap was "bright" and that it "oddly enough, sometimes retains its color in preservative." This latter is a peculiarity of this species, of *A. marcanoi,* and of the one next to be described. Most Antillean anoles with orange, red, or yellow dewlaps lose the pigments shortly after preservation; but this seems not to be the case in these cybotoids. Despite Noble's comments on dewlap color and its persistence in *A. longitibialis,* nowhere does he mention what are the characteristics of the bright dewlap color except to say that it is "yellowish." Thomas's (1964) field notes state that in males the dewlap is dirty yellow anteriorly to orange on the posterior three-quarters of the dewlap. It appears that the dewlap color in the two subspecies of *A. longitibialis* is fairly comparable.

Remarks. There is one specimen (MCZ 58,419, from 30 km NW of Oviedo, Pedernales Province) of whose status I am uncertain. This is an adult male 67 mm in snout vent length. It differs from both *A. l. specuum* and the new species described below in that it has a complete dark nuchal band, three complete dark dorsal bands between the limbs, and a pair of sacral blotches that almost form a fourth complete band. There are no distinctive head markings and the specimen is somewhat faded (collected in 1958). If it is an *A. l. specuum,* it is remarkably well patterned dorsally; the throat is now immaculate. The small ventral scales assure that it is not *A. cybotes.* The locality places it within the distribution of the former taxon but I refrain from assigning it to *A. l. specuum* since it differs in pattern details as noted above. I suspect that it is an exceptionally well patterned male *A. l. specuum,* but the cautions noted in the introduction are re-enforced here: without knowledge of habitat or color and pattern in life, one is strongly handicapped in confidently assigning older specimens to any of these taxa.

The name *specuum* is from the Latin for "of the crevices or caves" and alludes to the crevice-dwelling habits of this subspecies. The word *specuum* is genitive plural.

Specimens examined. A. l. longitibialis, **República Dominicana,** Isla Beata, just E of Punta Beata (ASFS V17,215–19); no other locality (ASFS V2,772–80, USNM 83,878, USNM 83,880, AMNH 41,415, AMNH 41,422, AMNH 41,424–32, AMNH 52,449–51, MCZ 17,686, MCZ 31,774, MCZ 37,480 82, UF FSM 21,572–78).

The new species referred to in the introduction is composed of two populations which differ from each other. Michael H. Strahm collected most specimens of the northern population. Accordingly, I associate his name with this new species, which I call:

Anolis strahmi, new species

Definition. A cybotoid anole characterized by large size (males to 79 mm, females to 64 mm snout vent lengths), supraorbital semi-circles always in contact, modally 2/2 scales between the supra-orbital semicircles and the interparietal, larger median dorsal scales (32 to 51 in snout-ear distance), subocular scales always separated from supralabial scales by one row of scales, usually three post-

rostral scales, more fourth toe lamellae (17–24), dewlaps deep orange to deep orange-brown, throats of males marked, or without dark flecking or scribbling, by population.

Head. Moderately massive, length from snout to posterior border of eye much shorter than either femur or tibia. Head scales mostly smooth in males and very weakly carinate in females. Five to nine scales across snout at level of second canthal scales. A very shallow frontal depression and a deeper parietal depression. Nares in front of and above canthal ridge composed of three or four scales. Anterior nasal scale in contact with rostral. Snout distinctly pointed when viewed from above and with a distinctive profile due to the raised nares.

Supraorbital semicircles in contact and are separated from the supraocular discs by 2 rows of granules. Supraocular discs consist of about 4 to 11 enlarged smooth to very weakly keeled (males) or keeled (females) scales separated by about 4 rows of scales and granules from the scales of the supraciliary rows. Two elongate supraciliaries are continued posteriorly by a double row of moderately enlarged scales. Canthus distinct, the first canthal scale the largest. Loreal rows five to nine, the lower rows larger and more regular. Supratemporal area scales are granular, grading rather abruptly into larger scales surrounding the interparietal depression. Interparietal is about the same size as ear opening and is separated from the supraorbital semicircles by one to three scales (modally two) or rarely unilaterally in contact.

Subocular scales are almost always separated from supralabials by one row of scales (very rarely in contact, very rarely by two rows of scales), anteriorly grading into loreals, posteriorly grading into large scales at the corner of the mouth. Usually six supralabials to center of eye.

Mentals are equally broad and long and almost equilateral, and are in contact posteriorly with one to ten small elongate postmental scales. Infralabials are broadly rectangular anteriorly, narrow posteriorly, in contact with three large tetrahedronal sublabials. Throat scales are small, granular, not keeled, and the anterior ones are elongate.

Trunk. Middorsal scales are in two or four abruptly enlarged rows, about four times as large as flank scales and 32–51 in snout-ear distance. Ventrals are small, about 1.5 times as large as

middorsal series, cycloid, smooth, and 31 to 61 in snout-ear distance. Two postanal scales are enlarged in males.

Gular fan. Very large; scales smooth, those along margin about twice as large as ventrals.

Limbs and digits. Hand and foot scales are smooth. Between 14 and 24 scales are under phalanges II + III of fourth toe. Largest scales of arm are smooth to very weakly unicarinate, those of leg smooth and both those of arm and leg are larger than ventrals.

Tail. Slightly laterally compressed, each verticil surmounted by three sharply keeled scales and ventrally by three pairs of unicarinate slightly smaller scales.

Anolis strahmi strahmi, new subspecies

Holotype: MCZ 132,371, an adult male, from 3 km NE of El Aguacate, Independencia Province, 854 m, República Dominicana, taken on 19 July 1975 by Michael H. Strahm. Original number ASFS V41,729.

Paratypes. All paratypes are from Independencia Province, República Dominicana. ASFS V41,730–34, same data as holotype; ASFS V41,284–94, same locality as holotype, 10 July 1975, M. H. Strahm; ASFS V28,453, ASFS V41,308 09, same locality as holotype, 14 July 1975; ASFS V44,991–94, same locality as holotype, 22 December 1976, A. Schwartz, W. B. Southerland; UF FSM 21,565-66, 2 km NE of El Aguacate, 900 m, 30 June 1974, F. G. Thompson.

Definition. A subspecies of *A. strahmi* characterized by modally eight scales in the supraorbital discs, dorsum is pale gray and is at best flecked with dark gray and often unpatterned, throat is usually unpatterned in both sexes but occasionally has some vague scribbling, and dewlap is very deep orange to orange-brown.

Description. An adult male with a snout–vent length of 78 mm and femur length of 25.5 mm; six snout scales at second canthal scales, seven vertical loreal rows, supraorbital semicircles in contact, scales between semicircles and interparietal 2 2; subocular scales separated by one row of scales from supralabials bilaterally; 11 scales in supraocular discs, six postmentals, three postrostrals, 3 3 canthals, 20 fourth toe lamellae on phalanges II + III, 41 median dorsal scales and 48 median ventral scales in snout-ear distance. In life, dorsum is pale gray with a few scattered darker gray dots, most prominent above the forelimb insertions; remnants of a postocular

truncate U are present, its very short arms abutting against the upper eyelids; supra- and infralabials contrastingly spotted with pale and dark gray; a very pale blue-gray subocular crescent; venter pale grayish, throat immaculate and without pattern; limbs and tail without any crossbands or other prominent markings; dewlap (shortly after death) deep orange (Pl. 4A11).

Variation. The series of 26 *A. s. strahmi* consists of nine males and 17 females. The holotype and another male (UF FSM 21,566) are the largest males with snout-vent lengths of 78 mm; the largest female (ASFS V41,288) has a snout–vent length of 64 mm. The smallest lizard (ASFS V44,994) is a female with a snout vent length of 42 mm. Femora measurements (in mm.) in all males are 15.7–26.4 ($\bar{x}$ = 21.5) and are 13.0–21.5 (18.9) in all females. Snout scales between the second canthals vary between five and eight ($\bar{x}$ = 7.0; M_o = 7–43% of the specimens); loreal rows are five to seven (M_o = 5–52%); supraorbital semicircles are in contact in all specimens. Scales between the supraorbital semicircles and the interparietal scale are modally 2/2 (14 specimens), with other counts of 1/0 (1), 1/1 (2), 1/2 (4), and 2/3 (1). Dorsal scales in snout-ear distance are 34–48 ($\bar{x}$ = 39.3) and ventrals in the same distance are 32–61 ($\bar{x}$ = 41.2). The subocular scales are separated from the supralabial scales by one row of scales bilaterally in all but two lizards which have either two rows of scales or are in contact unilaterally. Enlarged scales in the supraocular discs vary between five and 12 ($\bar{x}$ = 8.0; M_o = 8–36%); the same precautions made in the account of *A. l. speciuum* apply here. Postmental scales are four to seven ($\bar{x}$ = 5.3; M_o = 6–36%); postrostral scales are three to five ($\bar{x}$ = 3.5; M_o = 3–58%). Canthal scales are always 3/3. Fourth toe lamellae on phalanges II + III are 16–21 ($\bar{x}$ = 18.6); femur/snout–vent length ratio × 100 is 31.7–34.3 ($\bar{x}$ = 33.3) in males and 30.5–36.1 (32.9) in females.

Color notes on both males and females in life indicate the dorsal ground color is gray, remarkably similar to the color of the rocks on which the lizards live. Both sexes are patterned similarly dorsally; there are no dumbbells or flank stripes present (although the position of the latter is occasionally indicated by vague elongate dashes along its putative upper and lower margins). The dorsum is more or less randomly dotted or marked with scattered dashes aligned longitudinally; young males have vague dumbells which are

so reduced as to be only faint transverse lines hollowed laterally *i.e.*, they are mere vestiges of what presumably are basically dumbbells. The general aspect of the males and females is of a faint and randomly dotted or lineate pattern, but many adults and subadults completely lack any sort of dark body pattern elements. The postocular truncate U is represented by its outlines and these may be fragmented and very obscure. The same is true of the diagonal temporal line. The venter is dark gray to yellowish gray in females. The throat is marked with some confused scribbling, oriented longitudinally in one adult male (ASFS V41,285) and in one subadult male (UF/FSM 21,565; snout vent length 54 mm). Females generally have gray throats without markings, but one adult (ASFS V41,290; snout vent length 62 mm) has some vague darker scribbling and two other females have remnants of similar markings only very faintly shown on the posterior portion of the throat. In life, the limbs are crossbanded with pale and dark gray, but these markings are not obvious on the preserved specimens. A distinctive feature of males (and somewhat less so of females) is the spotted supra- and infralabials. A very pale blue-gray subocular crescent is present and moderately conspicuous in life.

The dewlaps in males are very deep orange to orange-brown and these colors are especially rich and almost velvety in texture. Color designations are Pl. 13J10 for one living male and Pl. 11I11 and Pl. 4A11 for two recently dead males. Females have the same basic intensity of coloration on their vestigial dewlaps.

Comparisons. Comparisons of *A. s. strahmi* with the subspecies on the south side of the Sierra de Baoruco as well as with *A. l. specuum* will be withheld until the former is described below.

Remarks. I have commented previously on Dr. Thompson's observations on the habitat of *A. s. strahmi.* Our own observations amply confirm his. On 10 July 1975 we searched several kilometers of the road below the post of El Aguacate and saw only very occasional lizards on the gray rocks of the roadcut and did not observe any on adjacent shrubs or herbs. In much of this distance, the roadcut is rather densely covered with vines, small shrubs, and herbs, but elsewhere it is almost bare with only scattered vegetational cover. We finally encountered *A. s. strahmi* in some abundance along an exposed section of roadcut which was about 30 m in length. The roadcut here was almost bare of plants with many

crevices and solution holes. Between 1330 and 1600 hrs this section of roadcut was shaded (due to the direction of its face rather than to any arborescent or herbaceous cover) and the lizards were seen in their retreats, their heads or foreparts extended outside the crevices in an alert manner. They were not easily alarmed, relying upon the extremely cryptic coloration of their gray dorsa agreeing very closely with the hue of the roadcut face. Two lizards were seen "sunning" themselves (in the shade) vertically, head down, on completely exposed rocky surfaces; one was observed clinging to the roof of a small solution hole. In addition to the 11 specimens collected during this 2.5 hour period, at least eight others were seen but not collected. They allowed close (1 m or less) approach of the collector before becoming alarmed and retreating into crevices or solution holes. Recovery time was brief; on several occasions, as we walked slowly down this 30 m stretch of road, we noted refuges of specific lizards. Upon returning a maximum of 10 minutes later the lizards had already reappeared at the crevice mouths (which were their individual retreats) or on adjacent rock faces. On subsequent visits we observed lizards in the same precise places as previously. Their agility and assurance on the rock faces were impressive.

On our third visit to the type locality on 19 July 1975, six lizards were collected between 1720 and 1830 hrs in the same stretch of roadcut. The adult male holotype was taken just below a slightly more covered section. About three or four other anoles were seen but escaped capture. Although the cliff face was completely in shade and the air was cool (but not cold) the rock faces were still warm to the touch.

On 22 December 1976, W. B. Southerland and I visited the type locality once again. Our arrival was at 1200 hr and we saw very few lizards. The roadcut was in shade and the shade increased until 1500 hr so that maximum insolation had occurred in the early morning prior to our arrival. However, the rocks were still warm to the touch. As the afternoon progressed, more *A. s. strahmi* appeared, so that about 12 were seen. Some large males, once disturbed, did not reappear on the roadcut face. Four specimens were taken: a male on an open rock face, a female on a dead stem 8 cm from the base of the cliff and two other females in or near crevices or cavities in the roadcut face. The female noted here on a dead stem is the only individual we observed or collected not on the rocks.

Above and below the road at the type locality are steep slopes. An outstanding feature of the immediate region is the eroded limestone terraces and jumbled rocks and boulders, all sparsely covered with herbs and scattered shrubs and with only occasional large trees. The general aspect of the area is rather bleak.

Two other observations at the type locality are pertinent. We encountered an active *Uromacer catesbyi* Schlegel foraging on the roadcut face occupied by *A. s. strahmi*. These snakes eat lizards but are rarely seen in this habitat type and prefer trees and shrubs. In a crevice at this site we also encountered a young *Epicrates striatus* Fischer; when young, these snakes eat lizards. It is not unlikely that both snakes were associated with this particular section of roadcut because of the ready supply of food (*A. strahmi*). Both snakes are diligent predators in that they search for prey by penetrating crevices, holes, cavities, and other possible hiding places. Elongate *U. catesbyi* is especially well adapted for this foraging pattern during the day and *E. striatus* forages similarly at night.

Anolis strahmi abditus, new subspecies

Holotype: MCZ 146,827, an adult male, from dirt road to Las Mercedes, 2.9 km from intersection (= 5 km SE, 2.9 km N of Pedernales), Pedernales Province, República Dominicana, 19–20 July 1975 by William E. Haas collector. Original number MCZ F-29,006.

Paratypes. All paratypes are from Pedernales Province, República Dominicana. MCZ 146,920, MCZ 146,828 47, same data as holotype; ASFS V41,908–12, same locality as holotype, 29 July 1975, M. H. Strahm; UF/FSM 34,423–27, 5 km SW, 2.5–3.0 km N of Pedernales, 8 August 1975, T. Wiewandt and D. Gicca; MCZ 151,879–901, 5 km SE, 2.9 km N of Pedernales, 30 September and 1 October 1976, W. E. Haas; MCZ 132,383, 5 km SE, 2.9 km N of Pedernales, 30 September 1976, N. Atkins and W. E. Haas; MCZ 151,849–54, MCZ 151,857–63, between 15 and 16 km N of Cabo Rojo, Alcoa road, 3 October 1976, W. E. Haas.

Definition. A subspecies of *A. strahmi* characterized by modally six or seven scales in the supraorbital discs; dorsum tan to grayish tan, at times marked with small brown to reddish blotches; lateral flank stripe tan to whitish present, dorsum with transverse dumb-

bells or hourglasses in both sexes; throat flecked or scribbled in both sexes with dark brown and dewlap deep orange.

Description. An adult male with a snout-vent length of 78 mm and femur length of 26 mm; six snout scales at second canthals, supraorbital semicircles in contact, scales between semicircles and interparietal 2 2, subocular scales separated by one row of scales from supralabials bilaterally; seven scales in supraocular disc, six postmentals, three postrostrals, 3 3 canthals, 19 fourth toe lamellae on phalanges II + III, 35 median dorsal scales and 40 median ventral scales in snout-ear distance. As preserved, the dorsum is grayish brown, with four dark brown dumbbell remnants, all much hollowed or with their lateral expanded ends virtually missing and an additional fifth dumbbell remnant postsacrally; a dull interocular bar and a truncate postocular U, both hollowed; lores, supra-, infra-, and sublabials mottled dark and pale brown; sides of body with elongate dark brown linate fragments, with two of the lowermost fragment-series in part outlining the flank stripe; limbs marbled or mottled dark brown and brown, the only clear transverse dark bar on the crus; both fingers and toes with a moderately clear dark brown crossband; venter grayish to tan, chin and throat dotted with dark brown, sides of abdomen flecked with grayish brown; dewlap pinkish 6 months after preservation.

Variation. The series of 68 *A. s. abditus* consists of 33 males and 35 females. The largest male (ASFS V41,911) has a snout-vent length of 79 mm and the largest female (MCZ 146,838) a snout-vent length of 63 mm. The smallest lizard (UF/FSM 34,425, a female) has a snout vent length of 39 mm. Femora measurements (in mm.) in all males are 16.0–27.4 ($\bar{x} = 21.7$) and are 13.2–20.8 (18.1) in all females. Snout scales between the second canthals vary between five and nine ($\bar{x} = 6.9$; $M_o = 7$–52% of the specimens); loreal rows are four to seven ($M_o = 5$–62%); supraorbital semicircles are in contact in all specimens. Scales between the supraorbital semicircles and the interparietal scale are modally 2/2 (35 specimens), with other counts of 1/1 (9), 1/2 (5), 2/3 (6), and 3/3 (8). Dorsal scales in snout-ear distance are 32–51 ($\bar{x} = 39.8$) and ventrals in the same distance are 31–53 ($\bar{x} = 40.2$). The subocular scales are separated from the supralabial scales by one row of scales in all but two specimens; these lizards have these scales in contact either bilaterally or

unilaterally. Enlarged scales in the supraocular discs vary between four and 13 ($\bar{x}$ = 7.3; M_o = 6 or 7–27% in each case). Postmental scales are four to 10 ($\bar{x}$ = 7.3; M_o = 6–33%); postrostral scales are three to five ($\bar{x}$ = 3.7; M_o = 3–43%). Canthal scales are most often 3/3, but one lizard has 2/2 and another 3/4 scales in this position. Fourth toe lamellae on phalanges II + III are 17–24 ($\bar{x}$ = 19.0); femur snout-vent length ratio ×100 is 28.7–38.4 ($\bar{x}$ = 33.5) in males and 30.5–36.3 (33.4) in females.

Color notes state that in both males and females in life the dorsum is tan to grayish tan with five narrow dumbbell or hourglass remnants; these dorsal pattern elements end above the flank stripe which is either tan or white. Despite its prominence in life, the flank stripe is outlined only by dark brown line fragments, including the remnants of the dorsal transverse dumbbells. A dark brown inter-ocular stripe and a postocular truncated U are both present and may be either prominent or vague; the U may be most conspicuous at its posterolateral "corners" on the superior temporal region. Some males (ASFS V41,910 12, MCZ 146,829) show a progressive degeneration of the dorsal pattern into a series of more or less random dumbbell-fragments and associated longitudinal lines or dots which are brown to reddish. In each of these lizards, the peculiar dorsal pattern is obviously a derivative of the customary dorsal dumbbells. Two females (ASFS V41,909, MCZ 146,838) are comparable to the above mentioned males in diminution of the dorsal pattern. In both sexes, the throat is marked with some sort of pattern; this varies from marbling or scribbling to longitudinal dark lines which is more common in females than males. The intensity of the throat markings is variable. The lores and supra-, infra-, and sublabials are contrastingly marked with dark and pale and the lip markings extend ventrally to give rise to the throat pattern. The male dewlaps are deep orange in life (Pl. 12F9); two dead males had comparable dewlaps (Pl. 12F9, Pl.12H8). The deep orange color of the dewlap center is slightly richer along the margin.

Comparisons. *A. s. abditus* requires comparison with the taxa *A. s. strahmi* and *A. l. specuum. Anolis cybotes* also occurs sympatrically with both subspecies of *A. strahmi,* but it is easily distinguishable in dewlap color (pale yellow, pale pink, almost white), smaller snout-vent length, and much larger ventral scales. *Anolis breviros-*

tris, a small gray dorsoventrally compressed species with a pale yellow dewlap and a paramedian double row of snout scales, also is syntopic with *A. s. abditus.*

The two subspecies of *A. strahmi* are very similar, although they are altitudinally and geographically separated. The dewlaps in both are deep and rich orange (to orange-brown in *A. s. strahmi*) and reach the same size in both sexes. *A. s. strahmi* differs from *A. s. abditus* in that the former has modally eight scales in the supra-orbital discs versus six or seven in *A. s. abditus.* Dorsal coloration in *A. s. strahmi* is pale gray versus tan to grayish tan in *A. s. abditus.* The dorsum is at best flecked and often unpatterned in *A. s. strahmi* males versus relatively prominent dumbbell or hourglass remnants in both sexes of *A. s. abditus.* Finally, throats in both sexes of *A. s. strahmi* are rarely marked versus throats in both sexes of *A. s. abditus* which are marked with flecking, dotting, scribbling, or lines. The dorsal color and pattern, as well as the throat markings, are the most distinctive characteristics separating the two subspecies.

A. s. abditus has not as yet been taken sympatrically or syntopi-cally with *A. l. specuum* (see Fig. 1); it is unlikely that these two species will be taken together since both are clivicolous. Though they seem to be ecological equivalents, it is possible that at some locality on the Península de Barahona they occur together. The two species should be easily differentiable, if they are sympatric. The dewlap in *A. s. abditus* is deep orange, whereas that of *A. l. specuum* is dull or dirty yellow to pale orange. *A. s. abditus* reaches a larger size (males to 79 mm, females to 63 mm) than does *A. l. specuum* (males to 72 mm, females to 59 mm). Although there are three to five postrostral scales in both taxa, the mode in *A. s. abditus* is three and in *A. l. specuum* is four or five. Two other scale relationships will aid in differentiating the two species. In *A. l. specuum,* there are more often 0/0 1/1 scales between the supraorbital semicircles and the interparietal (64% of the specimens) whereas in *A. s. abditus* there are more often 1/2–3/3 (79%) scales in this position. *A. l. specuum* more often (33%) has the subocular scales in contact with the supralabials than does *A. s. abditus* (3%). Although none of these scale counts or relationships is absolute, in combination they serve to differentiate the two species.

There are some striking resemblances between *A. l. specuum* and *A. s. abditus* in color and pattern. The former is brown with darker
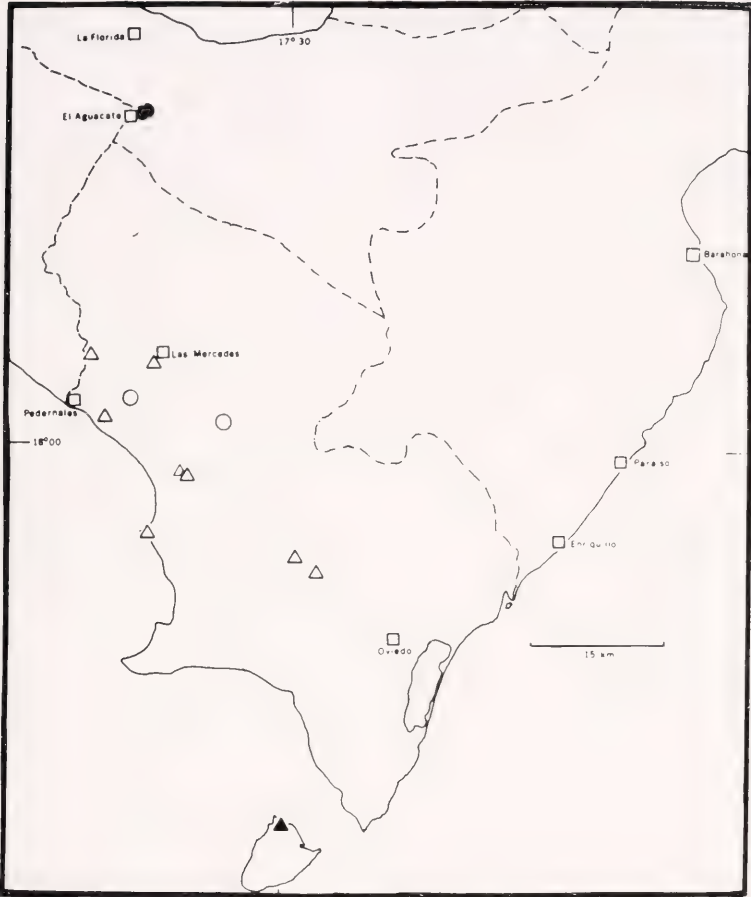
Figure 1. Map of the Península de Barahona, República Dominicana, Hispaniola, and Isla Beata. Pertinent population centers are indicated by labeled squares. Known distributions are shown for the anoles *A. longitibialis* (triangles) and *A. strahmi* (circles). The distributions are further designated for *A. l. longitibialis* (solid triangle), *A. l. specuum* (hollow triangles), *A. s. strahmi* (solid circles), and *A. s. abditus* (hollow circles).

brown markings whereas the latter is tan to grayish tan with brown markings. Both are prominently marked dorsally with 4 dumbbells; however, in *A. l. specuum,* the first dumbbell is well developed laterally and open anteriorly to yield a large almost ocellus-like spot. The dewlap colors of the two species are extremely distinctive since no *A. l. specuum* is known that has the deep orange dewlap of *A. s. abditus.* One final feature serves to distinguish the two species in this area. *A. l. specuum* males most often have the throat immaculate as adults (one adult male is known with a streaked throat) whereas the throat is invariably patterned in *A. s. abditus* males. All *A. s. abditus* females have marked throats whereas the throats of *A. l. specuum* females are variable — from immaculate to streaked with dark brown.

Remarks. There are only two localities for *A. s. abditus.* The first is a ravine (the type locality) between the Pedernales-Oviedo road and the village of Las Mercedes. At about 2.5 km N of the main road, the dirt road to Las Mercedes passes (for about 1 km) through a shaded and broad ravine with reddish rocky natural cliffs on both sides. These cliffs are creviced and have solution holes, but are separated from the road itself by low talus slopes which extend some five to ten meters between the cliffs and the roadway. The flora of the ravine stands in strong contrast to the *Acacia*-cactus desert which surrounds it; the ravine is distinctly more mesic, with trees and an understory of grasses, herbs and *Bryophyllum.* At the time of our 1975 visit the outside desert was exceptionally parched whereas the ravine was modestly luxuriant and moist. The ravine is almost at sealevel but at its northern end the road begins the ascent of the lower front ranges of the Sierra de Baoruco on which the village of Las Mercedes lies. The second locality is on the Alcoa road between Cabo Rojo and Aceitillar; I have not visited the site but William E. Haas (*in litt.,* 22 October 1976) wrote that it is "up a path just past km 16 on the Alcoa truck road, and the habitat is somewhat different [from the type locality] and the physiography a bit more so."

At the time of our 29 July 1975 visit to the type locality, the lizards were scarce at 1300 hr. The sun was almost directly overhead and the ravine was hot although fairly well shaded. As the afternoon progressed, the lengthening shadows of the western wall began to fill the ravine and by 1530 hr the lizards were moderately abundant.

They inhabited crevices and solution holes in the cliff faces (much after the fashion of *A. s. strahmi*). One male was seen foraging at 1630 hr on a shrub adjacent (1 m) to the cliff and had a large caterpillar in its mouth when collected. Foraging thus involves securing food elsewhere than directly on the cliff face itself. A very small juvenile was dislodged from the basal rosette of a moderately sized dead sisal plant (*Agave*) on the cliff face but escaped without being collected. One behavorial incident is worthy of report: we pursued a large male along the cliff face and the lizard finally leaped to an isolated large (2 m diameter) boulder, ran across its top at full tilt and literally launched itself off the far side of the boulder onto the ground. Several minutes later the same lizard was collected within a few centimeters of the boulder's base, immobile in the grassy and herbaceous ground cover. Whether its immobility was traumatic or whether it was "hiding" in a very unusual situation is unknown. This is one of only two instances when *A. strahmi* was secured in any situation other than a clivicolous one (the other exception is the female *A. s. strahmi* on the dead stem near the cliff base at El Aguacate). As with *A. s. strahmi*, *A. s. abditus* is impressively "at home" on its cliff faces. It is very agile, and its camouflage, tendency to remain immobile when approached — relying upon its cryptic coloration, and its prompt recovery time, all are extremely similar to those features in the behavior of *A. s. strahmi*.

DISCUSSION

It seems obvious that *A. longitibialis* and *A. strahmi* form a compact and closely related duo of cybotoid anoles whose distribution centers upon the Península de Barahona. Although I am convinced that they represent two separate species rather than subspecies, the latter interpretation is not to be lightly dismissed. There are no absolute meristic characters which separate the two, and they are similar in many features, not the least of which is their predilection for cliffs and vertical rocky surfaces to which they are unquestionably adapted. If, however, *A. longitibialis* and *A. strahmi* are conspecific, the peninsular distribution of the latter is peculiar in that it seems to be in enclaves surrounded on both east and west by (or interdigitating with) *A. longitibialis*. This arrangement can be

interpreted as a mosaic, where one species (*A. longitibialis*) inhabits open and xeric cliff faces and the other (*A. strahmi*) inhabits shaded, more mesic, and less rigorous cliffs. The dewlap colors of the two species are very distinctive and since dewlap color in eye-minded anoles is so important in species recognition and territorial defense, the very fact of the striking color differences of dewlaps in these two taxa strongly suggests that they are indeed species. The situation here is not so complex as that between *A. cybotes* and *A. marcanoi* (Williams, 1975): in this case two unquestioned species without strong meristic differences but with distinctive and contrasting dewlap colors and different body patterns are sympatric and even rarely syntopic. In these two species, however, there appear to be subtle differences in habitat preference, and as Williams (1975:9) pointed out the "balance of power" between them in any particular area may be tenuous. The same situation may exist in the geographical and ecological relationships between *A. longitibialis* and *A. strahmi* on the peninsula but presently the differences seem more overt.

More puzzling is the occurrence of two subspecies of *A. strahmi* on the north and south slopes of the Sierra de Baoruco. This is coupled with the striking difference in elevations involved (near sea level, and between 854 and 900 m). The habitats of the two subspecies are comparable — generally creviced cliff faces or roadcuts which can be regarded as cliff-face surrogates. But the similarity ceases with this description. The ravine near Pedernales, although it transects an otherwise hostile and xeric area, has relatively luxuriant vegetation and is well shaded. The El Aguacate roadcut is open and exposed to direct sunlight (the same is true for localities where *A. longitibialis* has been taken on the peninsula itself) and the lizards seem to shun those sections of the roadcut that are heavily vegetated and overgrown. Even sections of the roadcut that are exposed and open often lack or have minimal populations of *A. strahmi*. The area is quite cool in the afternoon and cold at night. One explanation for the apparently precise niche occupied by *A. s. strahmi* may well be that, at such high elevations, insolation of cliff faces and lack of vegetational cover will determine the diurnal rhythm of these lizards. Cliffs, exposed or not, facing in directions where the sunlight will not reach them until rather late in the morning are unsuitable because of lack of time exposed to the

warming effect of the sun. In contrast, vegetationally covered cliffs, even those oriented to achieve maximum early insolation, are too protected by vegetation to allow the lizards a sufficient period of activity during each day.

The disjunct nature of the two subspecies of *A. strahmi* may be more an artifact than a reality. There are few suitable cliff faces readily attainable by road in this entire region. It seems likely that *A. strahmi* inhabits suitable habitats around the general periphery of the Sierra de Baoruco. Cliffs and roadcuts on the peninsula along the eastern edge of the mountains between Barahona and Enriquillo were searched casually. These cliffs are often at sea level but are well shaded and generally face east. We found both *A. cybotes* and *A. brevirostris* here but not *A. strahmi* or *A. longitibialis.* Such negative evidence is questionable at best, although we did not find *A. cybotes* syntopically on cliffs or roadcuts with either of the clivicolous species. However, *A. cybotes* does occur sympatrically (but not on cliffs) with *A. l. specuum* and both subspecies of *A. strahmi.* It is interesting to note that in those places where *A. cybotes* inhabits cliffs and roadcuts it is much less adapted for such habitats than are the two clivicolous species. When pressed *A. cybotes* is more likely to leave the cliff face and jump to the ground to seek refuge under adjacent ground cover than are *A. longitibialis* or *A. strahmi* which seek sanctuary in crevices or solution holes.

Geographically it seems likely that there are more or less discontinuous populations of *A. strahmi* scattered around the periphery of the Sierra de Baoruco (but not across its summit) and the lower eastern regions of the adjacent Haitian Massif de la Selle. Populations should be looked for on the bare roadcut-cliffs between Fond Parisien and Soliette and on the northern face of the La Selle in Haiti near the Dominico-Haitian border south of Fond Verrettes. Although these cliffs seem suitable (more for *A. s. abditus* than for *A. s. strahmi*), it may be that an appropriate habitat niche occurs in this region which will accommodate the latter subspecies. If *A. s. strahmi* did occur there at suitable elevations on the northern face of the Massif de la Selle, it may now be extirpated due to extreme modification of habitat (the region has been denuded of much vegetational cover).

A. longitibialis, on the other hand, presents a more familiar pattern. It is a Barahona Entrapment xerophile derived from

primarily mesophilic *A. cybotes* with which, under favored circumstances, it is still sympatric. From the peninsula it has invaded Isla Beata and differentiated on the subspecific level. A phyletic sequence between these three species might well be: widely distributed, ecologically tolerant but primarily mesophilic *A. cybotes* with a pale dewlap → xeric and cliff adapted *A. longitibialis* with a pale dewlap → clivicolous and more mesic adapted *A. strahmi* with a vividly colored dewlap limited to disjunct enclaves where its ecological requirements are rather precisely met.

Another possibility that should not be overlooked is that the four taxa involved (*longitibialis, specuum, strahmi, abditus*) should be regarded as separate species. Certainly they are isolated from each other (*longitibialis* is insular; *specuum* occurs on the Península de Barahona; *strahmi* and *abditus* occur to the north and south of the Sierra de Baoruco massif, respectively). Regarding them as species has much to recommend it, but I have taken the more conservative course that no external characteristics are sufficiently obvious to make one seriously consider that there are four species involved rather than two. However, skeletal or electrophoretic evidence might well prove differently.

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LIZARDS OF THE *SCELOPORUS ORCUTTI* COMPLEX OF THE CAPE REGION OF BAJA CALIFORNIA

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ABSTRACT. *Sceloporus orcutti licki* as hitherto defined is shown to embrace two cryptic species, neither of which is subspecific in relation to the allopatric *S. orcutti:* an arboreal species, *S. licki,* and a petricole, *S. hunsakeri* sp.n., from 3 mi. E of San Bartolo (holotype MVZ 73,570); both are restricted to the Cape region of Baja California. All three species, *S. orcutti, S. licki* and *S. hunsakeri* have identical $2n = 34$ (XY ♂) karyotype patterns, but differ in numerous other respects. In these three species, the most succinctly diagnostic character states are: presence of a dorsolateral light stripe in *S. licki* only, 59 or fewer dorsal scales plus femoral pores in most (96% of 27) *S. orcutti,* and 61 or more in most *S. hunsakeri* (98% of 61).

INTRODUCTION

Field work in 1969 indicated that the Cape Region of Baja California (the area south of the Isthmus of La Paz) is inhabited by three distinct species of *Sceloporus* which are broadly sympatric and frequently syntopic with one another (Figs. 1, 2). Two of the three species, *Sceloporus licki* Van Denburgh and a species we describe here, are sufficiently similar to one another and to *S. orcutti* Stejneger that Smith (1939) considered them variants of a single race, *S. orcutti licki.* However, Hall's discovery in 1969 that the *licki* variant was arboreal and the other petricolous prompted reexamination of material from Baja California Sur. Specimens of the unnamed taxon have been available in museums since 1890.

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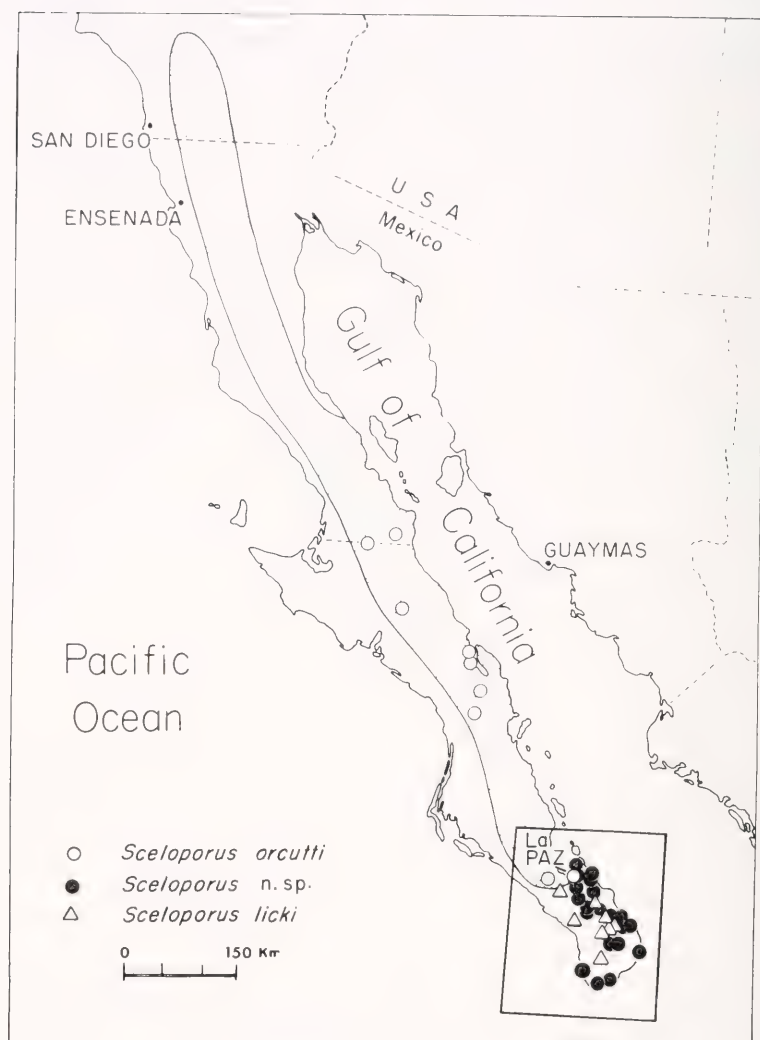University of Melbourne,
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Fig. 1. Distribution of the three species of the *Sceloporus orcutti* complex in Baja California.

Fig. 2.   Distribution of *Sceloporus hunsakeri, licki* and *orcutti* on or near the Cape region of Baja California.

Comparative material relevant to this problem has been examined from most of the major museums in the country. We are indebted to the curators and directors of these institutions. Cited specimens are referenced to collections by the following acronyms: CAS, California Academy of Sciences; CUM, University of Colorado Museum; LACM, Los Angeles County Museum; LMK, L. M. Klauber pers. coll.; LSJU, Leland Stanford Jr. Univ.; MCZ, Museum of Comparative Zoology, Harvard University; MVZ, Museum of Vertebrate Zoology, University of California, Berkeley; SDSNH, San Diego Society of Natural History Museum; UMMZ, University of Michigan Museum of Zoology; and USNM, U. S. National Museum of Natural History.

We name the newly recognized species for Dr. Don Hunsaker II, in recognition of his pioneering studies in the comparative ethology of the genus *Sceloporus* and for stimulating karyological study of its species by Hall.

Sceloporus hunsakeri, new species

Holotype: MVZ 73,570, adult male, tail complete, intact although fractured in two places in distal half, not regenerated, from 3 mi. E of San Bartolo ±500 ft., Feb. 17, 1960, R. G. Crippen, field no. 277.

Paratypes: Thirty-three, including eight topotypes, two of which were taken on the same date as the holotype (MVZ 73,572, 73,575) and six on March 14, 1960 (MVZ 73,579–84); two from 5 mi. SW of San José del Cabo, July 6, 1970, Richard L. Holland (CUM 45,880–1); two from Migriño, 33 mi. SSE of Todos Santos, July 5, 1969, RLH (CUM 40,779–80); one from ½ mi. N of Migriño, July 8, 1970, RLH (CUM 45,882); one from 1½ mi. N of Migriño, July 9, 1970, RLH (CUM 45,883); two from 7 km WNW of Buenavista, 100 m, Aug. 3, 1969, W. P. Hall (MCZ R1,222,413); one from bridge at Km 105.32 on Mex. Hwy. 1, Aug. 3, 1969, W. P. Hall (MCZ R122,242); one from Cabo San Lucas, Aug. 4, 1919, J. R. Slevin (MCZ 15,565); one from 2 mi. NW of Cabo San Lucas, P. Elias, M. Merrill, and J. Lazell, Jan. 29, 1972 (MCZ R131,704); one from Cabo San Lucas, Elias, Merrill and Lazell, Jan. 29, 1972 (MCZ R131,706); 10 from 6.4 mi. E of San Lucas, Playa Pública, T. Paul Maslin, Apr. 8, 1974 (CUM 51,401–10); and three from 6.5 mi. E of San Lucas, 300 ft., T. Paul Maslin, Apr. 9, 1974 (data from last 13 not included in tabulations herein). All of the type material is from

the Cape Region south and east of the Isthmus of La Paz in the territory of Baja California Sur, Mexico.

Other specimens examined. A total of 67, all from the Cape Region of Baja California Sur, Mexico, was examined only by Hall: Agua Caliente, 800 ft. (CAS 46,790–1, MVZ 11,709–11); 2.7 mi. W of Agua Caliente, El Chorro (LACM 18,880 2); Rancho Buena Vista (LACM 18,883); 4 mi. SE of Rancho Buena Vista, Cerro Agua Amargo, 23° 36′ N, 109° 37′ W (MVZ 50,070); Boca de la Sierra (CAS 91,457, LACM 18,879, SDSNH 30,188 9); Cabo San Lucas (CAS 16,532 3, 46,800–6, 46,808, SDSNH 32,903); 0.3 mi. SW of Cabo San Lucas (CAS 91,446); 7.7 mi. NE of Cabo San Lucas (CAS 91,319–20); El Triunfo (CAS 46,779, 46,823, 46,826–8); 1.3 mi. N of El Triunfo (CAS 91,476); La Paz (CAS 46,775, SDSNH 17,696 8); 10 mi S of La Paz (SDSNH 30,191 3); 12.4 mi. E of La Paz on road to Las Cruces (CAS 91,255); 12.9 mi. E of La Paz, Arroyo de los Pozos (CAS 91,367); 16 mi. E of La Paz (SDSNH 30,186); 19 mi. N of La Paz [N of Pichilinque Bay] (CAS 91,093); 19.5 mi. SE of La Paz, on road to Los Planes (CAS 91,105–6); 20 air mi. SE of La Paz, 1 mi. SW of La Trinchera (CAS 91,974–6); 21 mi. ESE of La Paz, 18.5 mi. from jct. road to Los Planes and La Paz airport road (CAS 91,222); Los Frailes (SDSNH 32,920); Bahia Los Frailes (CAS 15,739); 7 mi WNW of Los Planes near Lat. 24° (MVZ 73,587 8); Ojos Negros (USNM 37,675–6; San Antonio (CAS 46,830); San Bartolo (CAS 46,787, SDSNH 38,075); 1.1 mi. SE of San Bartolo (CAS 91,384–6); 3 mi. E of San Bartolo (CAS 90,972–5); 15 mi. S of San Bartolo (SDSNH 52,991). An additional 12, all young, were examined by both authors: seven topotypes, five of which were taken on the same date as the holotype (MVZ 73,571, 73,573–4, 73,576, and 73,578) and two on March 14, 1960 (MVZ 73,585–6); one from 2 mi. NW of Cabo San Lucas, Elias, Merrill and Lazell, Jan. 29, 1972 (MCZ R131,703); one from Cabo San Lucas, Elias, Merrill and Lazell, Jan. 29, 1972 (MCZ 131,705); and three from Boca de la Sierra, 2 mi. N of Miraflores, April 17, 1977, R. Seib (MVZ 144,800–2).

Diagnosis. A small (to 86 mm ♂, 71 ♀) member of the *spinosus* group of *Sceloporus* (as of Smith, 1939; Smith and Taylor, 1950), with supraoculars in a single row (undivided) rear two in contact with median head scales, no dorsal nuchal collar, dorsal scales 33–37 ($\bar{X}$ 35.1); femoral pores 12–18 (15.9); posterior supraocular usually (94%) in contact at least narrowly with a superciliary scale;

zero to 6 (1.9) supernumerary granules between supraoculars and superciliaries (i.e., granules in excess of a single row or parts thereof); internasals two only, rarely varying in number or position; subnasal usually (65.2%) present; preocular usually (72.3%) horizontally divided; scales between postparietals often (45.5%) four or five; number of single scales between subocular and supralabials often (64.6%) 2–4; preanal escutcheon scales 7–19; no evidence of continuous light lateral stripe in shoulder region; dark bars on throat of females and young usually not including a pair of central parallel lines; a central dark blue patch on throat in adult males; black patch on shoulder never containing a central light spot. The species is a petricole and has a $2n = 34$ karyotype.

Description of holotype. Four symmetrical postrostrals, laterals about $1\frac{1}{2}$ times as large as medial, squarish pair; a single lorilabial row contacting rostral between postrostrals and supralabials; no subnasal; two canthals; a large loreal separating 2nd canthal from lorilabials; latter in two rows posterior to middle of 1st canthal, except for interruption by one or two scales between rear of subocular and supralabials; latter 4–4 to below middle of eye; preocular divided; one enlarged, strongly keeled postocular in contact with subocular, upper postocular apparently destroyed by abrasion, others small, similar to temporals.

Two large, symmetrical internasals narrowly contacting 1st canthal, broadly contacting median pair of postrostrals and all three frontonasals; one small supranasal; two minute postnasals; median frontonasal somewhat larger than lateral frontonasals; two prefrontals, each intermediate in size between lateral and medial frontonasals, broadly in contact medially; frontal divided, posterior section 2/3 size of anterior, narrowly contacting interparietal; one large frontoparietal on each side, 1/2–2/3 size of posterior section of frontal; interparietal large, about as broad as long, widest posteriorly; a large parietal on each side, each about 3/5 size of interparietal; a well defined postparietal on each side, each over twice as wide as long, separated medially by 4 scales, narrowly contacting interparietal on one side only.

Supraoculars 5–5, undivided, anterior three separated from median head scales by a single row of small scales contacting posterior canthal, posterior two broadly in contact with parietal and inter-

parietal; four strongly imbricate superciliaries as seen from above, two more subimposed under junction of 3rd and 4th dorsal superciliaries; one row of small scales extending from rear edge of 1st superciliary (or very near it) posteriorly between all supraoculars and superciliaries except at posterior extremity, where 5th supraocular directly contacts (for about 3/5 of its length) rear superciliary; 2–2 small supernumerary scales (over and above one continuous row) in the area between supraoculars and superciliaries.

Auricular lobules 4–4 directly over ear opening, upper longest, next one broadest, lower one smallest and scarcely protruding over tympanum.

Infralabials 5–5 to below middle of eye; three pairs of postmentals, members of anterior pair in contact medially, those of 2nd separated by two scales, of 3rd by four; labiomental row separating postmentals and infralabials, except for one anterior scale in each series, allowing broad contact of 1st postmental and 1st infralabial; gulars all smooth and with a single apical notch, except below ear, where a faint keel and two notches separated by a median mucrone are present on a few scales.

Dorsal scales strongly keeled, strongly mucronate, in vertebral region more acutely pointed and with fewer and shallower notches and shorter accessory mucrones than in more lateral regions, in obliquely converging rows, 33 in least count from interparietal to level of rear edge of thighs held at right angles to trunk. Ventrals smooth, with a single apical notch except at sides, where they blend with lateral scales. Femoral pores 16–17, the two series separated by six scales. Preanal scales similar to other ventrals, except for an escutcheon involving eight scales in two transverse series near posterior edge of preanal area; escutcheon scales thickened, smooth-edged, not notched, somewhat similar to femoral pore scales but the glandular (?) area spread over the entire exposed surface, not restricted to one area, and not so deeply penetrant. A deep lateral nuchal pocket, without scales; no axillary or postfemoral pocket.

Scales on limbs are smaller in general than those on body, but otherwise grossly similar; scales on rear of thighs as large as scales preceding femoral pores, but mucronate, keeled and with accessory mucrones and notches; lamellar formula for fingers 9–12–16–17–12 (9–13–16–17–12) and for toes 8–12–17–20–15 (8–12–17–20–14).

Snout-vent 78 mm; tail 117 mm; snout-posterior margin of ear
opening 18 mm; maximum width of head, at ear level, 17 mm;
foreleg 32 mm; hind leg 49 mm; 4th toe from base of 5th, 20.5 mm.

In preservatives, color more or less uniform dark tan above, with
no markings except an iridescent bluish streak on some scales,
especially along keel; foreleg with weak crossbands, more conspicu-
ous distally; head somewhat lighter than trunk; tail with dim darker
brown bands, most distinct medially.

Melanization of ventral surfaces nearly but not quite complete,
with a light chin blending with a darker infralabial pigmentation
crossed by a few narrow diagonal light lines; central and entire rear
area of throat black with dark blue lateral highlights; black on
throat extending onto anterior chest area, but light areas remaining
in central lateral chest areas at level of axillae; throat color
extending dorsad as a shoulder patch, light margined (one scale
wide) posteriorly, entering lateral nuchal pocket anteriorly but not
passing beyond it; light posterior margin crossing arm insertion; no
light areas within shoulder patch. Sides of belly dark mauve,
blending with a broad black median border shot with dark iri-
descent blue areas; lateral belly patches not fully confluent medially
or with gular patch, although limited continuity exists in both areas;
black in groin continuous with belly patches but rear half of ventral
surfaces of thighs largely light; preanal area entirely light.

Variation. The 33 specimens in the type-series have 33–37 dorsals
(33, five; 34, six; 35, five; 36, thirteen; 37, four) with a mean of 35.1.
The range in the counts taken by Hall for the "other specimens" is
considerably greater (range 31–41; 31, one; 33, four; 34, three; 35,
nine; 36, eleven; 37, eighteen; 38, ten; 39, seven; 41, one) and the
mean 36.3 is also greater. The counts by Hall were taken at various
times under less controlled conditions and include several partially
decornified specimens which are difficult to count accurately be-
cause the underlying scales are very soft, easily distorted and
difficult to discern. Specimens reexamined by Smith with few
exceptions have 1–3 fewer dorsals than Hall originally counted.
Nevertheless we regard older counts that cannot now be rechecked
as useful indicators of a somewhat greater range than is represented
in the relatively small type-series.

The femoral pore counts taken by both authors are essentially
identical and our pooled results yield a range of variation in 169

counts from 12 to 18 (12, one; 13, five; 14, sixteen; 15, thirty-five; 16, fifty-eight; 17, forty-three; 18, eleven) with a mean of 15.9. There is no significant difference between counts in the two sexes (males, N = 98, 13–18, $\bar{X}$ 15.89; females N = 58, 12–18, $\bar{X}$ 15.84; 13 counts not allocated to sex, 13–17, $\bar{X}$ 15.84).

Head scale characters were recorded only for the 33 individuals of the type-series. In 66 counts on the contact of rear supraocular with a superciliary, only 4 (1.6%) had the rear supraoculars separated from the superciliaries (the first supraocular is in broad contact with the first superciliary in all). The supernumerary scales vary from 1 to 6 (0, nine; 1, seventeen; 2, twenty-one; 3, ten; 4, four; 5, three; 6, one) with a mean of 1.9.

The variation in other head scales, including very small scales, is exceptionally limited. The scales in the internasal area are especially constant relative to the variation occurring in most *Sceloporus*. All scales are as described for the holotype except: separate postrostrals four in 30, two in 1, five in 1, median pair fused with the supranasals on each side in 1, one pair of large internasals in 32, three in 1; internasals contacting anterior canthal on both sides in 21, separated by a separate small scale on both sides of two, on one side in four, by contact of a postnasal and lateral frontonasal on both sides of three, on one side in one, and in one specimen by a postnasal-lateral frontonasal contact on one side and by a separate small scale on the other. The internasals always contact the postrostrals (although the central two postrostrals are fused with the supranasals in one specimen) and frontonasals, so that always there are two scales in a straight median (or closely paramedian) line between median frontonasal and rostral. Subnasal present on both sides in 20, on one side in three, on neither side in 10; preocular horizontally divided on both sides in 21, on one side in four, on neither side in seven (indeterminate on one side in one, divided on other); postnasals 2–2 in nine, 2–3 in nine, 3–3 in 14, 4–4 in one; scales between postparietals two in two, three in 16, four in 11, five in four; postparietals contact interparietal on both sides in 29, on one side in three, on neither side in one; two enlarged, keeled postoculars in all; number of single scales contacting both subocular and supralabials 0–4 (59 counts: 0, three; 1, twenty; 2, twenty-three; 3, seventeen; 4, two); 1st canthal failing to contact lorilabials only on one side of one (lower edge split off as a separate scale); two frontoparietals on one

side in five, all others with 1-1; scales of 1st pair of chinshelds separated by one scale in one, of 2nd pair by three scales in two, and by two in 31, of 3rd pair by four (14), five (18), or six (1) scales; frontal divided into three scales in one, into four in one (in the latter, the anterior of three transverse divisions is split into right and left components).

All mature males possess a clearly defined preanal escutcheon, each scale of which contains a light colored flaky tissue surrounded by a narrow border of cornified black pigmented tissue. Scales in the center of the escutcheon are more strongly modified than those towards the margin. The structure is also discernible in females and young by scale thickness and the lack of an apical notch, but the modified scales can be reliably counted only in the adult males. In 11 such individuals from the type-series, counts range from 8 to 14 (8, two; 9, two; 10, three; 11, two; 13, one; 14, one) with a mean 9.3. In 33 comparable specimens examined only by Hall, the range is 7 to 19 with a mean of 12.5 (see Comparisons for details). All counts are more or less subjective, as frequently several scales are only partially modified to various degrees.

In live, fully melanistic males (68 mm s-v and larger, as recorded in color photographs taken in the lab, within a week of capture, when the animals were at or near optimum temperature), the central gular, chest, preanal, shoulder and shank areas are black, the lateral belly patches distinctly navy blue; four to five iridescent green diagonal stripes one to two scales wide divide the blue belly patches into darker ventral chevrons, each about three scales wide. The underside of the tail is abruptly lighter than the trunk and only faintly dusky. The underside of the foreleg, chin and infralabial areas are darker, and some evidence of narrow light bars is present on the lower lips and chin. Dorsally, the basic body color is an iridescent greenish bronze to light metallic green which grades to a slaty, metallic blue or purple along middorsum from between shoulders to over the tail base. This darker area is about seven to eight scales wide at the widest and grades into the lighter ground color rather than being sharply differentiated from it. In no specimen is there a light central spot in the shoulder patch.

Adult females and subadult males are light brown to dark greenish brown or slate above, with scattered scales exhibiting an

iridescent bluish apex; lips, tail and limbs barred, more strongly on distal parts. In both sexes, 3 4 dark bars separated by lighter stripes radiate from the eye on sides of the head. A black shoulder patch is always present, light-bordered both anteriorly and posteriorly in the young. In older animals of both sexes the anterior light border becomes obscured by encroachment of black, whereas the posterior border remains intact and distinct in all specimens. Typically the upper and lower extremities of the anterior border persist for a time as isolated light spots, and in due time only the lower persists, sometimes completely enclosed by black. In mature adults even that disappears completely. In no developmental stage is there ever a central light spot within the shoulder patch. Very small individuals show about 11 transverse rows of small, obscure, dark brown spots, larger and more distinct paravertebrally, on the trunk; the series continues onto the tail. This pattern soon fades with maturity, although the row of spots at shoulder level becomes briefly accentuated and weakly collarlike, before it becomes obscured by the general darkening of the dorsal surfaces; adult females may retain vestiges of the collarlike marking but it is completely indiscernible in adult males.

On ventral surfaces, the dark gular bars are bluish, and faint bluish belly patches shading laterally to tan are visible in mature females. The medial borders of the belly patches are comparatively dark but still considerably fainter than the gular bars. The patches are separated by about five to seven scale rows along the midline.

In all young specimens the throat, chin and lower lips are whitish but prominently barred, the dark lines twice as wide as the intervening spaces and converging toward the rear center of the throat. These markings persist throughout life, except that in mature males they are extensively obscured by the black area expanding from the rear center of the throat. The throat bars seldom form parallel lines on midthroat.

One adult male *S. hunsakeri* from the paratypic series had a karyotype (MCZ Karyology catalog no. Y14,683, main catalog no. MCZ R122,241) of 34 chromosomes in the typical primitive pattern for sceloporines (Paull et al. 1976). *S. licki* and *S. orcutti* have the same chromosome number (Cole 1970, Hall 1973, in prep.). The karyotyped male *S. hunsakeri* was collected while actively involved

in territorial defense and was maintained in the lab with a female *S. hunsakeri* and several *S. licki* for seven weeks before being sacrificed for karyology. The male was frequently seen courting the female throughout this time. He paid no attention to the *S. licki* housed in the same cage. When karyotyped, his testes still showed active spermatogenesis, with high frequencies of spermatogonial mitoses, meiotic prophases, second metaphases and maturing spermatids. We conclude from this that the male was sexually active at least from the period of collection, 3 Aug. 1969, through 24 Sept., when it was karyotyped.

Ecologically, *S. hunsakeri* appears to be a strict petricole and extremely wary. Many were observed 2 3 August 1969, when Hall was collecting in the Cape region of Baja California, but except for the two male *S. hunsakeri* collected while actively displaying to one another and a female trapped under a small bridge, all took alarm at a distance many times the 2 m length of the noose pole. In most cases, just at the sight of the collector's vehicle, they escaped into deep crevices or under massive boulders. None were observed in alluvial or wooded areas lacking massive rock outcroppings. Essentially all collection localities recorded for *S. hunsakeri* are rocky.

Comparisons

Past consideration of *S. licki* as a subspecies of *S. orcutti* was a product of 1) the similarities of *S. hunsakeri* and *S. licki* in size and squamation; 2) the close parallelism of *S. hunsakeri* and *S. orcutti* in ecology and coloration; and 3) the near parapatry of *S. orcutti* and *S. hunsakeri*. To establish *S. hunsakeri* and reestablish *S. licki* as valid species we must show: 1) that the differences between *S. hunsakeri* and *S. licki* are sufficient to rule out the possibility that these are not simply different morphs of a polymorphic population (as Smith [1939] originally believed); and 2) that the differences between *S. hunsakeri* and *S. orcutti* are sufficient to indicate the probable existence of *intrinsic* barriers to gene flow between the two populations.

S. hunsakeri vs. *S. licki*. Although *licki* and *hunsakeri* are essentially identical in body and head proportions, in femoral pore and body scale counts, and in most cranial scale characters, other differences are of a degree and nature that cannot be accounted for by allelic differences at a small number of loci. Most of the

differences are summarized in Table 1. The most constant differences in scutellation pertain to the relation of the posterior supraocular to the superciliaries (Fig. 3), irregularities of internasals (Fig. 4) and the size of the escutcheon (Fig. 7). In *S. hunsakeri* the modified escutcheon scales are in two or more transverse rows, whereas in *S. licki* usually only one scale row is involved, with three to five scales fully modified and a couple more partially so (i.e., at least half of the scale surface modified). A few additional scales, not counted in the tabulated totals, may show slight modifications of the scale tip. Though in *S. hunsakeri* more scales are involved in the secretion, not all are as sharply differentiated from the surrounding normal scales. The developmental field controlling differentiation appears to have a much smoother gradient so that the scales at the anterior and lateral peripheries of the escutcheon are all only partially modified. Thus the counts of these scales for both *S. hunsakeri* and *S. orcutti*, which have similar developmental patterns for this character, are not precise. Some females and juveniles show

Fig. 3.   Contrast between *S. licki* (left, MVZ 144,803) and *S. hunsakeri* (right, MCZ R122,241) in number of supernumerary scales between superciliaries and supraoculars, and in contact of posterior supraocular with superciliaries (actual field length is 8.6 and 9.1 mm respectively). In 144,803, rear supraocular and superciliary are completely separated by small scales and five supernumeraries. In R122,241, rear supraocular contacts rear superciliary, and two supernumeraries present.

TABLE 1. COMPARISON OF *S. HUNSAKERI, S. LICKI* AND *S. ORCUTTI**

Character state	hunsakeri	licki	orcutti
Snout-vent length, max.	87 mm (85)	78 mm (8)	109 mm (28)
Posterior supraocular contacting superciliary	62(66) 94%	0(16) 0%	3(20) 15%
Supernumeraries between supraoculars & superciliaries**	0-6(1.9) (33)	0-6 (3.1) (16)	
Specimens with internasal scale deviations	1 (33)	6 (8)	9 (10)
Subnasal present	43(66) 65.2%	6(16) 37.5%	18(20) 90%
Preocular divided horizontally	47(65) 72.3%	2(16) 12.5%	—
Scales between postparietals	2-5(3.5) (33)	2-3(2.9) (8)	2-4(2.6) (10)
Single scales between subocular and supralabials	0-4(1.9) (65) (94.9% 1 or more)	0-2(0.8) (16)	0-1 + (23.8% 1 or more)
Scales in preanal escutcheon 65 mm + s-v ♂♂	7 19(11.7) (33)	4 7(4.6)	—
Frontoparietals separated	33(33) 100%		43(61) 70.5%
Adult ground color	♂ iridescent bronze-green to blue; ♀ dull, slaty dark green to brown	♂♀ rich tan to brown; ♂ overwashed bluish-purplish iridescence	diagonally cross-barred

Character state	hunsakeri	licki	orcutti
Dorsolateral stripe, light tan to cream	none	2 scales wide on neck, wider, less sharply defined toward pelvis	none
Black shoulder patch	no center spot; white rear border	white to iridescent blue center spot tan rear border	—
Gular pattern	bars; rarely parallel paramedian lines; ad. ♂♂ mostly or all black-suffused	bars; often parallel paramedian lines; never black-suffused	no black suffusion
Lateral belly patches ♂♂	fused with gular patches; darkest laterally or all dark	not fused; darkest medially	not fused; no black suffusion
Habitat	petricolous, low to intermediate altitude	arboricolous, intermediate to high altitude	petricolous
Reaction	very wary	easily approached	very wary

*Parenthetic figures means and total specimens (or sides) counted.
**The small scales exceeding 1 complete row.

some degree of modification of the preanal scales but never to the extent seen in the adult males. The appearance of the escutcheon strongly suggests an organ specialized for the secretion of a substance to be rubbed against the substrate as the vent is wiped across it. Since fully developed escutcheons are only found in reproductively mature males, the secretion may have a pheromonal function possibly involved in maintaining reproductive isolation.

The scale differences between the two species, though not conspicuous, are diverse and distinctive. However, differences are strikingly apparent in color pattern and appear to be completely diagnostic in living and preserved material (Fig. 5). Color observations are based on the entire series of preserved specimens examined by Hall, on color transparencies of live specimens of both sexes and on the preserved material available to both authors. One set of

Fig. 4. Contrast between *S. licki* (left, MVZ 144,803) and *S. hunsakeri* (right, MVZ 144,800) in structure of internasal area; actual field length 11.5 mm in each (in median line). In 144,803 three posterior internasals, two primary internasals, latter separated from first canthal on each side by tiny scale posterior to an upper (left) and 2nd (right) postnasal; the four postrostrals irregular; supranasal on each side relatively large, frontoparietals in contact. In 144,800, primary internasals the only internasals present, separated from first canthal on each side by contact of upper postnasal and lateral frontonasal; this symmetry is typical.

Fig. 5.   Contrast between young male (39.5 mm s-v) *S. licki* (left, MVZ 73,577) and young male (35.5 mm s-v) *S. hunsakeri* (right, MCZ R131,703) in pattern of throat bars; actual field length 16.0 and 16.5 mm respectively. Parallel paramedian lines pronounced in 73,577, visible throughout life in both sexes since males lack a central rear gular patch; in R131,703 the lines are largely oblique, scarcely parallel at any point, and are obscured in adult and subadult males by a rear central gular patch.

differences associated with overall ground coloration and patterning appears to be correlated with ecological differences between the species. The remaining differences all relate to specific body areas presumably used in social signaling and species recognition.

The body color below the dorsolateral light stripe also shows some patterning of slightly lighter vertically elongated spots in both sexes of *S. licki*. In the field, differences in basic ground coloration and the conspicuously visible dorsolateral stripes of *S. licki* allow the collector to distinguish between these two species from distances of many meters. These differences are correlated with the basic colors of the preferred substrates frequented by each species. The relatively dull and uniform pattern of *S. hunsakeri* is adaptive to its habitat on unpatterned rocks, whereas the *S. licki* pattern is equally as disruptive as the light and shadow on or under the trees that constitute the habitat for that species.

Other color differences are all associated with body structures presumably involved in social signaling and or species recognition.

The dark shoulder patch seems likely to serve as an orientation mark for lateral displays (Fig. 6). In *S. hunsakeri* it may be set off in front by a light line or series of spots in incompletely melanized individuals. Faint ventral patches are visible in females of both species, but unlike the contrast in males, they are more intense medially, with the median dark edges separated by several scale rows.

Although karyotypes of *S. hunsakeri, S. licki* and *S. orcutti* are identical (Cole 1970, Hall 1973, in prep.), there is evidence that the reproductive seasons of *S. licki* and *S. hunsakeri* differ. Two *licki* males were karyotyped, one six days after capture 6 August (MCZ original number Y18,801 = MCZ 136,188), the other about seven weeks after capture (MCZ original no. Y14,689 = MCZ R122,233). Both showed completely regressed testes, with the seminiferous tubules collapsed to a few mm^3 within the loose and shriveled tunica, only a few mitoses and no hint of sperm or any stage of meiosis. On the other hand, the *S. hunsakeri* male karyotyped after 7 weeks of captivity still showed very active spermatogenesis and
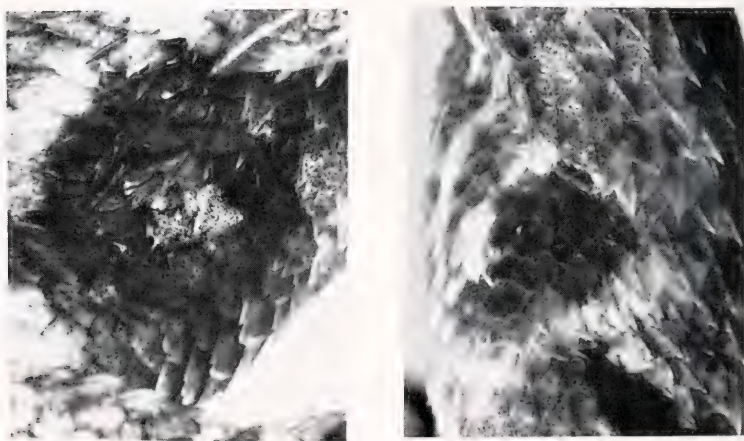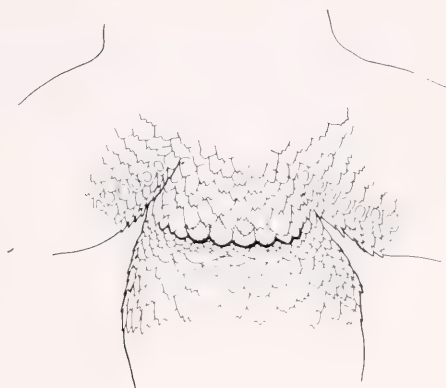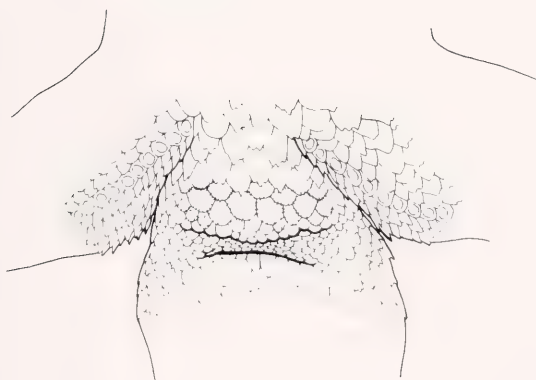

Fig. 6.   Contrast between young male (39.5 mm s-v) *S. licki* (left, MCZ 144,803) and a subadult male (61.5 mm s-v) *S. hunsakeri* (right, MCZ 73,575) in relation of dark shoulder patch to a central light spot; actual field length 5.8 and 12.0 mm respectively. A light dot, conspicuous in life but small here, within dark spot in *S. licki,* absent in *S. hunsakeri.*

Sceloporus licki
Paratype
CAS 1423

0 ⊢⊢⊢⊢⊢ 5 mm

Sceloporus n. sp.
CAS 46828

0 ⊢⊢⊢⊢⊢ 5 mm

Fig. 7.   Contrast between adult male *S. licki* (left, CAS 1,423) and adult male *S. hunsakeri* (right, CAS 46,829) showing development of preanal escutcheon scales. In *S. hunsakeri*, last row of preanals folded under and are not visible in illustration.

courtship behavior. The *S. licki* individuals held in the same cage with the *S. hunsakeri,* though apparently in good health, showed very little social or courtship behavior. Although this sample size is small, these observations along with the visual and pheromonal differences noted above, suggest these two species may have quite different reproductive seasons.

Therefore, although these two species are similar in most characters of proportion and squamation, they show many significant differences in other aspects of their biology, and we believe they should be considered genetically independent and ecologically differentiated sympatric species. Based only on these color pattern differences, even the oldest of the preserved specimens may be easily allocated to one or the other species.

S. hunsakeri vs. *S. orcutti.* It is evident that *S. hunsakeri* and *S. orcutti* occupy similar ecological niches characteristic of strict petricoles. They also have many aspects of coloration in common (e.g., see Smith, 1939). There is no evidence that their ranges contact, except for one *S. orcutti* and four *S. hunsakeri* with locality data of "La Paz" (which may only be a collecting headquarters). The Isthmus of La Paz is an alluvial outwash from the mountains to the south and is presumably of fairly recent origin. According to topographic maps of the area (Comisión Intersecretarial Coordinadora del Levantamiento de la Carta Geográfica de la República Mexicana, 1:500,000 scale, quadrangles 12R-VII, 12R-VIII, and 12Q-II), the maximum elevation of the divide across the Isthmus between the Pacific and Gulf slopes is less than 200 m. The depicted 200 m contour indicates that at least 20 km separates any area of the Cape over 200 m from any area of the Peninsula proper over 200 m. Except for the questionable specimens from "La Paz", there are no locality records for either *S. orcutti* or *S. hunsakeri* from this lowland. Papenfuss (person. commun.) has collected extensively in this area and he does not recall having observed *"orcutti"* or any potential *S. orcutti* habitat. Presumably *S. orcutti* and *S. hunsakeri* are dichopatric, although their ranges are close to each other (specimens with reliable localities are separated by about 40 km). In the absence of sympatry to assure that reproductive isolation exists, other criteria must be examined to determine the taxonomic status of these two isolated populations.

S. hunsakeri and *S. orcutti* differ conspicuously in morphology, unlike *S. hunsakeri* and *S. licki*. A considerable size difference and diagnostic scale characters are obvious from comparisons of Baja California Sur materials (Table 1). Northern *S. orcutti* reach an even larger size than this small sample indicates.

Head scales differ in percentages of given character states but not categorically in any character. The most constant distinction we discovered lies in complete separation of the rear supraocular from the rear superciliary in most (85%) *S. orcutti* and contact in most (94%) *S. hunsakeri*. Secondly, the internasal scales are quite irregular in number and/or position in *S. orcutti*, but are seldom unsymmetrical in *S. hunsakeri*. Thirdly, the major pair of internasals contacts the first canthals on neither side in ten *S. orcutti* and on 47 of 66 sides (71.2%) in *S. hunsakeri*. Lesser distinctions are noted in Table 1.

Finally, there is little overlap in either dorsal scale or total femoral pore counts for the two species. Dorsal scales for 28 southern peninsular *S. orcutti* examined by Hall range from 29 to 34 ($\bar{X}$ [±SEM] 31.77 ± 1.295) while 81 *S. hunsakeri* range from 31 to 43 ($\bar{X}$ 38.13 ± 1.884). The hypothesis of equivalency is rejected at the .005 level using the t test with 32 d.f. Total femoral pore counts range from 22 to 27 ($\bar{X}$ 23.83 ± 1.381) in 28 *S. orcutti*, whereas 84 *S. hunsakeri* range from 25 to 36 ($\bar{X}$ 31.56 ± 2.282) with equivalency rejected at the .005 level. A discriminant function can be generated from these data (Fig. 8) for 27 *S. orcutti* and 81 *S. hunsakeri* by adding the total femoral pore number to the dorsal scale count for each individual. This function separates all but two of the individuals examined. All *S. orcutti* except one have 59 or fewer dorsal scales plus femoral pores, whereas all but one *S. hunsakeri* have 61 or more. The mean value of the discriminant for 19 *S. hunsakeri* with localities within 32 km of La Paz (i.e., the Isthmus of La Paz) is 68.23 ± 2.96 compared with 68.03 ± 2.93 for all 81 *S. hunsakeri*. The four individuals from "La Paz" range from 69 to 71 with a mean of 70.0. Two *S. orcutti*, one from "La Paz" and one from 20 mi. W of La Paz are respectively 54 and 53, at the opposite end of the range of variation in *S. orcutti* from the values (60–74) for *S. hunsakeri*.

Color differences between the two species are completely diagnostic, insofar as we can compare them. *S. hunsakeri* does not
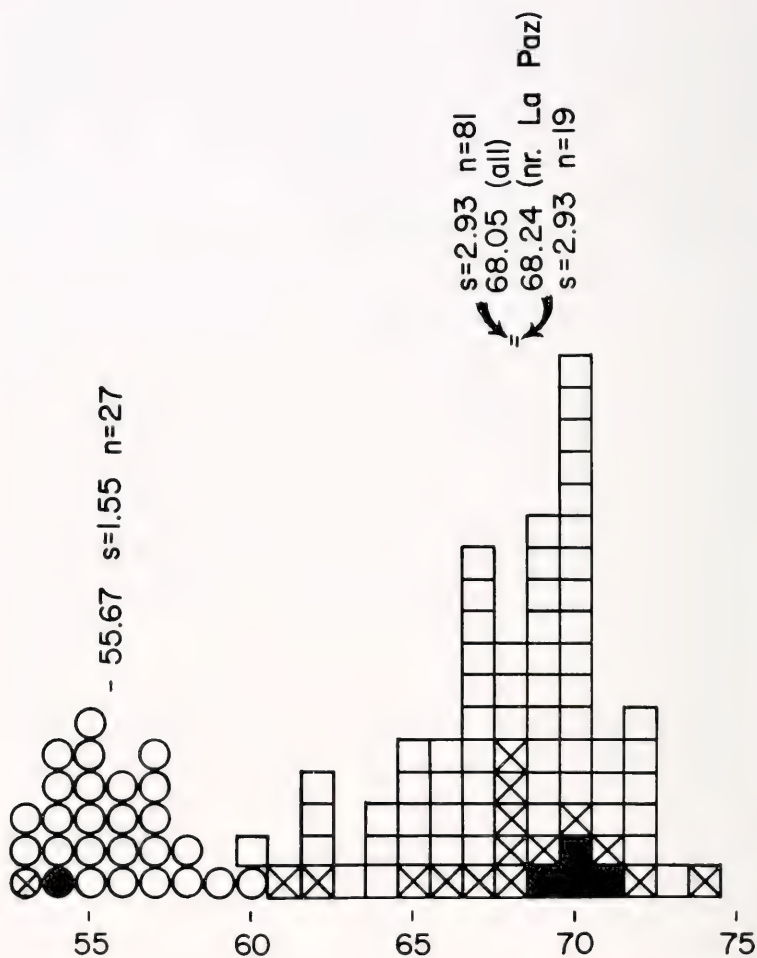
Fig. 8. Comparison of discriminant functions for *S. hunsakeri* and *S. orcutti* (most of the latter from Baja California Sur). *S. orcutti* specimens are indicated by circles, *S. hunsakeri* by squares. Solid symbols indicate specimens from "La Paz"; symbols containing an X indicate specimens with collection localities within 20 miles of La Paz.

possess the distinctive, narrow diagonal crossbars on both dorsal and ventral surfaces so conspicuous in northern *S. orcutti.* The barring, extensively obscured in adult *S. orcutti,* persists at least on the sides of the body in the largest specimens. Other differences are noted in Table 1. Southern *S. orcutti* appear to maintain these distinctions, although we do not now have substantial recent material to support this contention.

Clearly these data do not provide evidence for past or present introgression between the distinctly larger, larger-scaled *S. orcutti* and the smaller, smaller-scaled *S. hunsakeri.* To conclude this comparison we are left with the problem of assessing the taxonomic level of difference between populations which are and have been geographically separated. Our experience with the genus leads us to regard the observed differences as a strong indicator that the two taxa would be genetically isolated if they were in contact either through parapatry or sympatry, and therefore that *S. hunsakeri* should be recognized as a full species, rather than as a subspecies.

S. licki vs. *S. orcutti.* *S. licki* would never have been closely compared with *S. orcutti* if it had not been for the confusion of *S. licki* and *S. hunsakeri* from the very outset (see next paragraph), perpetuated by Smith (1939). Early workers referred or compared material representing *S. licki* to *S. undulatus consobrinus* apparently because of similarities in pattern observed also by Hall. Yarrow (1883:61) and Belding (1887:98) so identified materials taken in 1882 at "La Paz" by Belding, and Van Denburgh's (1895) primary comparison of *S. licki* was with *S. consobrinus.* That association does not now seem rational since the closest relatives of *S. licki* certainly occur in more nearly adjacent territories.

General comments on the S. orcutti complex

A single paratype of *S. licki* was recorded in Van Denburgh's description (1895:114) from San José del Cabo, taken Sept. 16, 1890, by W. E. Bryant. Given the probable lack of *S. licki* habitat there and the verified presence of *S. hunsakeri* in later collections, the Bryant specimen was probably the earliest acquisition of *S. hunsakeri.* Van Denburgh also recorded a dark central gular patch in one male of his Miraflores series (1895:112; 1922:357); that

specimen must likewise represent *S. hunsakeri,* since later collec-
tions from Miraflores confirm that both *S. hunsakeri* and *S. licki*
are present in the vicinity.

Unfortunately, the California Academy of Sciences collection
(including the *S. licki* type and all but three paratypes distributed to
other museums) was destroyed in the San Francisco earthquake and
fire. Nevertheless, Van Denburgh's type-description referred to the
striped form, which he clearly differentiated from *S. orcutti* by its
smaller and more sharply keeled ("rougher") dorsal scales, from *S.
magister* and *S. zosteromus* by smaller and more mucronate scales,
and from all of these species by color pattern. Each of the three
surviving *licki* paratypes is clearly the striped morph. Two paratypes
entered in the Stanford University collection at the time of the fire
have since been returned to the California Academy of Science. One
of these was designated by Smith (1939) as a neotype under its
Stanford University tag number (neotype: CAS 1423 = LSJU
2987a; when seen by Hall, both tags were still on the specimen). The
other specimen from this series is CAS 1426 = LSJU 2988. The third
paratype is from the Miraflores series, and is in the U.S. National
Museum of Natural History (USNM 23,749).

Stejneger (1893) described *S. orcutti* from USNM 16,330, from
Milquatay Valley, San Diego County, California, collected by C. R.
Orcutt. In reference to the type-locality it may be of interest to
record that the bottle containing the holotype also contains a rather
fragile note dated Aug. 14, 1934, signed by L. M. Klauber. We quote
it here to insure against loss of the information it contains: "Orcutt
once told me that the 'Milquatay' referred to was the flat just east of
Campo, San Diego Co., Calif. Milquatay is said to mean wheat field
in Indian, and almost any flat was known as Milquatay. The town
of Guatay (or Quatay) is not the type locality of *orcutti.*"

The preanal escutcheon of *S. hunsakeri* and *S. licki* discussed in
the preceding account occurs in *S. orcutti* and several other species
of the *S. spinosus* group as well. The development of the escutcheon
in *S. orcutti* is very similar to the pattern seen in *S. hunsakeri.*
However, its histology, functions, distribution in other species, and
general taxonomic value remain to be explored.

Dr. George Gorman and his students at UCLA have recently
begun a survey of the electrophoretic variability of the Baja
California *Sceloporus.* They inform us (person. commun.) that

genetic distances between representatives of *S. orcutti, S. licki,* and *S. hunsakeri* are all consistent with our separation of these populations at the specific level. They also report that there appears to be electrophoretic evidence suggesting that even *S. orcutti* as we have restricted its definition may be polytypic. However, we see no supportive external morphological evidence.

Given the many taxonomic problems involved in classifying allopatric populations, we do not here make any formal attempt to allocate *S. orcutti* complex populations on the Gulf of California islands to any of the three peninsular species. This cannot be done definitively until information on the biochemical genetics of both mainland and insular populations is more complete, although external morphology and coloration will yield preliminary indications. Prior to such examination, we suggest that the Espiritu Santo and Ballena island populations may be provisionally classified with *S. hunsakeri* (although some differences in coloration are evident), and that populations from the more northern islands be grouped with *S. orcutti.*

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APPENDIX

ADDITIONAL SPECIMENS EXAMINED
(All from Baja California Sur, Mexico, unless otherwise noted.)

Sceloporus licki. Neotype: Sierra San Lázaro (CAS 1,423 = LSJU 2,987). *Paratypes:* Sierra San Lázaro (CAS 1,426 = LSJU 2,988); Miraflores (USNM 23,749). *Other specimens:* Boca de la Sierra (LMK-SDSNH 30,187); 2 mi. NNW of Cerro San Antonio (SDSNH 53,136–43); El Sauce (=El Sauz), 4000 ft., Victoria Mts. (MVZ 11,702–08); Guamuchil Rancho (CAS 46,809); La Burrera (SDSNH 45,062–64, 53,132–35); Arroyo Palmellar, 6 mi. ENE of Rancho La Burrera (LACM 34,592–93); "La Paz" (USNM 53,392); 40 mi. S of La Paz, 2 mi. above El Valle Perdido (CAS 90,544, 90,558); Miraflores (USNM 64,472); nr. km 70, Mex. Hwy. 1, 8 km SE of San Antonio (MCZ 136,188); San Bartolo (CAS 46,780–1, 46,783–86; UMMZ 56,044; MVZ 144,809–13); 1.1 mi. SE of San Bartolo (CAS 91,383); 1.5 mi. E of San Bartolo, ±500 ft. (MVZ 73, 589); 3 mi. E of San Bartolo, ±500 ft. (MVZ 73,570).

Sceloporus orcutti. Holotype: California: San Diego Co., Milquatay Valley, 2500–2600 ft. elevation (USNM 16,330). *Paratypes:* Same locality (USNM 16,238, –29, 33, –34). *Other specimens:* 15 mi. S of Canipole (LMK-SDSNH); 43 mi. N of Canipole (LMK-SDSNH); Rancho Chenque (SDSNH 51,044–46); Coyote Bay, 13 mi. SE of Mulegé (MVZ 37,318); 12 mi. E of El Arco (SDSNH 17,471); La Paz (LMK-SDSNH 38,339); 20.0 mi. W of La Paz, ±500 ft. (MVZ 73,590); San Ignacio (MVZ 10,653, –54, –56, 13,597, –99; LMK-SDSNH 4,053, –54; UMMZ 76,482[2], 80,900); Misión Santa Gertrudis [Baja California Norte] (SDSNH 17,529–36).

B R E V I O R A

Museum of Comparative Zoology

THE LARGE PALAEOTRAGINE GIRAFFID, *PALAEOTRAGUS GERMAINI,* FROM LATE MIOCENE DEPOSITS OF LOTHAGAM HILL, KENYA

C. S. CHURCHER[1]

ABSTRACT. An isolated and slightly damaged left M[1] constitutes the first record of the species *P. germaini* in East Africa. This specimen matches in size and development of the buccal ribs and styles the upper molars of *P. germaini* from Oued el Hammam, Algeria.

An isolated and damaged left upper molar, probably M[1] (KNM-LT 414, field no. 138/67K), was collected by Dr. V. J. Maglio from Lothagam Hill, Kenya, in 1967. The tooth was found at Lothagam-I near the base of Member B (Patterson *et al.* 1970), and is deposited in the collections of the International Louis Leakey Memorial Institute for African Prehistory, Kenya National Museums, Nairobi.

The specimen (Fig. 1) is very slightly worn on the occlusal surface and derives from an immature individual. Minor damage has removed the mesial face of the crown, including the mesial half of the protocone, but the paracone is essentially entire. Slight damage to the distobuccal corner of the metacone has not destroyed the shape of the cusp or of the distobuccal wing of the hypoloph. Minor fragments of enamel are absent from the buccal surfaces of the apices of the paracone, metacone, and metastyle. The surface of the enamel is typically giraffid in its overall rugosity and thickness. The crown is tilted lingual on its roots in the anteroposterior (parasagittal) plane, and the roots tip distad. The mesial pair of roots is more damaged than the distal pair, all four roots are separate and are

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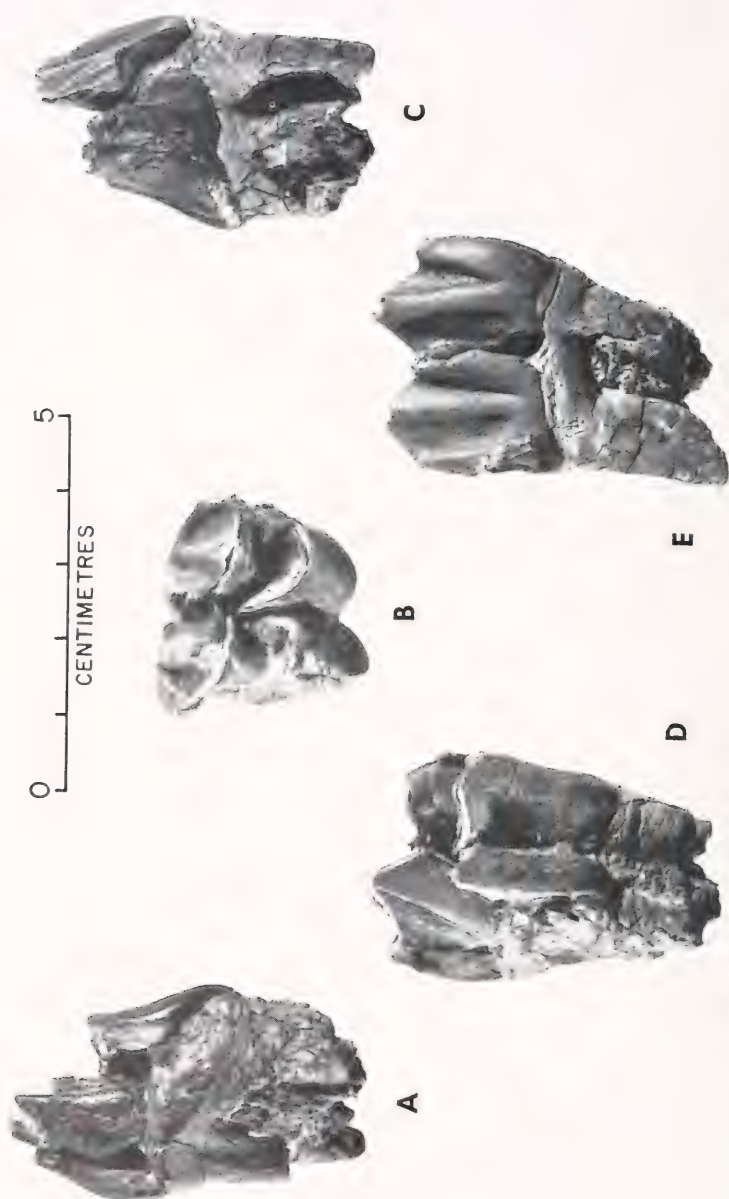
Figure 1. *Palaeotragus germaini*; left upper first or second molar from Lothagram-1, Kenya. A — mesial aspect; B — occlusal aspect with mesial towards A and buccal surface towards scale; C — distal aspect; D — lingual aspect; E — buccal aspect. A, C, D, and E are all oriented with roots nearest letters and crowns towards scale. Scale × 1, in cms.

round or oval in section. The exception is the distobuccal or metacone root which is grooved on its distal surface and crescentic in section.

The cusps are typically giraffid with tapered protocone and hypocone set buccally from the lingual cingulum. The paracone and metacone similarly are set lingually towards the mid-line of the crown. The buccolingual diameter over the mesial cusps (paracone and protocone) is greater than that over the distal cusps (metacone and hypocone). There is a well-developed median rib on the buccal surface of the metacone and a small pli is present distally in the postfossette on the wall of the hypoloph. A similarly located and formed pli, which is broken away, appears to have been present on the protoloph.

The specimen is attributed to *Palaeotragus germaini* Arambourg 1959 because of its similar size (Table 1) and because it matches well with Arambourg's (1959, Pls. XIV, XV) illustrations of first and second upper molars of that species (Fig. 2, A & B) from Oued el Hammam. The specimen resembles *P. germaini* in 1) the presence of strongly developed parastyles and mesostyles and 2) a strong rib on the buccal surface of the metacone of M^1, in the feeble junction of the paraloph and metaloph, and in the overlap of the mesostyle mesiobuccally to the distal end of the paraloph. Arambourg's specimens possess interlophar endostyles or pillars between the bases of the protocones and hypocones of the first and second molars. The Lothagam-1 specimen lacks any such endostyle. However, this structure is not always present in modern *Giraffa camelopardalis* (Fig. 2, F), *Okapia johnstoni,* or in fossil *P. primaevus* (Fig. 2, C; Churcher 1970, 1977). Therefore it cannot be considered a reliable diagnostic character. The specimen resembles *P. primaevus* in the presence of the metacone rib, and in the presence of plis on the buccal walis of the protocone and metacone. The specimen differs in that the ribs are more developed and the plis finer and directed mesiad rather than buccad as in *P. germaini* (Fig. 2, A & C).

The Lothagam tooth expresses the other characters ascribed to *P. germaini* by Arambourg (1959, 100-101), but many of these characters (e.g.˙ strong cingula or deep fossettes) are common to Giraffidae and are probably not diagnostic for species or genus.

The dimensions of the Lothagam *P. germaini* tooth fall within the ranges reported by Arambourg (1959) for M^1's of *P. germaini* from

Table 1. Comparative measurements of the first and second upper molars of *Palaeotragus germaini*, *P. primaevus*, *Samotherium sinense* and *S. neumayri* and of the upper molar from Lothagam-I. Measurements derived from illustrations are indicated by asterisks. All measurements are in mm.

	Lothagam-I, Kenya (KNM-I.T 414)	*Palaeotragus germaini* Oued el Hammam, Algeria. (Arambourg, 1959, p. 99; fig. 43.)		*Palaeotragus primaevus* Fort Ternan, Kenya. (Churcher, 1970, P. 23; Tab. III.)		*Samotherium sinense* China. (Bohlin, 1926, p. 55; Taf. VII.)		*Samotherium neumayri* China. (Arambourg, 1959, p. 99.)	
		M¹	M²	M¹	M²	M¹	M²	M¹	M²
Mesiodistal diameter over paracone-metacone	31.5	29–33.7	32.3–36	18.6–25.0	22e–28.0	39 or 40*	40 or 43*	34	40
Buccolingual diameter over cingula of paracone-protocone	30.3	27.5–32	30–34.2	19.7–23.2	22.1–25.5	43 or 42*	46 or 45*	38	42
Mesiodistal diameter over protocone-hypocone	26.6	27.5*	30*			37*	38*		
Buccolingual diameter over cingula of metacone-hypocone	27.1	27.0*	30*	18.4 22.3	21.7 24.0	43*	43*		
Buccal crown-height (reduced by wear)	25					22	30		

Oued el Hammam and marginally on or below the ranges for M²'s
(Table 1). In all instances, the measurements of the Lothagam tooth
are greater than any reported for *P. primaevus* from Fort Ternan
(Churcher, 1970), or for *Samotherium sinense* (Fig. 2, E) or *S.
neumayri* reported by Bohlin (1926) and Arambourg (1959) respec-
tively. (*S. sinense* is probably a junior synonym of *S. neumayri*
according to Erdbrink, 1976). The Lothagam specimen is assigned
to *Palaeotragus germaini* on the bases of both size and morphology.

Palaeotragus germaini was originally described by Arambourg
(1959) from Oued el Hammam or Bou Hanifa, Algeria. Churcher
(1978) assigned the large palaeotragines from Beni Mallal, Morocco
(Lavocat 1961), Bled ed Douarah, Tunisia (Robinson and Black
1974), and possibly Smendou, Algeria (Joleaud 1937) and Douaria,
Tunisia (Roman and Solignac 1934) also to this taxon. These North
African sites range from middle to late Miocene in age, with
Smendou and Douaria extending into early Pliocene times.

Arambourg (1959) described *P. germaini* as a large giraffid with
elongate neck and legs, and with the forelimb slightly longer than
the hind. The radius is longer than the tibia and the femur is short,
the metapodials are subequal, long, slender and laterally compressed
with subrectangular sections. Arambourg considered that *P. ger-
maini*'s upper molars were characterized by strong buccal walls,
interlophar endostyles, metacones separated from paracones, and
dep fossettes that are usually open lingually. He considered the teeth
to be strongly brachydont, but the tooth from Lothagam is not
more brachydont than teeth of similar size from modern *G.
camelopardalis* nor do his illustrations show teeth that are more
brachydont than that from Lothagam. The ossicones were consid-
ered to be long, supraorbitally placed, subtriangular in section and
oriented posterodorsally over the middle region of the skull. The
single ossicone known from Oued el Hamman is proportionately
smaller than those of *Samotherium* and is similar to those of other
species of *Palaeotragus*.

Arambourg described the Oued el Hammal skeletal material as
larger than that of other *Palaeotragus* species, similar in robustness
to that of *Samotherium,* and intermediate in size between that of
Samotherium and *Giraffa*. He considered that *P. germaini* exhibited
a parallel evolution separate from *Giraffa* or *Samotherium,* and its
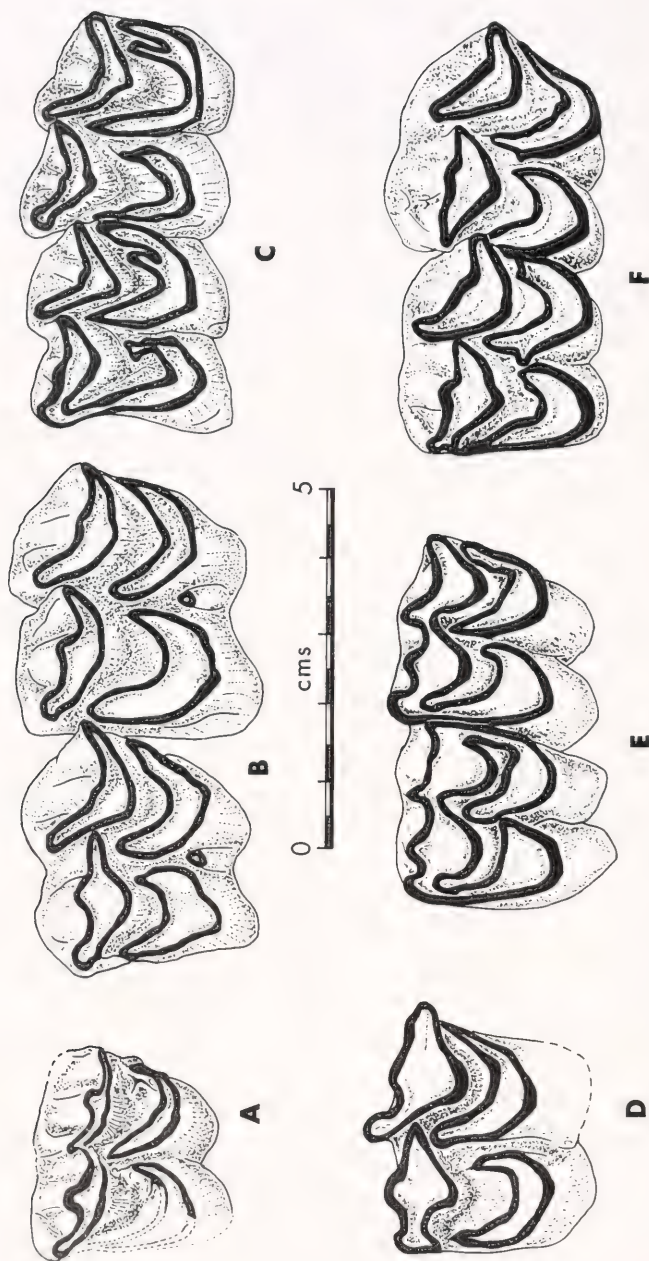lineage would thus be separate from those of the Giraffinae or

Figure 2. Occlusal patterns of first and second upper molars of selected Giraffidae. A — left M^1 of *Palaeotragus germaini* from Lothagam, Kenya; B — left M^1 of *Palaeotragus germaini* from Oued el Hammam, Algeria, redrawn from Arambourg (1959, Pl. XIV, fig. 1a); C — left M^{1-2} of *Palaeotragus primaevus* from Fort Ternan, Kenya, redrawn from Churcher (1970, p. 18, fig. 5) and cast of Kenya National Museum specimen FT 62 2700; D — right M^1 or M^2, reversed, of *Samotherium* sp. from Nakali, Kenya, drawn from Aguirre and Leakey (1974, p. 222, fig. 5); E — right M^{1-2}, reversed, of *Samotherium sinense*, redrawn from Bohlin (1926), Taf. VII, fig. 1); and F — left M^{1-2} of *Giraffa camelopardalis*, drawn from a recent specimen in the Royal Ontario Museum, Toronto, Canada. Scale in centimeters.

Sivatheriinae and would represent the more progressive and larger Palaeotraginae (Churcher 1978, Fig. 9). Arambourg assigned the Qued el Hammam giraffid to *Palaeotragus* on the proportions of the limbs, especially the elements of the hind limb. However, the characters of the molar teeth also place the taxon within the genus *Palaeotragus* rather than any other genus of the Giraffidae.

P. germaini was known previously only from North African sites of middle to late Miocene age, or possibly early Pliocene age. The Lothagam-1 late Miocene tooth represents the first East African record of the species. Some confusion may exist between some of the reported occurrences of *Samotherium* in Africa and *P. germaini*, especially when dental material is absent. The cervical vertebrae and two crushed ossicones from Fort Ternan that were assigned to *Samotherium africanum* by Churcher (1970) may in fact represent *P. germaini* or a form ancestral to it, since these ossicones are not excessively large and the single ossicone from Oued el Hammam cannot be considered necessarily typical. The identification of *Samotherium* by Aguirre and Leakey (1974) from the Nakali Tuffs of the Ngorora Formation, Kenya, suggests that both genera were present in East Africa during the late early to late Miocene. Their determination is founded on an isloated first or second upper molar (Fig. 2, D) which possesses a strong parastyle and mesostyle, a strong paracone rib, and reduced cingulum and metacone rib, which are all features of *Samotherium*.

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B R E V I O R A

Museum of Comparative Zoology

EVOLUTION OF LIFE HISTORIES: A COMPARISON OF *ANOLIS* LIZARDS FROM MATCHED ISLAND AND MAINLAND HABITATS

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ABSTRACT. Faunal comparisons between islands in the West Indies and the South and Central American mainland suggest that *Anolis* lizards play very different trophic roles in these two regions. Island anoles, with few predators, appear to be food limited relative to the heavily preyed upon mainland species. Theoretical considerations of species living under different competitive regimes suggest that island and mainland anoles should have evolved major differences in their life histories.

In order to evaluate the evolution of life history in the genus *Anolis,* I consider the degree of food limitation for anoles in comparable island and mainland habitats, the life history consequences of different selective regimes, and the correlation between observed life histories and theoretical expectations. Food availability on island and mainland sites was assessed from determinations of the standing crop of arthropods relative to the standing crop of anoles. A more direct assessment was accomplished by evaluating growth rates of *Anolis* juveniles. Both comparisons indicate that island anoles are food limited relative to mainland counterparts. Island anoles exhibit delayed maturity, long adult survivorship, large adult size, high sexual dimorphism ratios, and probably low reproductive effort in comparison with mainland anoles of similar size. For the most part, observed life histories fit the predictions based on current life history theory. However, for a given population, maximum body size, sexual dimorphism ratios, and offspring size are relatively invariant in expression. On the other hand, growth rate, rate of egg production, and age at sexual maturity vary as a function of food availability.

INTRODUCTION

In this paper I evaluate the effects of the competitive milieu on evolution of life history in the lizard genus *Anolis*. Various observations suggest the island and mainland members of this large group

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differ in the way that their populations are regulated. Anoles of the South and Central American mainland have numerous competitors for their insect prey and also have many predators; these anoles play minor roles in the middle levels of their complex food webs (Rand and Humphrey, 1968). On the other hand, anoles of the West Indies have few competitors or predators. There are fewer species of birds on these islands than in comparable mainland habitats and many types of insectivorous and lizard-eating birds are totally absent. These missing species include motmots, antbirds, woodhewers, ovenbirds, and puffbirds (Bond, 1971). Moreover, West Indian bird faunas do not exhibit density increases as a result of fewer species; density of insectivorous birds is lower in the West Indies than in comparable mainland habitats (Recher, 1970; Terborgh, pers. comm.). At a given West Indian site there tend to be fewer species of frogs (possible competitors for small insect prey) and snakes (possible predators on lizards) than at a comparable mainland site. The number of lizard species is also often lower than on the mainland (Rand, 1961; Schwartz and Thomas, 1975). Army ants which compete with anoles on the mainland have never reached the West Indies. It is this poverty of potential competitors that allows Williams (1972) to conclude that competition among West Indian anoles is, for all practical purposes, intrageneric.

Trophic level differences suggest that island anoles, with few predators, may be food limited relative to the heavily preyed upon mainland species (Slobodkin et al. 1967; Wiegert and Owen, 1971). Recent theory predicts that such differences in mode of population regulation might have profound effects on *Anolis* life histories (MacArthur and Wilson, 1967; Gadgil and Bossert, 1970; Gadgil and Solbrig, 1972; Pianka, 1970, 1972).

The effect of the competitive milieu on the allocation and utilization of energy result in the predictions listed in Table 1. Heightened competition in saturated environments will either 1) reduce the overall amount of energy that an organism can gather per unit time or 2) force changes in the allocation of time and energy devoted to conflicting demands, or both will occur (Pianka, 1972). The consequences of this are important. The absolute amount of energy that can be used for reproduction is reduced. Thus a relatively low reproductive effort is predicted for populations in saturated environments. Moreover, selection will usually favor

Table 1.   Predictions of relative differences in life history between island and mainland *Anolis* lizards.

		ISLAND ANOLES: Food Limited	MAINLAND ANOLES: Not Food Limited
1.	Reproductive effort	Low	High
2.	Sexual maturity	Late	Early
3.	Relative size of offspring	Large	Small
4.	Size	Large	Small
5.	Sexual dimorphism in size	High	Low

individuals with attributes that make them successful in competitive situations. In *Anolis,* selection for large size can be expected to be particularly efficacious because larger individuals are usually dominant over smaller individuals in competition for space, which provides an advantage for obtaining food and mates (Rand, 1967; Trivers, 1976). Sexual dimorphism in size is a means by which competition for food between male and female *Anolis* is reduced (Schoener, 1967). High sexual dimorphism ratios are expected when competition is intense. Since juveniles fare poorly in competition with established adults, selection should favor long adult life with reproduction occurring in more than one breeding season (Murphy, 1968). Tinkle et al. (1970) predict that lizards living in saturated environments will have relatively large eggs and hatchlings because of the relationship between size and competitive ability. In sum, island anoles should be K-selected in the sense of MacArthur and Wilson (1967).

On the other hand, if mainland anoles are generally limited by their predators, they should be r-selected relative to island anoles that are limited by food resources (Pianka, 1970, 1972). Because the risk of death is high for all age classes of mainland anoles, fitness is maximized by high reproductive effort. Attributes that maximize present reproduction will be favored by selection because the chance of future reproduction is small. Because age at first reproduction and size are closely and positively related (Fenchel, 1974), selection for early reproduction (which is the most effective way to increase r) will parallel selection for small adult body size.

In order to evaluate the evolution of life history in the genus *Anolis,* I have considered three main questions: Are island anoles food limited relative to mainland anoles? If so, what have been the

life history consequences of the different selective regimes? Do the
observed life histories conform to theoretical expectations?

To evaluate the hypothesis that island anoles are food limited
relative to mainland anoles, I first compare the standing crop
biomass of *Anolis* predators and their arthropod prey in com-
parable island and mainland habitats. A lower ratio of prey to
predator biomass on islands than on the mainland would provide
indirect evidence supporting the hypothesis. More direct evidence is
sought in comparisons which involve the relative allocation of
energy to feeding and social interactions as opposed to growth and
reproductive effort. The hypothesis will also be tested with data on
population turnover. Higher individual persistence in island versus
mainland populations would provide evidence that predation pres-
sure is lower in island than in mainland habitats. Next, various life
history attributes of island and mainland anoles are contrasted to
determine if island and mainland anoles differ in body size, age at
sexual maturity, sexual dimorphism ratios, reproductive effort, and
size of offspring. Finally, I discuss the evolution of life histories in
Anolis.

MATERIALS AND METHODS

Comparisons of island and mainland *Anolis* are based on data
that I collected from cacao plantations on Dominica (an island)
during August 1971, March 1972, and July 1972 and in Costa Rica
(mainland) during April and May 1971, August 1971, and February
1972. Cacao plantations were chosen because different localities
have similar climates; cacao requires rainforest climates with high,
evenly distributed rainfall. In such environments seasonal differ-
ences in lizard reproduction are minimal (Licht and Gorman, 1970;
Sexton et al., 1971) facilitating comparisons of different sites.
Moreover, the closed canopy of a mature cacao plantation and the
shade required by the trees themselves make the understory of a
cacao plantation similar to that of an undisturbed rainforest
(Leston, 1970).

Sites and anoles studied

The island site was located on the windward side of Dominica at
Londonderry Estate 2 km N of the Melville Hall Airport at an
elevation of about 15 m. Weather stations in this area frequently

average over 2500 mm of rain a year and even during the relatively dry period, mid-January to mid-March, rainfall is usually more than 100 mm a month (Beard, 1949; Hodge, 1954). Rainfall at Melville Hall Estate for August 1971 was 268 mm, for March 1972 was 265 mm, and for July 1972 was 108 mm (Christopher Maximae, pers. comm.).

Dominica has a single species of anole, *Anolis oculatus*. On the basis of geographical variation in size and color pattern four subspecies have been described (Lazell, 1972). *A. oculatus winstoni* is found in lowland habitats on the windward side of the island. Subsequent references to *A. oculatus* will apply to this subspecies. *Anolis oculatus* are common in such diverse habitats as beach strand and undisturbed forest but appear to be most abundant in man-made "forests" such as cacao and orange groves. In cacao plantations *A. oculatus* occupy all structural components of the habitat, i.e. individuals are seen on the ground, on trunks, and in the canopy.

The mainland study site was located in the Atlantic lowlands of Costa Rica about 45 km W of Limon (Limon Prov.) on Finca La Lola, the cacao experimental station of the Instituto Interamericano de Ciencias Agricolas (IICA, Turrilaba) at an elevation of 33 m. Average annual rainfall at La Lola for the years 1949–1967 was 3501 mm (Soria et al., 1969). There are two relatively dry periods a year (February-March and September), but rainfall rarely falls below 100 mm a month. Rainfall at La Lola for April 1971 was 266 mm, for May 1971 was 111 mm, for August 1971 was 106 mm, and for February 1972 was 332 mm (Alfredo Paredes, pers. comm.).

Although seven species of anoles are recorded from nearby forests, only two are commonly found in the cacao plantations (Talbot, 1977). Of these, *A. limifrons* is by far the most abundant, being found in all localities where shade is present. In the cacao, individuals are usually found less than 2 m above the ground but seldom on the ground itself. In contrast, the terrestrial *A. humilis* is restricted to older cacao stands where understory vegetation is sparse.

Mark-recapture studies

Mark-recapture studies, conducted during three visits over about a year, were made in mature cacao plantations characterized by a continuous canopy and sparse understory. In Dominica, the 625 m²

study site included 43 regularly spaced cacao trees and six large breadfruit trees (Fig. 1). In Costa Rica, the 652 m² study site (in Experimental Section 19 of Finca La Lola) included 45 regularly spaced cacao trees and two large *Hura crepitans* (Fig. 2). Insecticides or other chemical treatments were not used on the study sites during this study or for many years previously.

During census periods, anoles were captured by hand and information on size, sex, individual identification number, and location were recorded in the field. Anoles were released shortly after capture where they were caught. Snout-vent length (SVL) was measured to the nearest mm for each capture and during some census periods weight (W) was determined to the nearest one-tenth of a gram (Pesola scales). Sex of adults and all but the smallest juveniles was readily distinguishable by the presence of the large dewlap in males only. Additionally, male *A. oculatus* of all sizes have enlarged post-anal scales which females lack. Individuals were identified by clipping the terminal phalange of toes in unique combinations involving not more than one toe.

Population size was estimated from mark-recapture data. For *A. oculatus,* I estimated population size with the Peterson method using a normal approximation to place 95% confidence intervals around the mean (Seber, 1973). Census data for these estimates were collected on 17–20 March and 30 March–1 April, 1972. For *A. limifrons,* population size was estimated with a regression procedure (Marten, 1970) using data of five census periods during April and May 1971.

Adult survivorship on the study sites was determined from the proportion of marked adults collected during the two site visits after the initial marking period.

Diet analyses

Anoles were collected[2] for stomach-content analysis in cacao plantations adjacent to and similar in vegetation structure to the mark-recapture sites. On Dominica, this collection was made on two days in August 1971, and in Costa Rica, on six days in early May 1971. Collections were made in late afternoon on rainless days so that all individuals had an equal time to feed. Individuals were

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[2]These collections have been deposited in the Museum of Comparative Zoology, Harvard University.

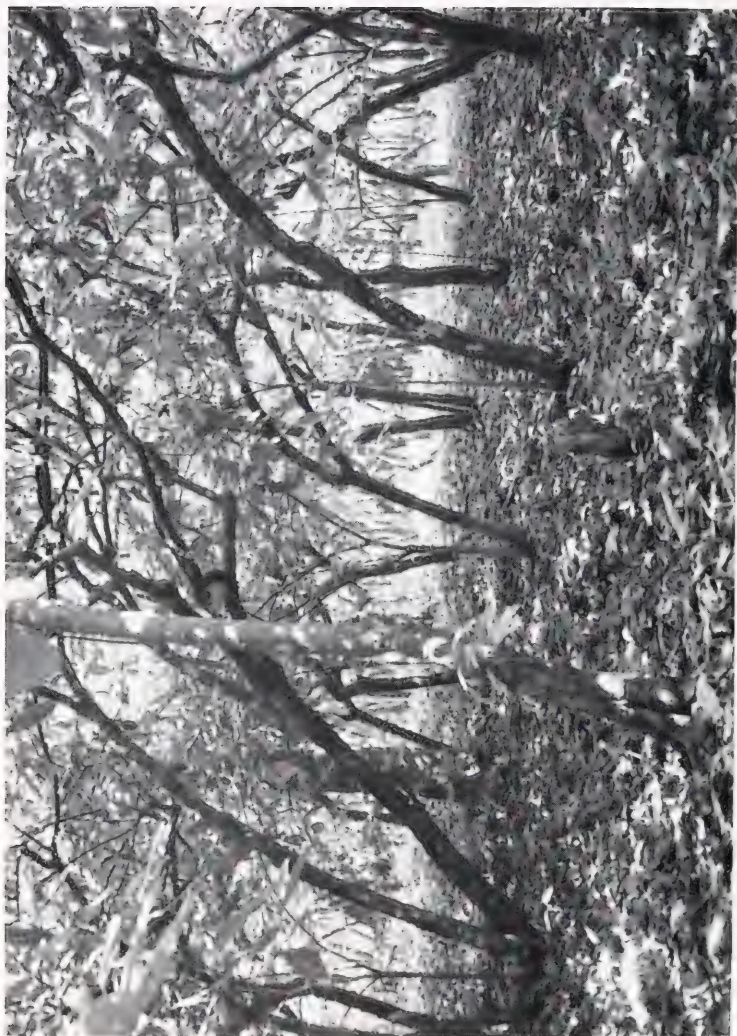Fig. 1. Study site in cacao plantation in Dominica, W.I.

Fig. 2. Study site in cacao plantation in Costa Rica.

collected by size in proportion to their occurrence in the popula-
tions. Specimens were killed within an hour of capture and pre-
served in alcohol.

Stomach contents were analyzed using the following techniques.
The length of each item found in the stomach proper was measured
and the average width and depth were estimated to the nearest 0.1
mm with an ocular micrometer. The volume of each arthropod was
determined by multiplying these three dimensions. Arthropods were
assigned to one of 15 taxonomic categories (Table 2).

Anolis *body size and reproductive condition*

For each lizard in the above collections SVL and head length
(HL) were measured. Head length was measured as the distance

Table 2. Composition of arthropod collections made by sweeping understory
vegetation on the Dominica and Costa Rica cacao sites. Values are percentages of
total numbers in each collection and do not include collembola and mites.

| | DOMINICA | | COSTA RICA | |
	cacao foliage	forest foliage	cacao foliage	forest foliage
Lepidoptera larvae	0.2	0.0	1.9	0.3
Lepidoptera adults	0.3	2.7	5.8	0.7
Orthoptera	1.9	0.5	2.3	4.1
Blattidae	0.1	0.0	0.0	1.1
Hymenoptera: Formicidae	40.8	52.5	10.3	21.4
Hymenoptera: Other	10.7	3.1	18.5	12.1
Homoptera	5.5	5.8	10.6	6.4
Hemiptera	1.5	0.0	1.8	0.7
Coleoptera adults	1.2	2.3	13.3	11.2
Diptera adults	32.3	20.6	29.3	21.7
Holometabolous larvae (except Lepidoptera)	0.1	0.0	0.1	0.1
Araneida	4.5	11.8	5.5	6.3
Isopoda	0.0	0.0	0.1	2.4
Isoptera	0.3	0.0	0.0	9.6
Miscellaneous	0.5	0.7	0.5	1.9
Sweeps	700	450	250	350
Total arthropods	3522	3180	1952	1219
No. ≥ 5 mm/1000 sweeps	243	44	972	526

from the anterior edge of the ear opening to the tip of the snout. The sex of each specimen was confirmed by dissection and the reproductive condition of females was indexed by the number of oviducal eggs and the diameter of the largest ovarian follicle.

The relation of head length and weight to SVL was determined by a least squares analysis. A single regression equation was appropriate for each of the three species because separate analyses for males and females did not alter the equation significantly ($p > 0.05$).

Lizards were classified as adult male, subadult male, adult female, and juvenile. Females were considered adult (sexually mature) at SVLs not less than that of the smallest female with oviducal eggs. For species in which males are considerably larger than females, subadult males are equal in range of SVL to adult females (after Schoener, 1968). Subadult males are small, sexually mature males (Licht and Gorman, 1970; Sexton et al., 1971) that appear to be excluded from the breeding population by the larger adult males (Rand, 1967; Andrews, 1971a) and thus form a separate class. Juveniles, defined as immature individuals, were sometimes divided into two groups: juvenile I and juvenile II, with smaller and larger individuals, respectively.

The total live weight of anoles on each of the study areas was estimated using the following technique. I divided the *A. limifrons* collected in May 1971 and the *A. oculatus* captured in March 1972 into SVL categories separated by 1 mm increments. The appropriate regression equation was used to convert SVL to weight. Weight was then multiplied by the number of individuals in each SVL category and the results were summed within classes to give the total weight per class. These values were adjusted for the estimated number of individuals per class on the study areas.

Behavioral studies

Information on foraging behavior was collected through a series of standard 30-minute observation periods (e.g. focal-animal sampling, Altmann, 1975). Foraging behavior was typified by adult females because foraging is more clearly defined in females than in (adult) males (Andrews, 1971a). On Dominica, observations were made between 6 and 18 August 1971 on the capture-recapture area. On the Costa Rica site, observations were made between 29 April

and 10 May 1971 on both the capture-recapture area and the collection area.

Characteristics of arthropod communities

Arthropod abundance, size distribution and taxonomic composition on the cacao study sites and also in undisturbed forests nearby were determined from sweep samples of understory foliage. Sweep samples provide representative collections of the kinds of prey eaten by anoles that forage in this stratum (Andrews, 1971b). The limitations and assets of sweep sampling as an ecological technique are discussed in previous literature (Southwood, 1966; Janzen and Schoener, 1968; Janzen, 1973a).

On the cacao sites, sweep collections for arthropods were made within two days of the collections of anoles and were taken on the same areas as the anole collections. The forest site on Dominica (Palmist Ridge) was located 5 km SW of the cacao site at an elevation of about 275 m. Rainfall is approximately 4000 mm y. This ridge top forest is extensive, with a high (max. 44 m) and fairly open canopy. The understory is sparse enough to walk through easily at most points. This site is further described by Soriano-Ressy et al. (1970). Sweep samples were taken in this forest in March 1972. The forest site in Costa Rica was located 2 km from Finca La Lola near the road between Limon and Siquirres and at a similar elevation to the cacao site. The forest area was relatively small (perhaps less than 1 km²) and was surrounded by cacao and areas recently clear cut. Trees had been selectively removed from the forest and therefore in some places the understory vegetation was dense enough to prohibit easy access. Sweep samples were taken in this forest on 29 February 1972.

Methods used for sweep sampling are described by Janzen (1973a). The total number of sweeps on each site ranged from 250 to 700 with sets of 50 separated for statistical purposes. Arthropods were manually sorted from the leaves and detritus immediately after collection and then preserved in alcohol. Sampling was conducted only during sunny or intermittently cloudy conditions and at the same time of day (1000–1200 hours) on both sites. The same methods of taxonomic categorization and measurement of length were used for these arthropods as for the arthropods taken from the *Anolis* stomachs. However, dry weight in each length class was

estimated using regression equations (Sage, 1974, Appendix Table 2) rather than from a volumetric determination. The following relationship for adult insects was used for most length classes:

$$\text{Ln } Y = -7.761 + 0.3498X - 0.003931X^2$$

where Y = dry weight in grams and X = length in mm. For Lepidoptera larvae and Orthoptera of 15 mm and greater, I used equations specific for these taxa.

RESULTS AND DISCUSSION

Prey Availability: Size, Abundance, and Taxa

Size-frequency distributions of arthropods collected in cacao plantations show that large individuals were poorly represented in the island sample (Fig. 3). Only 4.8% of all individuals were 5 mm or greater in length on the Dominica site in contrast with 12.8% on the Costa Rica site (p ≤ .001, Kolmogorov-Smirnov two-tailed test). This contrast between sites is accentuated when dry weight in each arthropod length class is plotted (Fig. 4) and further illustrated by summing total dry weights per 1000 sweeps, 6.4 g for Dominica and 17.8 g for Costa Rica. Moreover, significantly fewer arthropods were collected on the Dominica site than on the Costa Rica site (Table 2, p = 0.02, Mann-Whitney two-tailed test). The Dominica site averaged 247 arthropods per 50 sweeps and the Costa Rica site, 391 arthropods per 50 sweeps. Thus the low abundance of arthropods on the Dominica site is related to, in part, the low numbers of large individuals.

The collection of arthropods from forest understories on Dominica had significantly fewer large arthropods than did the collection from the Costa Rica site (Table 2, p ≤ .001, Kolmogorov-Smirnov two-tailed test). The island site also had a lower dry weight biomass of arthropods per 1000 sweeps than did the mainland site, 6.5 g as opposed to 8.1 g, respectively. However, the Dominica forest collection had significantly more individuals per 50 sweeps than did the Costa Rica forest collection (p = .02, Mann-Whitney U test, two-tailed). This is the result of large numbers of one very small myrmicine ant in the Dominica collection.

The taxonomic composition of the arthropod collections on the two sites is contrasted in Table 2. Formicidae dominate the island collections (41–53%) with the one myrmicine species contributing respectively 27.4 and 46.7% of all arthropods collected from the
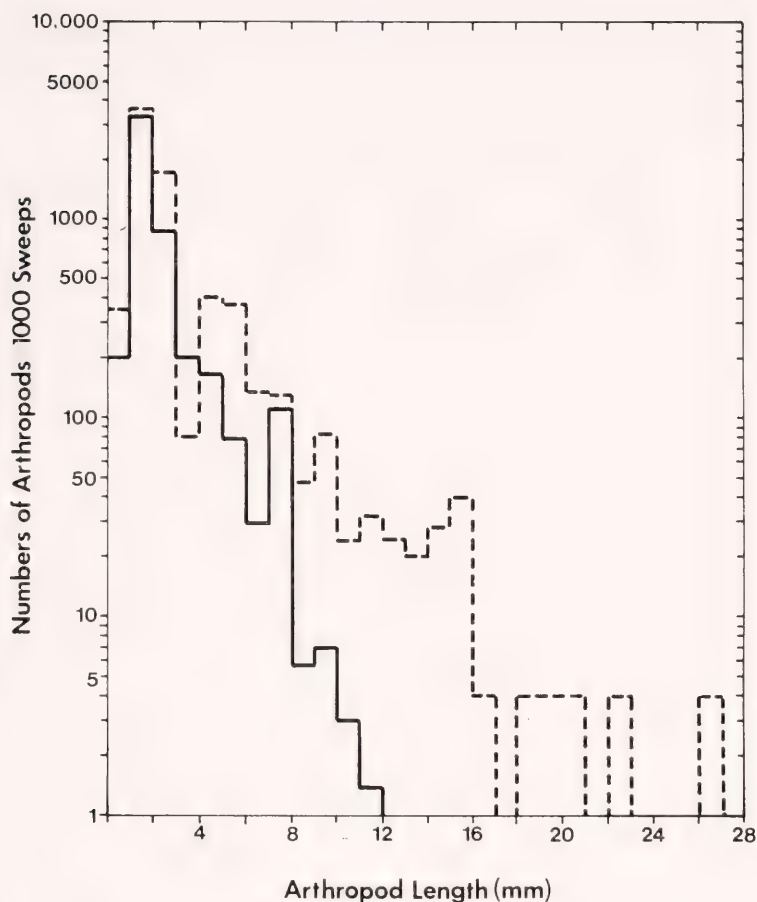
Fig. 3. Size-frequency distributions for arthropods collected in understory foliage in cacao plantations in Dominica (—) and La Lola, Costa Rica (----). Arthropods of 28 mm or more in length are not shown (2 in Dominica and 1 in Costa Rica).

cacao and forest foliage. In contrast, Formicidae contributed only 10–21% of all arthropods from the mainland site.

In general, large arthropods are well represented in sweep sample collections from mainland rainforests. On the Costa Rica site, 526 arthropods 5 mm or greater in length were collected per 1000 sweeps and this comprised 15.1% of all arthropods. Comparable figures are
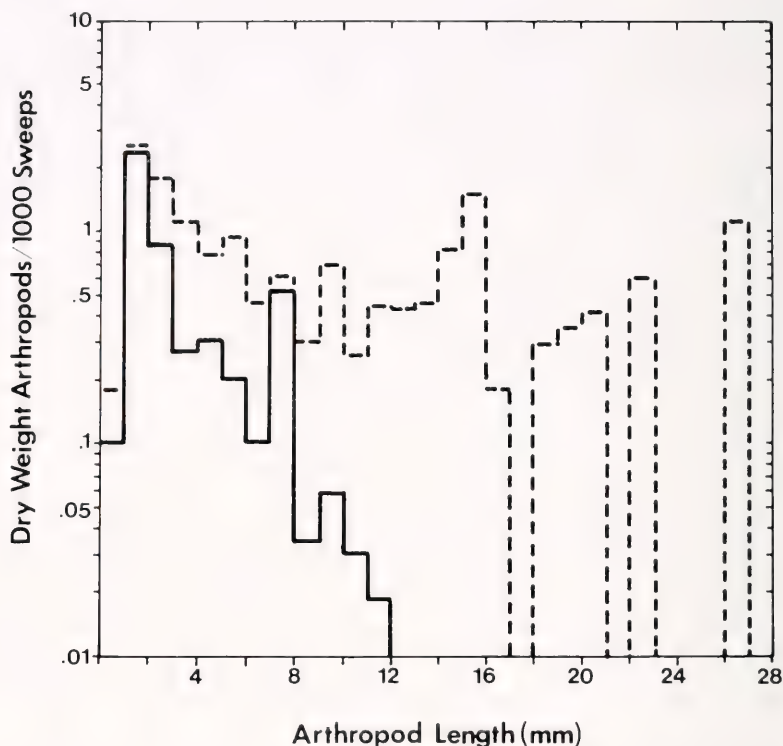
Fig. 4. Dry-weight — frequency distributions for arthropods collected in understory foliage in cacao plantations. Conventions as in the preceding figure.

available for two other lowland rainforests in Costa Rica. In wet and dry season collections, I (Andrews, 1971b) found 510–525 arthropods 5 mm or greater in length per 1000 sweeps and these comprised 22.4–31.6% of all arthropods. In a dry season collection, Janzen and Schoener (1968) found 201 arthropods 5 mm or greater in length per 1000 sweeps and this comprised 25.2% of all arthropods. In comparison, very few large arthropods were collected on Dominica, the one island locality for which comparable data are available. I collected only 44 individuals 5 mm or more in length per 1000 sweeps and only 0.6% of all arthropods collected were in this size category (Table 2).

More extensive comparisons of island and mainland arthropod communities have been made in second growth habitats. Allen et al. (1973) and Janzen (1973a, b) sweep sampled comparable sites on Puerto Rico and nearby smaller islands and on the mainland in Costa Rica. Both studies found a significantly lower abundance of arthropods in the island than in the mainland collections.

Population Densities

Anoles were two to three times more abundant on the island than on the mainland study site (Table 3). The total population size of *A. oculatus* was estimated at 299–363 individuals and of *A. limifrons,* 123 individuals. I assume that gains and losses to the adult populations during the census intervals were small because of their fidelity to established territories (Rand, 1967; Ruibal and Phili- bosian, 1974a; Andrews and Rand, unpub. mainland data) and because mortality would be slight during the census periods. The Peterson estimate for *A. oculatus* juveniles is probably reasonable because the census period spanned only two weeks. However, the regression technique used for *A. limifrons* adults gave unrealistically high values for *A. limifrons* juveniles. This was the result of the large

Table 3. Population composition, density, and biomass of *A. oculatus* on the Dominica study site and *A. limifrons* on the Costa Rica study site. Estimates for each class are followed by 95% confidence limits. Asterisked values for juveniles indicate the total number captured during the census period. Two totals for *A. oculatus* are given, one for each estimate of juvenile numbers.

	A. oculatus	*A. limifrons*
Site area (m²)	625	652
Number of Individuals		
Juveniles	170 (138–241)	—
	106*	46*
Subadult males	44 (22–∞)	—
Adult females	111 (80–198)	—
Adult males	38 (28–65)	—
Total adults	—	77 (72–82)
Total numbers	299–363	123
Total biomass (g)	1056–1121	96

number of unmarked individuals that were captured during the seven week census period. The census period was long enough to allow recruitment from eggs. Moreover, because of a lower site fidelity of juveniles than adults (Rand, 1967), appreciable numbers of unmarked individuals may have moved into the study area and marked individuals moved away from it. A conservative estimate of juvenile population size is the total number of juveniles captured on each site during the census period (Table 3). Only 22 *A. humilis* were encountered on the mark-recapture area; the inclusion of its numbers would increase the number of anoles on the mainland site very little.

For similar habitats, the commonest species on islands characteristically have higher population densities than the commonest mainland species (Table 4). In non-forested and disturbed habitats, some island species become extremely abundant. For example, densities of 1400 and 2000 individuals per 1000 m² are recorded for the grass anoles, *A. poncensis* and *A. pulchellus,* on Puerto Rico. Population densities of more than 400 individuals per 1000 m² are typical of trunk-ground anoles in disturbed habitats (e.g. *A. oculatus, A. lineatopus, A. acutus, A. sagrei).* The island species listed with relatively low densities share habitats with species of equal or greater abundance. On Bimini, although *A. distichus, A. carolinensis,* and *A. angusticeps* are generally uncommon compared to *A. sagrei,* the range of combined densities on five sites where all four species were present was 197 935 individuals per 1000 m² (Schoener and Schoener, unpub. data). *Anolis lineatopus* and *A. opalinus* had a combined density of 312 individuals per 1000 m² on Jamaica.

In contrast to the island examples, the highest densities recorded for anoles in disturbed mainland habitats are all less than 200 individuals per 1000 m². On Barro Colorado Island in Panama, *A. auratus,* a mainland counterpart of the West Indian grass anoles, had an estimated population density of 137 individuals per 1000 m² (Andrews, unpub. data) even when population densities were unusually high (A. S. Rand, pers. comm.).

Anole densities are lower in forests than in more open and disturbed habitats on both islands and on the mainland. On Abaco, Schoener and Schoener (unpub. data) estimate population densities for *A. sagrei* of 167–235 individuals/1000 m² on forest sites and 439 969 individuals/1000 m² on secondary sites over a two year period. Fleming (pers. comm.) found only six *A. limifrons* per 1000

m² in forest plots in the Atlantic lowlands of Costa Rica, in contrast to my estimate of 189 individuals 1000 m² in cacao plantations. Greater densities of some anoles in disturbed habitats compared with forested habitats has also been noted in Mexico by Henderson and Fitch (1975).

Anolis density estimates on islands and on the mainland may be even more disparate than indicated in Table 4. Sparse populations are usually not chosen for ecological study because of difficulty in obtaining sufficient data to accurately estimate population size. Since *Anolis* densities are generally lower on the mainland, mainland site selection is more likely to be biased towards high density situations.

Population densities have not been determined for any South American anoles. Work by Rand and Humphrey (1968), Fitch et al. (1976) and Duellman (in press) indicate that the most conspicuous characteristic of *Anolis* communities in this region is the extremely low densities of all species. An on-going study (Miyata, 1977) is being conducted, in part, in disturbed habitats where some species are encountered fairly frequently. It is obvious that low densities have generally discouraged ecological research on anoles in South America.

Diets

The island cacao site is characterized by low arthropod abundance, arthropod size distributions skewed towards small sizes, high frequencies of ants and a high density of *Anolis* lizards relative to the mainland site. These differences in the prey community should be reflected in the diets of the island and mainland cacao anoles.

Daily food intake of the cacao anoles was assessed from the quantities of food material found in their stomachs (Fig. 5). The two mainland species consistently had greater volumes of prey in their stomachs per gram body weight than did the island species. The differences were the greatest for the adult females of *A. limifrons* and *A. humilis* which had about twice the prey volume as did the similarly sized juveniles of *A. oculatus.* The greatest similarities were for adult males of the two mainland species which had mean prey volumes comparable to those of similarly sized *A. oculatus.*

Metabolic rate, and thus energy requirements, are a function of temperature in lizards (Bennett and Dawson, 1976). Since *A. oculatus* and *A. limifrons* seem to have similar thermal regimes,

Table 4.   Population densities of island and mainland *Anolis* lizards. Original values converted to number per 1000 m².

ISLANDS

Species	Habitat	Locality	No. 1000 m²
A. oculatus	cacao	Dominica (Table 3)	466–573
A. lineatopus	brush heap	Jamaica (Rand 1967)	1091
A. cristatellus	park	Puerto Rico (Rand 1961)	145
A. poncensis	cactus patch	Puerto Rico (Rand 1961)	1398
A. gundlachi	forest	Puerto Rico (Turner and Gist 1970)	200–280
A. pulchellus	grassland	Puerto Rico (Gorman and Harwood 1977)	2000
A. acutus	park	St. Croix (Ruibal and Philibosian 1974a)	430
A. sagrei	various sites	Abaco (Schoener and Schoener, MS)	167–969
A. sagrei	various sites	Bimini (Schoener and Schoener, MS)	77–685
A. distichus	various sites	Bimini (Schoener and Schoener, MS)	9–109
A. carolinensis	various sites	Bimini (Schoener and Schoener, MS)	18–69
A. angusticeps	various sites	Bimini (Schoener and Schoener, MS)	35–231
A. opalinus	pasture-scrub	Mandeville, Jamaica (Jenssen 1973)	142
A. lineatopus	pasture-scrub	Mandeville, Jamaica (Jenssen 1973)	170

MAINLAND

| Species	Habitat	Location (Reference)	
A. limifrons	cacao	Costa Rica (Table 3)	189
A. nebulosus	oak woodland	Mexico (Jenssen 1970)	90
A. polylepis	forest	Costa Rica (Andrews, unpub. data)	29
A. limifrons	forest	Panama (Andrews, in prep., Sexton 1967)	39 165
A. limifrons	forest	Costa Rica (Fleming, unpub. data)	6
A. humilis	forest	Costa Rica (Fleming, unpub. data)	11
A. cupreus	forest	Costa Rica (Fleming and Hooker 1975)	11 145
A. cupreus	wooded ravine	Costa Rica (Fitch 1973a)	57–141
A. cupreus	gallery forest	Costa Rica (Fitch 1973a)	184 191
A. auratus	grassland	Panama (Andrews, unpub. data)	135
A. tropidonotus	pine woodland	Honduras (Jackson 1973)	9
A. lionotus	stream edge	Panama (Campbell 1973)	13 100
A. poecilopus	stream edge	Panama (Campbell 1973)	13 100
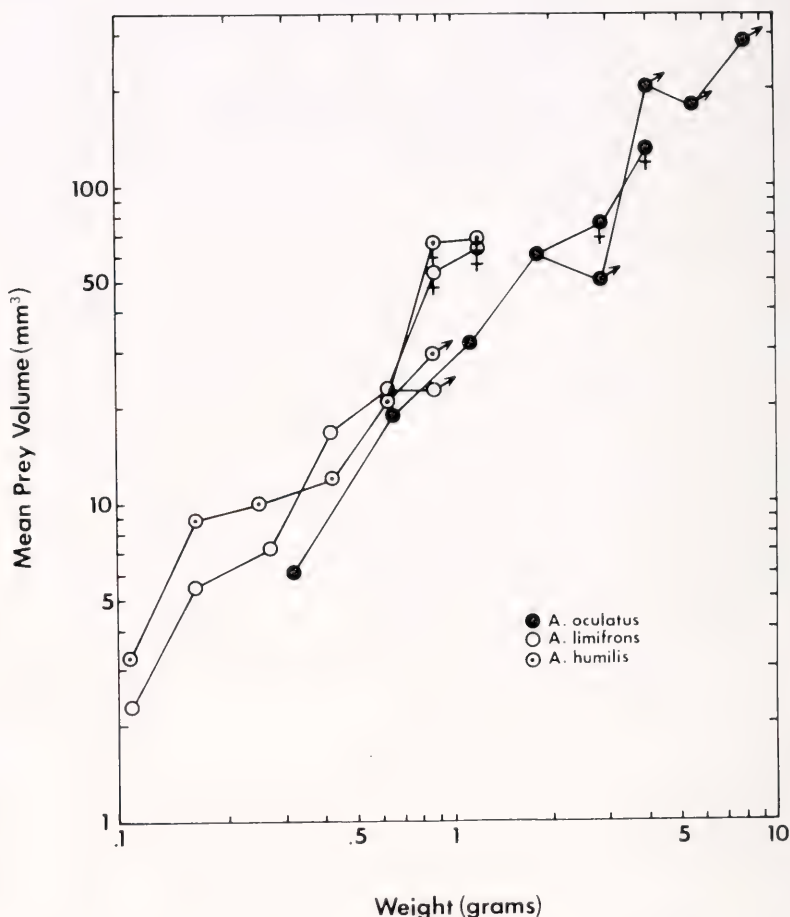
Fig. 5. Mean volumes of prey per individual for *A. oculatus*, *A. limifrons*, and *A. humilis* expressed as a function of body weight. Head lengths converted to weight equivalents with equations in Table 10.

their energy requirements should not differ on this basis. Ruibal and Philibosian (1970) measured mid-day body temperatures for *A. oculatus* in a cacao plantation near my study site. Lizards had a mean body temperature of 29.8° C for a range in air temperature of 28.6 29.8° C. A. R. Kiester and I measured mid-day body temperatures for *A. limifrons* along a path at La Lola and at the forest site in

May 1971. Body temperatures at these sites should bracket those in the cacao site because they had somewhat more open and more closed canopies respectively. Sixteen adult *A. limifrons* along the path had a mean body temperature of 30.1° C (S. E. = 0.44) with a range in air temperature of 28.0–32.0° C. In the forest, six adults had a mean body temperature of 29.3° C (S.E. = 0.21) with a range in air temperature of 28.4–30.3° C. Mid-day body temperatures of both *A. oculatus* and *A. limifrons* averaged about 30° C.

In some qualitative aspects the prey size utilization curves for the three cacao anoles are similar (Figs. 6–8). The distributions by prey numbers are all strongly skewed towards the smaller prey sizes, *i.e.* the items eaten most frequently by all species were small. Such distributions seem to be typical for anoles (Schoener, 1968; Sexton et al., 1972) and probably reflect log-normal distributions of size in insect communities (Schoener and Janzen, 1968). The distributions by prey volume are more normal in appearance although still skewed towards small prey sizes for some lizard classes. Arthropod length is related to volume (or weight) by a power function (Schoener, 1969a). Therefore, large items, although eaten relatively infrequently, contribute substantially to the volume of prey eaten and thus are more important than frequency would indicate.

Larger individuals of all species tended to take larger prey than small individuals. This was particularly clear for *A. oculatus* where differences were significant for all such comparisons ($p \leqslant .01$, Kolmogorov-Smirnov two-tailed test, Siegal 1956). Females tended to take larger prey than equally sized sub-adult males but differences were not significant (K-S two-tailed test, $p > 0.05$).

For *A. limifrons,* the classes listed in order of decreasing prey size are: adult female, juvenile II, adult males and juvenile I ($p \leqslant 0.05$ for all pairwise comparisons, K-S two-tailed tests). Thus, males took relatively small prey for their size. For *A. humilis,* males and females took prey of similar sizes but significantly larger prey than did the juvenile classes.

Although qualitatively similar, the prey size utilization curves of the island and mainland anoles differ markedly when absolute prey sizes are considered. The sampled population of *A. oculatus* took significantly smaller prey than did the *A. limifrons* population ($p \leqslant .001$, K-S two-tailed test). This difference is also illustrated from comparisons of lizard size classes (Fig. 9). The largest males were
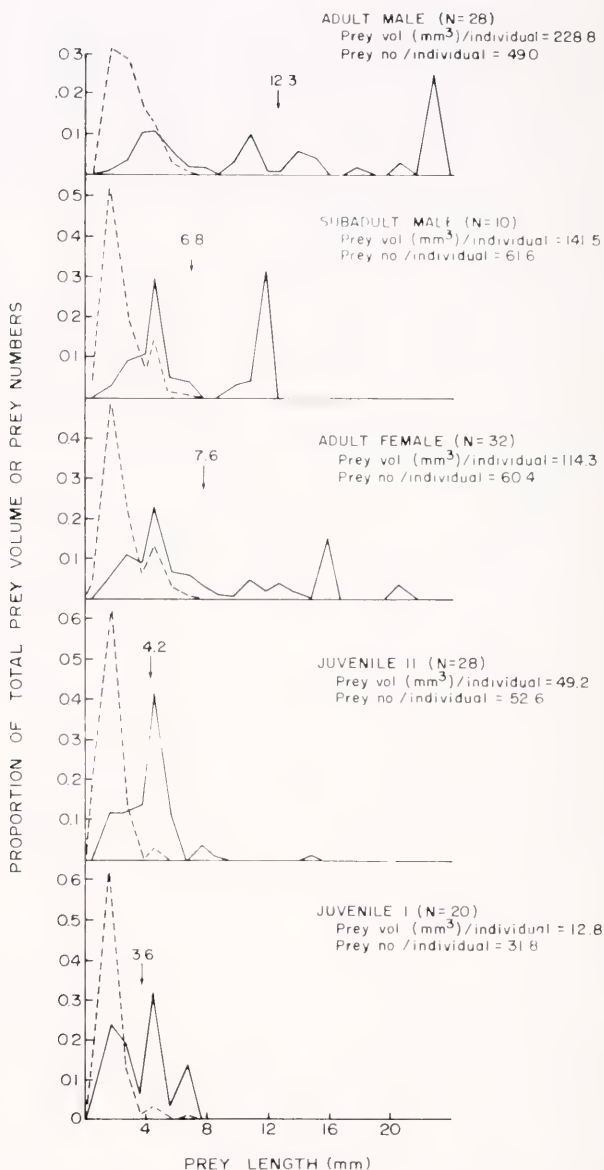
Fig. 6. Prey utilization curves by the fraction of prey numbers in each prey-length class (----) and the fraction of prey volume in each prey-length class (—) for *A. oculatus*. Arrows indicate mean prey sizes for the volume distribution.
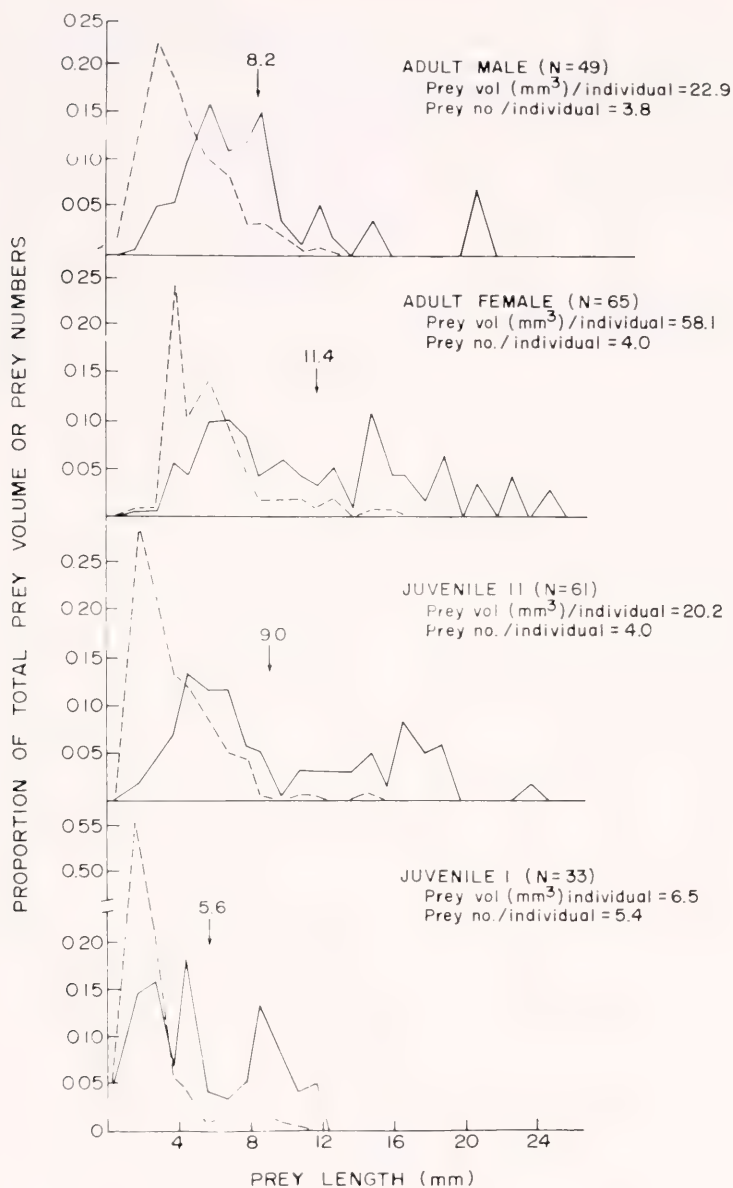
Fig. 7. Prey utilization curves for *A. limifrons*. Conventions the same as for the preceding figure.
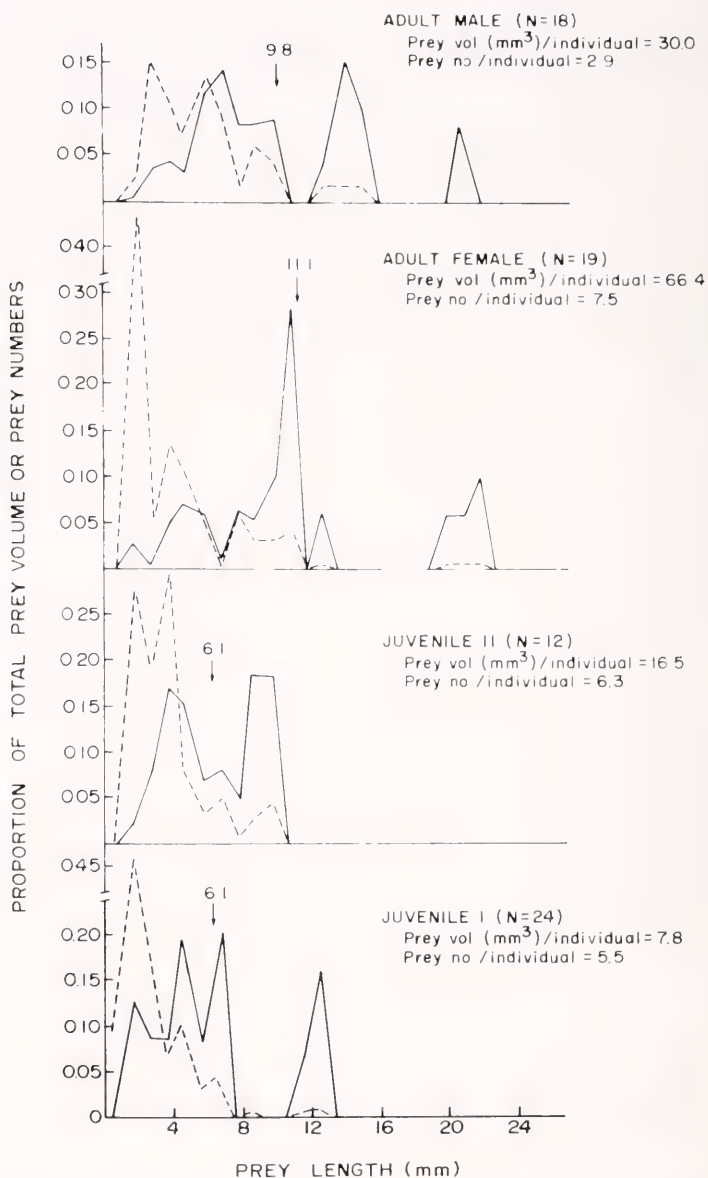
Fig. 8. Prey utilization curves for *A. humilis*. Conventions the same as Figure 6.

the only *A. oculatus* that averaged larger prey than any *A. limifrons* and this was a result of three large orthopterans eaten by one individual which strongly influenced the mean. Mean prey sizes for *A. humilis* are not plotted but are very similar to those of *A. limifrons* (compare class means in Figs. 7 and 8). However, in the comparison of the prey size distributions for the entire collection of both species, *A. limifrons* was found to take significantly larger prey than did *A. humilis* (p ⩽ .001, K-S two-tailed test). Associated with the differences in prey sizes were the numbers of prey found per anole individual — 32–62 for *A. oculatus* as opposed to 4–5 for *A. limifrons* and 3–8 for *A. humilis*.

The three species also differed in the taxonomic composition of their diets. For *A. oculatus*, the most frequently eaten arthropods
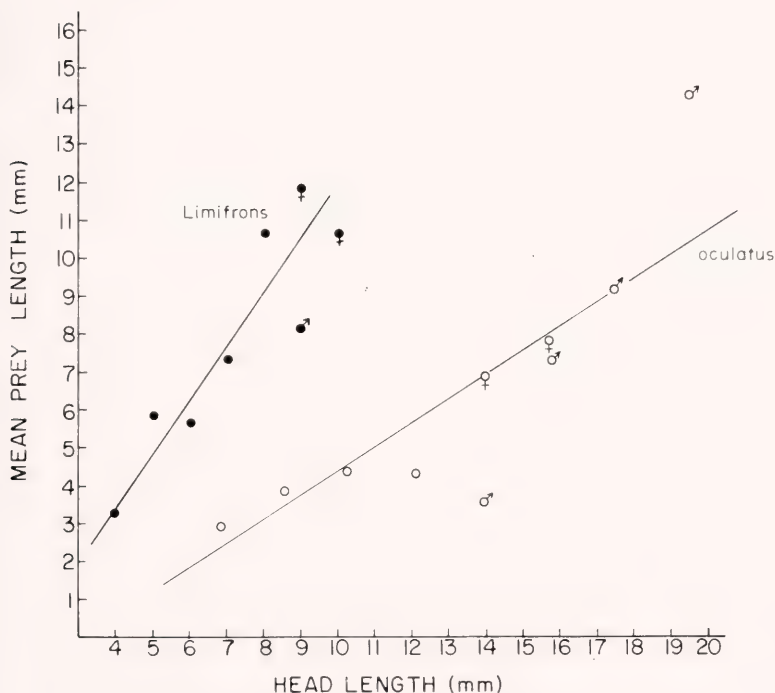

Fig. 9.   Mean prey length for the volume distribution (see Fig. 6) as a function of head length for *A. oculatus* and *A. limifrons*.

were Formicidae (ants) which contributed 44 57% of all items
(Table 5). Formicidae, Isoptera, and miscellaneous (mostly psocids,
collembola, and mites) arthropods were the most important con-
tributors to prey volume although decreasingly so for the larger
anoles with contributions of 77, 61, 58, and 39% for juveniles, adult
females, subadult males, and adult males, respectively. For *A.
limifrons*, no one taxon was outstanding in frequency but Lepidop-
tera larvae were the most important contributor to volume for all
classes (27 44%) while Homoptera, spiders, and Orthoptera were of
lesser importance (Table 6). For *A. humilis*, frequency of various
taxa was more consistent, with holometaboulous larvae (mostly
Diptera and Coleoptera), spiders, miscellaneous, and Isopoda being
consistently highly ranked (Table 7). Again the most important
contributor to volume was Lepidoptera larvae (25–28%).

Stomach content analyses show that the diet of the island *A.
oculatus* is made up of numerous small insects, primarily ants, and

Table 5. Dietary composition of *A. oculatus* on the Dominica site in August
1971. Values shown are the decimal fraction of total numbers and volume (mm³)
for each class.

	Juvenile		Adult Female		Subadult Male		Adult Male	
	No.	Vol.	No.	Vol.	No.	Vol.	No.	Vol.
Lepidoptera L.	.001	.011	.003	.002	.002	.005	.012	.088
Lepidoptera Ad.	—	—	.001	.006	—	—	.001	.001
Orthoptera	.002	.020	.004	.035	.006	.025	.005	.300
Blattidae	.002	.023	.005	.041	.002	.006	.001	.002
Hymenoptera:								
Formicidae	.460	.256	.502	.244	.570	.224	.444	.206
Hymenoptera: Other	.036	.011	.008	.001	.010	.005	.009	.042
Homoptera	.006	.006	.006	.010	.005	.007	.005	.001
Hemiptera	.006	.004	.004	.004	.002	.001	.001	.001
Coleoptera Ad.	.084	.039	.067	.058	.063	.009	.191	.102
Diptera Ad.	.052	.080	.015	.144	.014	.356	.008	.067
Holometabolous L.	.012	.020	.019	.006	.013	.005	.005	.002
Araneida	.033	.019	.012	.087	.014	.005	.015	.005
Isopoda	—	—	—	—	—	—	—	—
Isoptera	.077	.377	.113	.210	.119	.274	.180	.126
Misc.	.229	.135	.242	.153	.181	.078	.124	.056
Total N	2110		1934		616		1373	
Total Volume	1633.8		3656.0		1415.2		6407.6	

Table 6. Dietary composition of *A. limifrons* on Costa Rica site in May 1971. Values shown are the decimal fraction of total numbers and volume (mm³) for each class.

	Juvenile		Adult Female		Adult Male	
	No.	Vol.	No.	Vol.	No.	Vol.
Lepidoptera L.	.153	.437	.123	.273	.179	.318
Lepidoptera Ad.	.014	.017	.054	.097	.043	.038
Orthoptera	.002	.004	.042	.125	.027	.039
Blattidae	.019	.066	.034	.120	.005	.001
Hymenoptera: Formicidae	.074	.008	.069	.008	.109	.033
Hymenoptera: Other	.108	.030	.061	.011	.038	.023
Homoptera	.108	.129	.088	.076	.147	.090
Hemiptera	.026	.005	.019	.004	.005	.003
Coleoptera Ad.	.053	.030	.161	.078	.125	.084
Diptera Ad.	.110	.056	.050	.024	.125	.049
Holometabolous L.	.026	.030	.004	.001		
Araneida	.165	.099	.119	.056	.087	.230
Isopoda	.045	.071	.142	.076	.071	.064
Isoptera	—	—	—	—	—	—
Misc.	.096	.017	.034	.051	.038	.028
Total N	418		258		184	
Total Volume	1445.4		3776.1		1122.0	

of the mainland *A. limifrons* of a few large insects, primarily Lepidopteran larvae. This dichotomy seems typical of most island and mainland anoles so far studied (Rand, 1967; Schoener, 1967, 1968; Schoener and Gorman, 1968; Andrews, 1971a, b; Sexton et al., 1972; Lister, 1976; Scott et al., 1976). If the frequency of prey by length is considered, it seems generally true that the majority of the prey of island anoles (population or class) are less than 5 mm in length and the majority of the prey of mainland anoles are 5 mm in length or more. Ants are conspicuous in the diets of island anoles only. A "giant" anole, *A. cuvieri* of Puerto Rico, seems to be an exception (Rand and Andrews, 1975), but generalizations discussed here may not apply to such a large species. This problem is discussed in the Overview Section.

Although intraspecific comparisons indicate that head and body dimensions of anoles are related to prey size (Schoener, 1968; Schoener and Gorman, 1968), comparisons between species, and

Table 7. Dietary composition of *A. humilis* on the Costa Rica site in May 1971. Values shown are the decimal fraction of total numbers and volume (mm^3) for each class.

	Juvenile		Adult Female		Adult Male	
	No.	Vol.	No.	Vol.	No.	Vol.
Lepidoptera L.	.091	.281	.085	.276	.132	.254
Lepidoptera Ad.	.014	.009	.028	.090	.019	.070
Orthoptera	.039	.136	.021	.030	.076	.189
Blattidae	.005	.021	.007	.007	.019	.036
Hymenoptera: Formicidae	.082	.032	.042	.008	.094	.039
Hymenoptera: Other	.039	.012	—	—	—	—
Homoptera	.029	.036	.042	.087	.057	.037
Hemiptera	.048.	.014	—	—	—	—
Coleoptera Ad.	.048	.028	.014	.006	.132	.042
Diptera Ad.	.043	.020	.063	.135	.019	.001
Holometabolous L.	.173	.207	.507	.196	.132	.058
Araneida	.149	.039	.092	.026	.094	.089
Isopoda	.101	.142	.070	.137	.113	.127
Isoptera	—	—	—	—	—	—
Misc.	.139	.028	.028	.001	.113	.058
Total N	208		142		53	
Total Volume	386.2		1261.6		540.8	

particularly between species that occupy different habitats, show that lizard size alone is a poor indicator of prey size. For example, most sizes of *A. limifrons* eat larger prey than do *A. oculatus* even though *A. oculatus* is by far the larger species. Moreover, *A. oculatus* has a relatively longer head and greater weight per unit SVL than *A. limifrons*. There is apparently no direct functional relationship between the size and body proportions of anoles and the size of prey eaten. For *A. oculatus*, the linear relationship between lizard body size and mean prey size may result from interference competition where larger individuals monopolize the largest prey through social dominance over smaller individuals.

Anolis activity patterns

Both diets and population densities suggest that island anoles may have to spend more time and energy foraging and interacting with other individuals than do mainland anoles. If turnover rates and caloric values of stomach contents are comparable, then for

similar energy requirements, the utilization of small prey will necessitate more active foraging by island than by mainland anoles. This prediction is borne out by results of observations on adult females on the cacao sites (Table 8). *A. oculatus* individuals were considerably more active than *A. limifrons* during foraging as judged by the number of shifts in position and the number of movements that were directed towards potential prey. *A. oculatus* made about twice the number of major shifts in position (greater than one body length) than did *A. limifrons*. *A. oculatus* was observed to attack prey about five times more frequently. The greater activity of *A. oculatus* was associated with a relatively shorter prey attack distance with 70% of the 60 prey capture attempts made at 10 cm or less as opposed to only 25% of the 8 such attempts for *A. limifrons*. Although *A. oculatus* females fed more on the ground than did *A. limifrons* females (85% versus 38% of attacks), the success rate of both species was similar; about 80% of prey capture attempts resulted in capture.

Where anole densities on islands are greater than on the mainland, the activities and associated energetic costs of social interactions will be greater for island than for mainland anoles. Social interactions in reptile populations appear to increase as a function of population density (Brattstrom, 1974). Presumably, increased density is associated with increased levels of interactions between males and females as well as increased levels of aggression between individuals of the same sex. Ruibal and Philibosian (1974b) found a linear increase in aggressive encounters with density for both male and female *A. acutus*. Brad Lister (pers. comm.) recorded the

Table 8. Indices of foraging activity of adult female *Anolis* on the island and mainland cacao sites.

	A. oculatus	A. limifrons
n	18	12
Hours of observation	9	6
Position shifts/h	12.1	5.2
Prey capture attempts/h	6.7	1.3
% successful attempts	82	75
Mean prey distance (cm)	19	30
% captures on ground	85	38

activities of adult male *A. sagrei* in areas with densities of 13 and 50 individuals per 231 m² on Abaco Island in the Bahamas. He found that this approximately four-fold increase in male density was associated with a 15–20 fold increase per anole in such socially relevant activities as chases and displays (headbobs and dewlaps).

High activity rates of island anoles may only be possible because of the relaxation of predation in island environments. With low risk of predation, island anoles maximize fitness by moving frequently to capture prey and to engage in social interactions with neighbors. In contrast, mainland anoles live in environments where a moving lizard has a relatively high probability of attracting the attention of a predator (Andrews, 1979). Mainland anoles maximize fitness by feeding infrequently on large, high yield items.

Observations by Toft (1976) address this point. Diurnal members of frog communities in tropical rainforests exhibit one of two foraging patterns. The poisonous dendrobatids and some bufonids are active foragers, moving almost incessantly and eating very small items such as ants. In contrast, the palatable frogs (mostly lepto-dactylids) are sit-and-wait predators on relatively large arthropods. Their foraging behavior is much like that of the arboreal sit-and-wait anoles. The conspicuous behavior of dendrobatids and bufonids may be possible only because they are distasteful to most predators.

Survivorship

Survivorship of adult *A. oculatus* on the island site was considerably greater than of adult *A. limifrons* on the mainland site (Table 9). Nine months after the original census of the *A. limifrons* population, none of the males that were present on the site in May were recaptured and only one (6.6% of females captured) female was recaptured. In contrast, a high proportion of the originally marked *A. oculatus* were recaptured in following censuses. After 7 and 11 months respectively, 32.6% and 25.0% of males and 62.9% and 53.5% of females were recaptured.

Although there are few long-term population studies on anoles, the evidence at hand suggests that adult survivorship is greater for island than for mainland anoles. Annual adult survivorship of *A. acutus* on St. Croix ranged from 27–40% for females and 0–19% for males (Ruibal and Philibosian, 1974a). Schoener and Schoener (1978) found annual survivorships up to 20–50% for some classes of

A. sagrei, A. distichus, and *A. angusticeps* on Bimini and Andros.
Several populations of *A. opalinus* also had many adult individuals
that lived for more than one year (T. A. Jenssen, pers. comm.). On
the other hand, both capture-recapture data and seasonal changes in
population composition suggest complete annual turnover of adults
for mainland *A. polylepis* (Andrews, 1971b), *A. limifrons* in Costa
Rica (Table 9; Fitch, 1973b), *A. limifrons* in Panama (Andrews and
Rand, in prep.; Sexton et al., 1963), *A. nebulosus* (Jenssen, 1970),
A. cupreus (Fitch, 1973a; Fleming and Hooker, 1975), and other
mainland anoles (Fitch, 1973b).

Size. Relationships

The island and mainland cacao anoles are markedly different in
size (Table 10). *A. oculatus* is large and exhibits a pronounced
sexual dimorphism in adult maximum size. Males reached 79 mm
SVL or about 11 g and females 63 mm SVL or about 5 g. In
contrast, *A. limifrons* and *A. humilis* are small with slight sexual
dimorphism in size. Female *A. limifrons* reached 41 mm SVL and
female *A. humilis* 40 mm SVL at weights of about 1.3 g and males
were a few mm less in SVL. This difference in size and in degree of
sexual dimorphism is typical of the differences between island and
mainland anoles.

Sexual dimorphism ratios (SDR's) of Greater Antillean and
mainland species are contrasted in Figure 10. Species size is indexed
by maximum SVL of males and females (Williams, 1972). In this
comparison, the number of sympatric species (as many as 6-7) are
similar in both the island and mainland faunas. This comparison is

Table 9. Survivorship of adult anoles on cacao sites. For *A. oculatus* this
included all individuals $\geq$ 48 mm SVL.

	A. oculatus	*A. limifrons*
No. adults initially marked	44 ♂	23 ♂
	85 ♀	32 ♀
Time elapsed	7 months	3 months
Total captured (% marked)	46 ♂ (32.6)	18 ♂ (55.6)
	62 ♀ (62.9)	17 ♀ (47.1)
Time elapsed	11 months	9 months
Total captured (% marked)	44 ♂ (25.0)	18 ♂ (0.0)
	71 ♀ (53.5)	15 ♀ (6.6)

Table 10. Body size relationships of the *Anolis* populations in this study. Head length (HL) and weight (W) are given as a function of snout-vent length (SVL) with HL and SVL in mm and W in grams. Regression equations determined by least squares analysis (r^2 follows equations in parentheses).

| Species | Maximum SVL | | ♀ SVL at Sex. Mat. | Regression Equations | |
	♂	♀			
A. oculatus	79	63	48	HL = .260 + .272 SVL (.99)	W = .000024 SVL$^{2.98}$ (.98)
A. limifrons	39	41	35	HL = .966 + .234 SVL (.97)	W = .000048 SVL$^{2.73}$ (.92)
A. humilis	37	40	35	HL = 1.151 + .241 SVL (.99)	
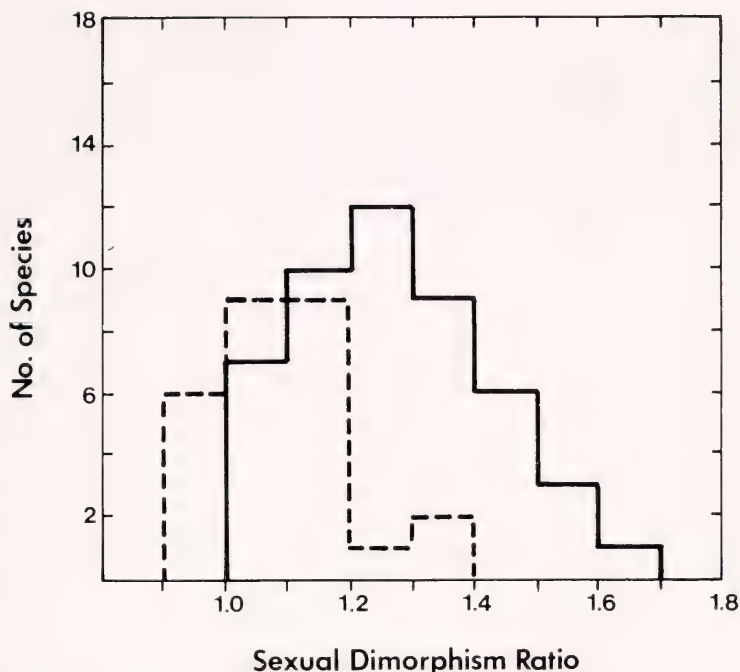
Fig. 10. Sexual dimorphism (male maximum SVL/female maximum SVL) ratios for Greater Antillean (solid line) and mainland (South and Central America) (dashed line) *Anolis*. Data for the Greater Antillean species are from Schoener (unpublished measurement tables, only species with a sample size of 15 or more individuals were used). Data for mainland species are given in Table 12.

also a conservative test of the prediction that island anoles will have higher SDR's than mainland anoles (Table 1) because of lower SDR's in the Greater Antilles than on the one- and two-species islands of the Lesser Antilles (Schoener, 1977).

Island species are found to have significantly greater sexual dimorphism ratios than do mainland species ($p \leqslant .001$, 2×2 Chi-squared test, Siegal 1956). Fitch (1976) has also measured SDR's of mainland *Anolis*. Excluding those species for which I present data, the range of SDR's (0.80–1.36) and mean SDR (1.07) for the tropical anoles in his data set are very similar to mine (Fig. 10) and further support the prediction of relatively high sexual dimorphism ratios for island anoles.

An even more relevant analysis is suggested by Schoener's (unpublished MS) demonstration that ecomorphs, which are species occupying similar structural habitats, are also similar in their sexual dimorphism ratios. Although 6–7 ecomorphs have been described (Rand and Williams, 1969), the present discussion is restricted to species whose structural habitat includes shrub level vegetation. Thus plotting the SDR's of bush-grass and trunk-ground anoles as a function of maximum male SVL shows that island and mainland species form exclusive groups (Fig. 11). For any given male size, the island bush-grass species have higher sexual dimorphism ratios than mainland counterparts. Furthermore, the island trunk-ground species have greater SDR's than all but one mainland trunk-ground species. Thus, even when similar ecomorphs are compared, the island anoles have greater SDR's than mainland species.

Comparisons of size are difficult since there is a wide range of size of different species as indexed by maximum male size both on islands and on the mainland. In the Greater Antilles the range in species size increases with the number of species per island, and on Cuba, the most extreme case, the range is from 38–191 mm (Williams, 1972). Although Cuba has by far the largest *Anolis*, the range of species sizes in the Greater Antilles is generally similar to that for mainland species where the range is from 38 to about 150 mm (Williams, pers. comm.). On the one- and two-species islands of the Lesser Antilles the range in species sizes is smaller, from 47–128 mm; extreme sizes are absent. Thus the range in species size is related to species richness; the greater range for Greater Antillean than for mainland anoles is possibly due to ecological opportunities that are not present on the mainland (Williams, 1972).

To avoid this problem I compare the relative abundance of various sized species within *Anolis* communities on islands and on the mainland.

Relatively large species are common and frequently dominant members of anole communities in the West Indies. On single species islands in the Lesser Antilles maximum male SVL's tend to range between 65 and 95 mm (Williams, 1972). On islands with two species, one tends to be larger and the other smaller than the average for solitary anoles (Williams, 1972). However, both members of these species pairs are frequently co-dominants in the habitats where they occur together (G. Gorman, pers. comm.). There are many
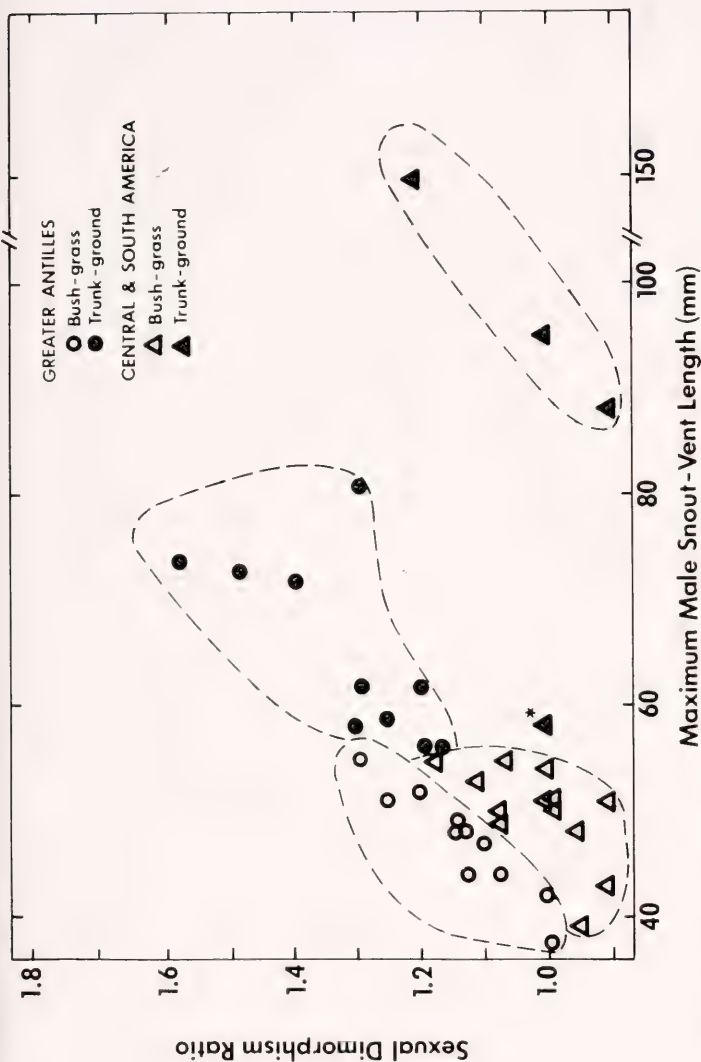
Fig. 11. Sexual dimorphism ratios expressed as a function of male maximum SVL for bush-grass and trunk-ground ecomorphs. Both sexual dimorphism ratios were plotted for the four mainland species which had two sample populations. Data sources as in Fig. 10. *A. lemurinus* is noted by an *. Although this species is a trunk-ground anole, it commonly perches in dark recesses at the base of trees (Fitch, pers. comm., Andrews, unpub. data). It is much less conspicuous than most trunk-ground anoles which typically perch in relatively high and exposed locations.

species in the Greater Antilles with maximum male sizes of 55 mm
SVL or less (Schoener, unpub. measurement tables). Despite this,
small bush-grass anoles and large trunk-ground anoles that are
sympatric may have comparable densities (Schoener and Schoener,
1971a, b; Jenssen, 1973) or large trunk-ground anoles may have
greater densities than sympatric bush-grass anoles (Turner and Gist,
1970; Rand, 1967).

In contrast to the island situation, *Anolis* communities on the
mainland are either dominated by small species or are comprised
entirely of species with low population densities. According to Fitch
et al. (1976): "Throughout Mexico and Central America one or
another of the seven species mentioned [*A. humilis, A. limifrons, A.
cupreus, A. sericeus, A. nebulosus, A. subocularis,* and *A. tropi-
donotus*] tend to dominate habitats suitable for anoles". To his list I
would add *A. polylepis,* the dominant in southwestern Costa Rica.
All of these species are small, with males not exceeding 55 mm in
maximum SVL. Furthermore, all species occupy shrub-level struc-
tural habitats. Large congeners are rarely encountered relative to
the small dominants. Examples of large species with low population
densities are *A. frenatus* in Panama (Andrews and Rand, unpub-
lished data), *A. capito* in Costa Rica (Andrews, 1971b), *A. attenu-
atus* and *A. woodi* in Costa Rica (Fitch et al., 1976), and *A.
biporcatus* and *A. pentaprion* in Costa Rica and Panama (Andrews,
unpublished data; Fitch, unpublished data).

In South America, the species most frequently encountered may
be relatively large in size. It appears that the structure of *Anolis*
communities in South America may be quite different than in
Central America and Mexico, but because all species are infre-
quently encountered, much more information is necessary before
such a generalization is possible.

Because of the high abundance of large species on islands,
comparisons of population density (Table 4) provide a minimal
contrast between *Anolis* community structure on islands and on the
mainland. For example, the total live weight of *A. oculatus* on the
island study was estimated at 1094 g (including 173 juveniles) and
the total live weight of *A. limifrons* on the mainland site at 96 g
(Table 3). The 2 3 fold difference in numbers becomes a ten-fold
difference in biomass.

Reproduction (females)

For lowland *Anolis* species, reproductive activity is associated with rainfall (Licht and Gorman, 1970). Judging from studies on sites with rainfall regimes similar to those of this study, reproduction probably continues year round for *A. oculatus* and *A. limifrons*. Possibly some dimunition occurs in the number of females with oviducal eggs during January-March (Licht and Gorman, 1970; Fitch, 1973c). Data on reproductive condition was collected during times of the year that both *A. oculatus* and *A. limifrons* females should have been producing eggs (August 1971 and April-May 1971, respectively). The majority of adult females on the cacao study sites were reproductive as measured by the presence of oviducal eggs (Table 11). A greater proportion of female *A. limifrons* were considered reproductive by this criterion than female *A. oculatus* (p ≤ .01, 2 × 2 Chi-squared test, Siegal, 1956). Using reproductive condition as an index of the rate of egg production (Licht and Gorman, 1970), the data of Table 11 suggest that the rate of egg production by *A. limifrons* females might be greater than for the *A. oculatus* females.

A general comparison of reproductive effort or proportion of energy budgets allocated to reproduction (Hirshfield and Tinkle,

Table 11. Reproductive condition of female *Anolis* in study populations expressed as the number of individuals with oviducal eggs.

	Repro. class (no. of eggs)	Number of Females	% females with eggs
A. oculatus	0	13	
Aug. 1971	1	22	63
Dominica	2	0	
A. limifrons	0	6	
May 1971	1	53	91
Costa Rica	2	6	
A. humilis	0	4	
May 1971	1	13	80
Costa Rica	2	2	

1975) for island and mainland anoles is not now possible. Such comparisons require information on the rate at which eggs are produced during the breeding season as well as their caloric worth. Rates of egg production under field conditions are known for only two tropical species. *A. aeneus* on Grenada laid eggs at intervals of about 12 days (Stamps, 1975) and *A. limifrons* (both Panamanian and Costa Rican populations) at intervals of 7–8 days (Andrews and Rand, 1974). Although reproductive condition through the annual cycle has been determined for many anoles (Licht and Gorman, 1970; Sexton et al., 1971; Andrews, 1971b; Gorman and Licht, 1974; Sexton and Brown, 1977), such data cannot be used to index the rate at which eggs are laid unless environmental conditions are comparable. One confounding factor is that anoles retain eggs under dry conditions (Stamps, 1976). Thus, two oviducal eggs may indicate retention rather than high rates of production. A second influence is the year to year variation among species in fat accumulation during dry periods and its utilization for egg production during the breeding season (Licht and Gorman, 1970; Fleming and Hooker, 1975). Fat storage would facilitate high rates of egg production over short periods. Both of the above factors make the interpretation of reproductive condition data difficult. Associated energy costs of reproduction, such as territorial defence or preparing egg laying sites, are even more poorly known than the direct costs of eggs *per se*.

OVERVIEW

We are now in a position to evaluate the evolution of life histories in island and mainland *Anolis*. A critical portion of the information that has been reviewed concerns present-day conditions in these two environments. The expectation that island and mainland anoles will differ in life histories is based on supposed differences in the way that their populations are regulated. Therefore, I first consider the evidence that island anoles are food limited relative to mainland anoles.

Determinations of arthropod and *Anolis* abundance suggest that food availability is less on islands than on the mainland. My Dominica site had a ten-fold greater live weight of anoles but about one-third the dry weight of arthropods than the Costa Rican site had. Although I measured standing crop, measurements of site

productivity for arthropods would presumably enhance the difference between sites. Assuming the rate of population turnover is roughly a function of individual size, production of small arthropods would be roughly comparable on both sites due to the similar representation of arthropods $\leqslant 8$ mm in length (Figs. 3 and 4). Production of large arthropods would be greater on the mainland site because such individuals were almost absent in the island collection. Limited arthropod data from other islands support my findings (Janzen, 1973b). More conclusively, the evidence for high anole densities on islands is well documented (Table 4) and would be strengthened by use of biomass rather than numbers of individuals because of the relatively large size of common island anoles.

The sizes and kinds of arthropods in anole diets suggest that island anoles eat more non-preferred items than do mainland anoles. Like many generalized predators, anoles prefer large items to small ones (Andrews, 1971b, unpub. data; Schoener, 1969a); the number of large prey eaten should be some function of their availability to a feeding lizard. Small items, particularly ants, are relatively more abundant in island than mainland habitats and more abundant in the diets of island than mainland anoles as well. The large numbers of prey in the stomachs of island anoles is a necessary consequence of small average prey sizes. Thus, a comparison of diets suggest that while mainland anoles have the "option" of feeding on large, high yield prey items, island anoles do not.

The above comparisons constitute indirect evidence that anoles on islands are food limited relative to anoles on the mainland. In addition, comparisons of processes that are potentially energy limited would provide more direct evidence in support of this hypothesis. The growth of juveniles is such a process and is, in fact, considerably slower for island than mainland species. For comparable lowland habitats, island juveniles grew at one-half to one-third the rate of mainland juveniles (Andrews, 1976). The low growth rates of island anoles may reflect low food availability or a relatively high allocation of energy to foraging and social activities or both.

The data at hand suggest that island anoles are food limited relative to mainland anoles. The data on survivorship are in accord. Mainland anoles have greater population turnover than island anoles, presumably reflecting the greater predation intensity in

mainland than island habitats. The hypothesized dichotomy in selective regimes for island and mainland anoles is strongly supported. The consequences of such differences are predictable, at least in theory. I now review the life histories of island and mainland *Anolis*.

First, is age at maturity later for island than mainland anoles? Island females were estimated to reach sexual maturity in 5–9 months as opposed to 2–4 months for mainland females (Andrews, 1976). Comparing species with similar female size, *A. lineatopus* (Jamaica) becomes sexually mature in 156 days and *A. polylepis* (Costa Rica) in 100 days. However, in *Anolis*, size at sexual maturity is a linear function of maximum size (Andrews and Rand, 1974). Thus, the later maturity of island than mainland anoles must be a function of their lower growth rates. Moreover the low growth rates of island anoles are facultative; with augmented food, rates of growth may be more than doubled (Andrews, 1976). This means that age of maturity in female *Anolis* on islands will vary with food availability.

Two observations support the prediction that reproductive effort is lower for island than for mainland anoles. First, less energy is available for the growth of juveniles on islands than on the mainland. Energy may likewise limit reproduction for island females. On the other hand, island females have the potential to lay eggs at rates comparable to those of mainland females (Andrews and Rand, 1974). Second, hatchling size is primarily a function of female size (Andrews and Rand, 1974). Island females do not have larger hatchlings than mainland females which may be related to constraints of the arboreal life styles of anoles. However, the slope of the linear function relating hatchling weight to female weight is considerably less than one. Therefore, proportionally, the caloric investment per offspring (ignoring associated costs) will be considerably less for large than for small species. For comparisons in which island species have larger females than mainland species, relative investment per offspring would be lower for island females even if rates of egg production in the two groups were the same.

High SDR's are characteristic of West Indian *Anolis*. The male is larger in all cases. However, if sexual dimorphism is solely a function of the need to partition food by size (Schoener, 1967, 1968; Schoener and Gorman, 1968), it should not matter which sex is the

larger. On the mainland, the situation is quite different. For 21 of the 59 populations measured by Fitch (1976) and myself, females were larger than males.

One explanation for the larger size of males than females is sexual selection. Trivers (1972) points out that when females are clumped in space but dispersed in time by asynchronous breeding that one male can monopolize breeding. The more females potentially monopolized, the more intense will be male-male competition for this resource. These assertions are particularly applicable to *Anolis* because: 1) adult males are often associated with more than one female (Rand, 1967; Andrews 1971a), 2) females potentially mate just prior to the ovulation of each egg (Crews, 1973), and 3) male size is positively related to reproductive success (Trivers, 1972). Because of the potential for males to monopolize many females, sexual selection should be particularly effective in insular situations where *Anolis* densities may be high.

In addition to sexual selection, factors that promote fitness in females may also explain the larger size of males than females in the West Indies. Because size at first reproduction is linearly related to maximum size (Andrews and Rand, 1974) for the same growth rates, the smaller the species size the sooner females can lay eggs. If we ignore other factors, early maturity should be advantageous because age at first maturity is such an important contributor to r_{max} (Cole, 1954). Furthermore, decrease in female size lowers metabolic requirements faster than it lowers offspring size. For example, reduction of female weight from 4 g to 2 g reduces standard energy requirements by about 40% but offspring weight by only about 20%. In highly competitive situations, it may be advantageous for females to have low energy demands and yet be able to produce relatively large offspring. Thus female size may be a compromise between low energy demands and early reproduction and the ability to produce competitive offspring. This might explain Schoener's (1969b) observation that there is less variation in median female size than in median male size between islands differing in number of congeners.

The prediction that mainland anoles will be smaller in size than island anoles is supported by community level comparisons; in mainland habitats common species are generally small and in island habitats common species are both small and large. I have argued that small size is one of a suite of r-selected life history attributes

adaptive in mainland *Anolis* habitats where predator pressure is high. However, large species do occur in these habitats. The large mainland anoles appear to fall into one of two ecological categories, each minimizing the risk of predation in different ways.

The very low densities of many large species such as *A. capito* and *A. frenatus* are associated with dietary specialization on large prey items. The mean length of 62 prey items eaten by 23 adult *A. capito* was 16 mm when calculated by prey numbers or 30 mm when calculated by prey volume (Andrews, 1971b). Adult *A. frenatus* eat similarly sized prey (Scott et al., 1976; Andrews, unpub. data). Individuals of 15 mm in length or more constitute less than 0.4% of arthropods taken by sweep sampling at lowland rainforest sites in Central America (Andrews, 1971b; Janzen and Schoener, 1968, Guapiles site). Therefore large anoles that specialize on rare resources must themselves be rare. Although small arthropods are much more abundant than large ones, large anoles are probably large prey specialists because the low foraging rates are adaptive in their rainforest habitats (Andrews, 1979). The tendency of the large trunk-ground species such as *A. capito, A. frenatus,* and *A. woodi* to "freeze" rather than to flee when disturbed (Fitch, pers. comm.; Andrews, 1971b) also suggests that they avoid detection by predators by long periods of immobility and highly cryptic coloration.

The mainland anoles that are both large and relatively abundant seem to be adapted to specialized habitats where predator pressure may be relatively low. The "aquatic" anoles have maximum male sizes ranging from 70–100 mm SVL (Table 12, Fitch 1976). Campbell (1973) found densities of *A. poecilopus* and *A. lionotus* up to 100 individuals per 1000 m² in Panama. Escape from avian predators may be relatively easy in the boulder strewn, stream side habitats where these anoles live. The "rock" anoles, with maximum male SVLs of about 80 mm, are locally abundant in Mexico (Fitch and Henderson, 1976). Here also, predator pressure may be low.

In contrast, the overriding determinant of *Anolis* life histories on islands is competition for food. Large size is one of the K-selected attributes which maximize fitness in situations where resources are limited. The contention by Case (1978) that the increased size of territorial lizards on islands is a function of a greater availability of food resources is not supported by the *Anolis* data. Both insect

standing crops and the growth rates of juveniles in comparable island and mainland habitats indicate that the ratio of resource supply to resource demand by anole populations is relatively low on islands. Although food availability may provide one constraint to the maximization of body size in island habitats, it does not explain the relative increase in size of island anoles.

The dichotomy in the life histories exhibited by island and mainland anoles generally conforms to the initial predictions (Table 1). However, life history theory implies that life history attributes are invariant expressions of the genome. It is obvious from examination of *Anolis* life history attributes that while some attributes are relatively constant in expression, others are extremely plastic. In *Anolis,* attributes such as maximum size, sexual dimorphism ratios, and offspring size have easily definable values for a given population. These indicate selection for fitness under environmental conditions that are "constant" across many generations. On the other hand, growth rate, age at sexual maturity, and rate of egg production are highly variable under experimental conditions and presumably in the field as well. There has been a recent recognition that such variability may be highly adaptive in heterogeneous or fluctuating environments (Hickman, 1975; Hirshfield and Tinkle, 1975; Nichols et al., 1976). The ability of the food limited island anoles to exploit temporally or spatially abundant food by increasing rates of growth or egg production is not surprising considering the importance of early maturity and reproductive effort to individual fitness.

The life history model proposed here must be qualified in one important respect. It was developed by focusing on the major selective forces acting on island and mainland *Anolis* that live in lowland tropical environments. Although the available data support the predicted island-mainland dichotomy, only two anole ecomorphs, the bush-grass and the trunk-ground species, have contributed to these data. The anoles we know the least about, very large species, canopy species, and species that live in extreme environments, are also the most likely to prove exceptions to the model (Andrews, 1976). The trophic position of the very large anole species may very well differ from small species since many are frugivorous (Brach, 1976; Schoener, unpub. data) and some include

Table 12. Sizes and sexual dimorphism ratios of South and Central American *Anolis*.

Species	Maximum SVL ♂	Maximum SVL ♀	SDR	Source	Structural habitat
A. auratus	51	51	1.00	Sexton et al. 1971 (Panama)	grass
A. barkeri	101	78	1.29	Meyer 1968 (Mexico)	aquatic-stream edge
A. biporcatus	87	97	.90	Rand (pers. comm., Panama)	canopy
A. capito	88	97	.91	Andrews (unpubl. data, Costa Rica)	trunk-ground
A. carpenteri	41	44	.93	Echelle et al. 1971 (Costa Rica)	—
A. chrysolepis[1]	69	67	1.03	Vanzolini and Williams 1970 (S. Am.)	ground
	70	80	.88		
A. cupreus[1]	55	47	1.17	Fitch et al. 1972 (Costa Rica)	bush-ground
	50	46	1.08		
A. frenatus	150	120	1.25	Scott et al. 1976 (Panama)	trunk-ground
A. fuscoauratus	43	47	.91	W. E. Duellman (pers. comm., Ecuador)	bush-ground
A. humilis	38	40	.95	Table 2 (Costa Rica)	ground
A. intermedius	54	54	1.00	H. S. Fitch (unpub. data, Costa Rica)	bush-ground
A. lemurinus[2]	58	60	.97	H. S. Fitch (unpub. data, Costa Rica)	trunk-ground
A. lemurinus	79	79	1.00	H. S. Fitch (unpub. data, Mexico)	
A. limifrons	50	50	1.00	Sexton et al. 1971 (Panama)	bush-ground
	39	41	.95	Table 2 (Costa Rica)	bush-ground
A. lionotus	76	70	1.09	Campbell 1973 (Panama)	aquatic-stream edge

A. nebulosus	49	46	1.07	Jenssen 1970 (Mexico)	bush-ground
A. onca	87	67	1.30	A. S. Rand (pers. comm., Venezuela)	bush-ground
A. ortoni	48	50	.96	W. E. Duellman (pers. comm., Ecuador)	bush
A. poecilopus	71	66	1.08	Campbell 1973 (Panama)	aquatic-stream edge
A. polylepis	53	48	1.10	Andrews 1971a (Costa Rica)	bush-ground
A. punctatus	82	77	1.06	W. E. Duellman (pers. comm., Ecuador)	twig-branch
A. sericeus	50	48	1.04	H. S. Fitch (unpub. data, Mexico)	trunk (?)
A. tropidogaster	51	51	1.00	Sexton et al. 1971 (Panama)	bush-ground
A. tropidolepis	59	58	1.02	Fitch 1972 (Costa Rica)	
A. tropidonotus	55	52	1.06	Jackson 1973 (Honduras)	bush-ground
A. trachyderma	51	56	.91	W. E. Duellman (pers. comm., Ecuador)	bush-ground
A. vociferans	56	57	.98	Myers 1971 (Costa Rica)	bush-ground

[1] SDR determinations available for many populations; only those for extreme SDR's are given.

[2] The two *lemurinus* are considered distinct species because of the size differences and confused state of the taxonomy of Central American anoles.

other anoles in their diets (Rand and Andrews, 1975; O. J. Sexton, pers. comm.). Furthermore, the environment may place physiological constraints on anoles in some habitats that override the biotic factors considered here. As examples, *A. onca,* which occupies xeric coastal regions of Venezuela, has a very high SDR for a mainland anole (Table 12), and the low growth rates of *A. tropidolepis* in Costa Rica may be a function of low environmental temperatures in its cloud forest habitat (Fitch, 1972). Whether or not a distinct island-mainland dichotomy can be extended to such "atypical" species is yet to be resolved.

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B R E V I O R A

Museum of Comparative Zoology

A NEW PALEOCENE PALAEANODONT AND THE ORIGIN OF THE METACHEIROMYIDAE (MAMMALIA)

KENNETH D. ROSE[1]

ABSTRACT.   A new genus and species of palaeanodont, *Propalaeanodon schaffi,* from the late Paleocene (late Tiffanian) Polecat Bench Formation of the Bighorn Basin, Wyoming, is the oldest and most primitive known metacheiromyid. *Propalaeanodon* foreshadows *Palaeanodon* in the reduction of its postcanine teeth. It resembles epoicotheriids in the presence of postcanines along the entire length of the horizontal ramus, and resembles the slightly older *Amelotabes,* in particular, in the retention of seven postcanines. *Propalaeanodon* thus provides additional evidence for uniting the Metacheiromyidae and the Epoicotheriidae in the suborder Palaeanodonta, and it strongly suggests that the Metacheiromyidae evolved from the Epoicotheriidae, probably during the Tiffanian.

Two humeri from the same stratigraphic level as the holotype are tentatively referred to *Propalaeanodon.* They possess specializations typical of Eocene palaeanodonts, including a prominent deltopectoral crest and a large supinator crest. These features indicate that *Propalaeanodon* was, already in the late Tiffanian, a highly specialized fossorial animal.

The systematic position of the Palaeanodonta is uncertain. They have been considered to be related to the orders Xenarthra or Pholidota or both by all recent students and, indeed, they are the only known fossil group that evolved specializations similar to those in these two orders. Although it is possible that palaeanodonts were an early radiation of probably myrmecophagous, fossorial mammals merely convergent to these orders, the evidence now available enhances the probability that the three groups share a special relationship.

INTRODUCTION

The edentate-like members of the rare mammalian suborder Palaeanodonta have long been considered early relatives of the Xenarthra, the Pholidota, or both. As now known, they are restricted to the earlier Tertiary of western North America. Palaeanodonts are classified in two families, the Epoicotheriidae and the

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Metacheiromyidae. To date, nine genera and fifteen species have been recognized, several of which were described quite recently (West, 1973; Rose et al., 1977; Rose, 1978). They range in age from Tiffanian (late Paleocene) to Orellan (middle Oligocene).

Recently the dentary of a primitive new palaeanodont was discovered by Charles Schaff, Museum of Comparative Zoology, in late Tiffanian rocks in the northern Bighorn Basin, Wyoming. The oldest and most primitive metacheiromyid, it sheds new light on the origin of this peculiar family and further documents the unity of the Palaeanodonta. Two palaeanodont humeri, collected much earlier from the same stratigraphic interval, probably represent the same new species.

Abbreviations of institutional names cited herein are as follows:

AC Pratt Museum, Amherst College, Amherst, Massachusetts.

AMNH American Museum of Natural History, New York.

MCZ Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

PU Princeton University Museum, Princeton, New Jersey.

UM University of Michigan Museum of Paleontology, Ann Arbor, Michigan.

SYSTEMATIC PALEONTOLOGY

Suborder PALAEANODONTA Matthew, 1918
Family METACHEIROMYIDAE Wortman, 1903
PROPALAEANODON, gen. nov.

Type species. Propalaeanodon schaffi, sp. nov.

Included species. Type only.

Distribution. Late Paleocene (late Tiffanian) ot the Bighorn Basin, Wyoming.

Diagnosis. Only metacheiromyid with seven postcanine teeth that extend to the back of the horizontal ramus. All postcanines single-rooted except P_4, which is two-rooted. Postcanines small, peglike, separated by short diastemata, and with rounded crowns, in these features resembling *Palaeanodon;* but crowns higher and more pointed than in *Palaeanodon.* Dentary slender, slightly smaller than in *Palaeanodon ignavus;* deepest beneath first postcanine (P_1), shallowest beneath last postcanine (M_3), as in *Palaeanodon.* Medial buttress prominent but less so than in *Palaeanodon.*

Etymology. In allusion to its resemblance to, lower stratigraphic level than, and probable relationship to *Palaeanodon.*

PROPALAEANODON SCHAFFI, sp. nov.
Fig. 1A and B, 2A, and 3B

Holotype: MCZ 20122, left dentary with P_{2-3}, alveoli for P_1, P_4, M_{1-3}, and posterior margin of canine alveolus.

Hypodigm. Holotype and tentatively PU nos. 13928, 13929.

Horizon and Locality. Latest Paleocene (late Tiffanian), "Silver Coulee beds" of Polecat Bench Formation (of Jepsen, 1940), Jepsen Valley Quarry, NW¼, Sec. 27, T.57N., R.100W., Park County, Wyoming.
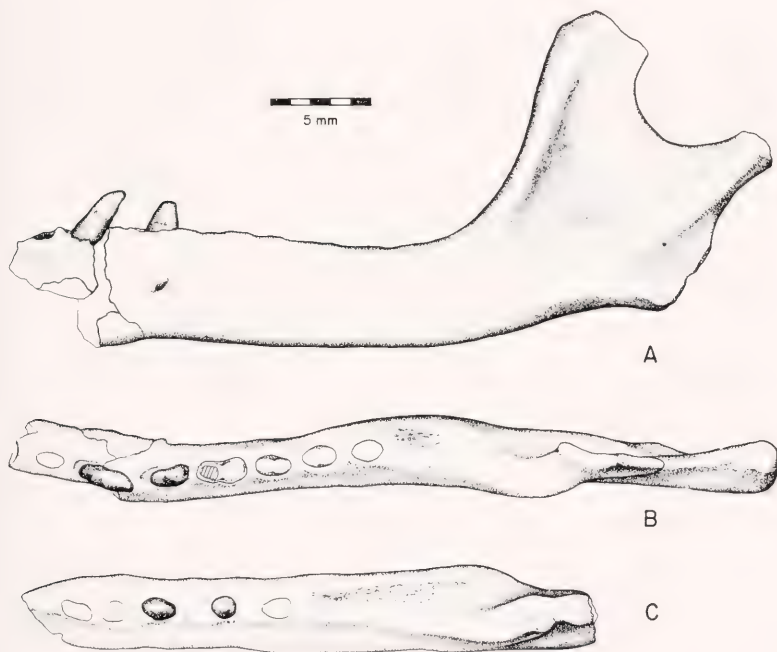
Figure 1. Lateral (A) and dorsal (B) views of holotype of *Propalaeanodon schaffi,* MCZ 20122, left dentary with second and third postcanines (P_{2-3}). Dorsal view of left dentary of *Palaeanodon* sp. (C), showing extended edentulous part of ramus behind fifth postcanine; reconstructed from UM 63611 and 66243.

Figure 2. Medial views of left dentaries of palaeanodonts. (A) *Propalaeanodon schaffi,* holotype, MCZ 20122. (B) *Palaeanodon* sp., reconstruction based on UM 63611 and 66243. (C) *Amelotabes simpsoni,* holotype, PU 14855 (right dentary, reversed).

Diagnosis. Only known species of the genus; measurements in Table 1.

Etymology. For Charles R. Schaff, expert collector and preparator, who discovered the holotype.

Description. Only two teeth are preserved in the holotype, although the dentary is nearly complete and provides much information about the mandibular morphology of *Propalaeanodon schaffi.* The horizontal ramus is intact as far forward as the posterior margin of the canine alveolus. This alveolar margin reveals that the canine was large, as in other palaeanodonts, and its

root robust, a feature also indicated by thickening of the dentary anteriorly.

The dentary contained seven postcanine teeth, presumably four premolars and three molars, which were greatly modified from the primitive eutherian condition. Seven is a greater number of teeth than in any other metacheiromyid, indeed more than in any other palaeanodont except *Amelotabes,* which also has seven (Rose, 1978). *Alocodontulum,* in which the lower dentition is unknown, has seven upper postcanines (Rose et al., 1977, 1978), and thus probably had seven lowers as well. The postcanines of *Propalaeanodon* occur along the entire length of the horizontal ramus, as in
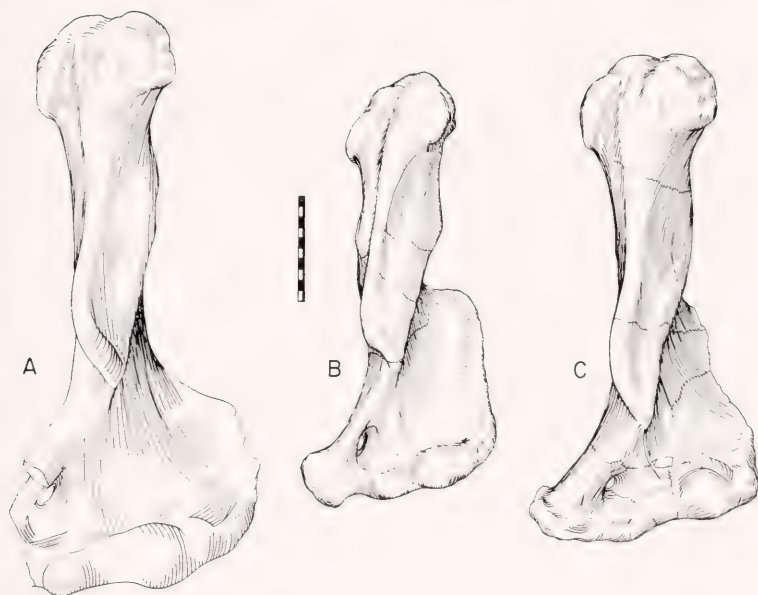
Figure 3. Left humeri of palaeanodonts. Scale is 10 mm. (A) Early Eocene metacheiromyid *Palaeanodon ignavus,* based on AMNH 15088 and 16832; after Matthew (1918), but with corrected orientation of proximal end. (B) ?*Propalaeanodon schaffi,* PU 13928. (C) Early Eocene epoicotheriid *Pentapassalus woodi,* part of holotype, AC 2766. Note that this species is referable to *Pentapassalus* (Rose, 1978), not to *Palaeanodon* (Guthrie, 1967; Emry, 1970). The supinator crests in (A) and (C) are incomplete and have not been reconstructed because of the variable development of this crest in different taxa of palaeanodonts; they were in any case larger than depicted.

TABLE 1

Dimensions of the holotype of *Propalaeanodon schaffi*, MCZ 20122.
(Measurements are in mm to nearest .05 mm)

	Length	Breadth
P_1 alveolus	1.35	0.85
P_2 alveolus	damaged	
P_2 crown	1.25	1.00
P_3 alveolus	2.40	1.15
P_3 crown	1.80	1.10
P_4 alveolus	2.80	1.10
M_1 alveolus	2.00	1.15
M_2 alveolus	2.00	1.15
M_3 alveolus	1.60	1.00
P_1-M_3	17.10 (approx.)	

Depth of mandible, lingually at P_1: 6.10 (approx.)
Depth of mandible, lingually at M_3: 4.80

epoicotheriids but not in later metacheiromyids, in which the back of the horizontal ramus is edentulous. All teeth in *Propalaeanodon* are single-rooted except P_4, which has two roots (probably a primitive feature). Judging from the alveoli, M_1 and M_2, and possibly P_3, had single roots that were faintly bilobate. The roots of all postcanines were tapered and closed, as in *Palaeanodon*. The epoicotheriids *Amelotabes* (Fig. 2C) and *Tubulodon* are similar in having a two-rooted P_4, but in these taxa several other postcanines are also two-rooted. In *Pentapassalus* M_1 has a bilobate root but P_4 is single-rooted (Gazin, 1952). The postcanines in *Palaeanodon* are all single-rooted (Fig, 1C, 2B).

The crowns of P_2 and P_3 are preserved. P_2 has become dislodged from its alveolus as a result of damage to the front of the jaw and appears higher than P_3. Both teeth are peglike with rounded crowns apparently devoid of enamel. In these characters they closely resemble the postcanines of *Palaeanodon* (Fig. 1C, 2B and Rose, 1978), although they are slightly larger, particularly longer, higher crowned, and less rounded. As in *Palaeanodon* they show no cusp pattern on the crowns, nor is there any evidence of direct occlusion with the upper teeth. Occlusal wear is discernible in molars and even in premolars of some epoicotheriids. The alveolus of P_4 indicates

that it was the largest cheek tooth, a feature in common with *Amelotabes* but in contrast to *Palaeanodon*. There is a slight size reduction from P_4 to M_3.

All postcanines are separated by short diastemata. At the alveolar margin, the alveoli of P_{2-4} slightly exceed the size of the roots they contain; this probably obtained for the molars as well. These traits are characteristic also of *Palaeanodon,* some advanced epoicotheriids, and many toothed xenarthrans.

The ascending ramus and condyle of *Propalaeanodon* resemble those of *Pentapassalus pearcei* and *Metacheiromys tatusia* (Gazin, 1952; Simpson, 1931). The coronoid process is slightly smaller than in contemporary proteutherians (*sensu* Butler, 1972) and rises at an angle of about 110° to the ventral border of the mandible. The condyle, which is narrower transversely than in most toothed xenarthrans and contemporary proteutherians, is situated relatively low but above the level of the tooth row. Its convex articular surface is directed dorsally and backward, as in *P. pearcei.* The mandibular foramen is also relatively low, being situated on the posterior projection of the tooth row. The internal mandibular groove extends from just anterior to this foramen to a point beneath M_1.

As in all metacheiromyids, there is a prominent medial buttress, forming anteriorly a low, narrow ridge lingual to the molars. The dorsal surface of the buttress is roughened, particularly behind M_3. On the external surface of the mandible the masseteric fossa, though rather poorly defined, is deeper than in most other palaeanodonts. The fossa is bounded in front by a crest formed by the thickened anterior border of the coronoid. A more rounded ridge running forward from the condyle forms its lower limit. The horizontal ramus is rather slender and shallow, deeper in front than in back, as in *Palaeanodon.* A small mental foramen is present beneath P_3.

Two palaeanodont humeri from Princeton Quarry are probably referable to *Propalaeanodon schaffi* (Princeton Quarry is about ½ mile northwest of Jepsen Valley Quarry and at about the same stratigraphic level). They are the only other palaeanodont specimens from the same stratigraphic interval as the holotype. PU 13928, a complete left humerus (Fig. 3B), and PU 13929, a distal end of a left humerus, are of appropriate size for *Propalaeanodon.* They are smaller than the humeri of *Palaeanodon ignavus* (Fig. 3A) and *Pentapassalus woodi* (Fig. 3C and Rose, 1978) and slightly larger

TABLE 2

Dimensions (mm.) of humeri in certain palaeanodonts.
(Known humeri of *Palaeanodon* are too incomplete to allow accurate measurements.)

	?Propalaeanodon schaffi, PU 13928	*Metacheiromys dasypus*, AM 11718	*Pentapassalus pearcei* (from Gazin, 1952)	*Pentapassalus woodi*, AC 2766
length	39.3	74.0	37.0	47.1
length of deltopectoral crest (from proximal end of greater tuberosity)	26.3	54.7	28.0	35.5
length of supinator crest (from distal end of humerus)	19.7	38.8	22.0	20.8a
greatest transverse breadth of distal end of humerus	19.8	34.0	21.7	22.6

a = approximate

than the humeri of *Pentapassalus pearcei* (Gazin, 1952). However, all these specimens are essentially similar in structure (see Table 2 for comparative dimensions).

The deltopectoral crest is broad and well developed in PU 13928. It may be relatively slightly longer than in *Palaeanodon,* but this is not certain because the known humeri of the latter are fragmentary and poorly preserved (AMNH nos. 15088, 16831, 16832). The crest is relatively shorter than in *Pentapassalus* and *Metacheiromys* (see Simpson, 1931: 340–342). Its distal end is developed into an anteromedially directed prominence for the insertion of the pectoralis major. Proximolaterally the crest gives rise to a low process for the insertion of the deltoid. A less well-defined crest extends distally from the lesser tuberosity almost to the entepicondylar foramen and bears a small teres tubercle midway along the shaft, on which the teres major inserted, as in *Metacheiromys dasypus* (Simpson, 1931).

The supinator crest is somewhat smaller than in *Pentapassalus pearcei* and *Metacheiromys dasypus* and lacks the hooklike, dorsally projecting flange characteristic of the latter two species.

Nonetheless, this crest is very large and served as the site of origin for the powerful supinator muscle and carpal extensors, and probably the brachioradialis. The median epicondyle (the point of origin of the pronator teres and the carpal flexors) is also large, although smaller than in *Palaeanodon* and *Pentapassalus.* These features of the humerus indicate an animal highly adapted for fossorial habits (Reed, 1954; Hildebrand, 1974). Although the development of the deltopectoral crest in palaeanodonts is (as Emry, 1970, asserts) more like that of manids than of armadillos, the development of the supinator crest is more extreme, even in PU 13928, than in either manids or xenarthrans.

DISCUSSION

Propalaeanodon is the second known Paleocene palaeanodont and the only known Paleocene metacheiromyid. A number of resemblances to epoicotheriids were described above — e.g., seven postcanines, teeth present at the back of the horizontal ramus, two-rooted P_4 — but these are primitive features of palaeanodonts. *Propalaeanodon* resembles *Palaeanodon* (Fig. 1 and 2) in the manner of reduction of its postcanines to peglike teeth (all but one single-rooted) with rounded crowns that apparently lack enamel. Like *Palaeanodon,* its postcanine teeth are housed in tapered alveoli that are larger than the roots and separated by diastemata. Although some of these features also evolved in advanced epoicotheriids (e.g., Bridgerian *Tetrapassalus mckennai,* Chadronian-?Orellan *Xenocranium pileorivale;* Simpson, 1959; Colbert, 1942), the total suite of features evolved much earlier in the metacheiromyids. Thus when metacheiromyids had already achieved these traits, contemporary epoicotheriids, as now understood, retained relatively unreduced teeth with enamel and with very short or no diastemata between them. *Tetrapassalus* and *Xenocranium* are more specialized than *Propalaeanodon* in having fewer teeth and a shortened dentary, but they are more primitive (and typically epoicotheriid) in showing occlusal wear on the teeth.

As metacheiromyids reduced the number of postcanine teeth, they retained a long dentary, hence leaving the back of the horizontal ramus edentulous. The trend in the Epoicotheriidae was toward shortening the dentary as teeth were lost. The antiquity and primitive grade of *Propalaeanodon* results in resemblances to both

metacheiromyids and certain epoicotheriids and highlights the extent of parallelism that has occurred within the Palaeanodonta.

Propalaeanodon is one of those rare fossils that is morphologically intermediate between two well defined families, and it strengthens the alliance of the Epoicotheriidae and the Metacheiromyidae in the suborder Palaeanodonta. Because of its very early acquisition of advanced traits found also in *Palaeanodon* and its stratigraphic and geographic proximity to *Palaeanodon,* I believe *Propalaeanodon* is best regarded as a primitive metacheiromyid, probably lying in or very near the ancestry of *Palaeanodon.* Its very late Paleocene age makes derivation of the Metacheiromyidae from an epoicotheriid similar to early late Tiffanian *Amelotabes* highly probable. Moreover, the primitive aspect of *Propalaeanodon* suggests that metacheiromyids did not become distinct from epoicotheriids before the Tiffanian.

The humeri tentatively referred to *Propalaeanodon* possess specializations characteristic of fossorial mammals (see Simpson, 1931 and Rose, 1978 for additional functional interpretations). They are of interest in demonstrating that the humerus was already highly specialized in this late Paleocene palaeanodont. The deltopectoral crest is very similar to that in *Palaeanodon.* The supinator crest may have been slightly larger than in *Palaeanodon,* but no specimen of *Palaeanodon* preserves a complete supinator crest.

AFFINITIES OF THE PALAEANODONTA

Resemblances of palaeanodonts to Xenarthra and Pholidota have been enumerated by several authors (Matthew, 1918; Simpson, 1931; Emry, 1970). Two questions arise from these comparisons: To what extent are these features demonstrably synapomorphic with one or the other of these orders? To what extent do they reflect parallelism or convergence?

Detailed comparisons led Matthew (1918) to conclude that the Palaeanodonta are definitely related to the Xenarthra and probably to the Pholidota as well. He found no morphologic obstacles to direct descent of both orders from *Palaeanodon,* but for geographic and faunal reasons he deemed this origin of Xenarthra unlikely. He speculated that "early Tertiary faunas of South America ... must be derived apparently from some late Cretacic fauna, unknown to us

but presumably inhabiting some part of North America" (Matthew, 1918: 653). Simpson (1931) detailed many characters to support alliance of the Metacheiromyidae and the Xenarthra, but he concluded that they are not so closely related to the Pholidota. Nearly four decades later, Emry (1970) critically reviewed Simpson's criteria, presenting arguments that he believed vitiated them. In Emry's view, the Metacheiromyidae were directly ancestral to the Manidae, and he included both in the order Pholidota. He rejected any special relationship between palaeanodonts and Xenarthra. Emry therefore discontinued formal recognition of the suborder Palaeanodonta, questioning whether epoicotheriid-metacheiromyid ties were really closer than metacheiromyid-manid relationship.

A primary concern of these and other authors has been that known palaeanodonts were too specialized too early in the record to be direct ancestors of xenarthrans, since contemporary and differently specialized xenarthrans were known from South America (e.g., the early Eocene dasypodid *Utaetus*). In particular, tooth reduction was regarded as "prematurely specialized." The discovery of a primitive epoicotheriid (Rose, 1978) and now a primitive metacheiromyid, both from the late Paleocene and both with much less reduced dentitions, may obviate this objection. Meager evidence attests to the presence of dasypodids in the Riochican of Patagonia (Simpson, 1948), and these are possibly contemporaneous with the Paleocene palaeanodonts. However, while the age of the Riochican is usually given as late Paleocene, its precise correlation with North American land mammal ages is uncertain (Simpson, 1978). At least part of the Riochican is considered by some authors to be younger than late Paleocene, i.e. equivalent to the Clarkforkian and early Wasatchian (e.g., Marshall et al., 1977). It is known that the teeth of early xenarthrans had enamel and developed gabled wear surfaces (Simpson, 1932). Therefore *Propalaeanodon* itself, whose postcanine teeth apparently had already lost enamel and did not develop wear facets, may have been too specialized to be directly ancestral to the Xenarthra (but not Pholidota). These objections do not apply to *Amelotabes,* and nothing now known about it precludes it from possible direct ancestry to Xenarthra or Pholidota. Some postcranial features, such as the extreme development of the supinator crest in palaeanodont humeri, are more specialized than in any known xenarthrans or pholidotans. However, some members of both groups possess an expanded, though smaller, supinator crest.

If known palaeanodonts are ancestral to either Xenarthra or Pholidota, secondary reduction of the supinator crest must have occurred. This would not be required, however, if either or both orders were derived from more primitive palaeanodonts in which the supinator crest was less developed.

Paleogeographic evidence must also be considered. There was no land connection between North and South America in the late Cretaceous or in the Paleocene (Freeland and Dietz, 1971; Malfait and Dinkelman, 1972). Therefore if palaeanodonts gave rise to xenarthrans, they could only have reached South America by rafting (Patterson and Pascual, 1972). In view of the specializations of metacheiromyids and the probability that Metacheiromyidae did not evolve before the Tiffanian, their resemblances to xenarthrans are more likely the result of convergence than of true affinity. Among known fossil forms, epoicotheriids are the most likely candidates for xenarthran ancestors, although this is probably dependent on the existence of earlier representatives than are now known. Derivation of manids from early palaeanodonts is possible and may be supported by the presence of an early manid, *Patriomanis,* in the Chadronian of North America. However, contemporary (or possibly older) manids have long been known from the Quercy Phosphorites of Europe (e.g. von Koenigswald, 1969) and a middle Eocene manid was recently reported from Messel, Germany (Storch, 1978). A direct land connection between North America and Europe existed until the end of Sparnacian (early Eocene) time (McKenna, 1972), hence it was presumably possible for manids to disperse in either direction before the middle Eocene. If manids evolved from palaeanodonts, it is most parsimonious to postulate North America as the place of origin, with subsequent dispersal to Europe.

There can be little question that palaeanodonts were the closest ecological analogues of xenarthrans and pholidotans in the early Tertiary. It may be that palaeanodonts represent an early independent radiation convergent to these orders. Evidence presented here and in other recent studies, however, strengthens the possibility of relationship among these groups. Once again it appears reasonable, as Matthew (1918: 655) wrote sixty years ago, "that there is, after all, a real affinity between the Pholidota and Xenarthra."

ACKNOWLEDGMENTS

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BREVIORA

Museum of Comparative Zoology

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DESCRIPTION OF A NEW HAWAIIAN GOBIID FISH OF THE GENUS *TRIMMA*

PHILLIP S. LOBEL[1]

ABSTRACT. A new gobiid fish species, *Trimma taylori* from Hawaii is described. A key to the nine nominal species of *Trimma* and a discussion of the Hawaiian gobies are included. The genus *Trimma* is reviewed and a preliminary assessment it presented of the possible relationships of *Trimma*. The nominal species of *Trimma* as now recognized may eventually be seen to comprise more than one group.

INTRODUCTION

Gobiid fishes are among the least known of the tropical marine fauna due to their generally miniscule size and secretive habits. Despite the difficulty of collecting and identifying such small reef fishes, a great number of species (over 1500) and genera (ca. 550) have been described (E. Lachner, pers. comm.). This high species diversity of gobiids rivals and exceeds that of most other fish families. However, the full extent of goby species diversity is far from known. For example, *Trimma* presently contains eight nominal species but an additional 25 to 30 remain to be described (D. Hoese, pers. comm.). The primary task of gobiid systematists at this time remains the study of species identification and distribution. The new goby described herein is the first *Trimma* to be found in Hawaiian waters. This species brings the total number of Hawaiian fishes to 682 (see Randall 1976).

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TABLE 1

Morphometric Comparison of *T. taylori* and *T. caesiura* [mean (range)] in percent of standard length

	TRIMMA TAYLORI			TRIMMA CAESIURA		
	Holotype	N=12 incl. Holotype	N=6	Holotype	N=5 incl. Holotype	N=2
Sex	♂	♂	♀	♂	♂	♀
Standard length mm	15.5	13.7(11.8–15.5)mm	13.8(13.1–14.9)mm	26.7	24.4(23.0–26.7)mm	20.3(19.8–20.8)mm
Greatest depth of body	22.6	21.0(18.7–22.8)	22.5(19.1–31.2)	20.2	21.6(18.9–25.2)	21.9(20.2–23.6)
Body width behind gills	15.3	12.5(9.5–15.3)	11.4(9.8–15.2)	17.8	16.1(13.6–17.8)	12.6(11.6–13.5)
Head length	25.0	27.6(24.1–31.0)	28.6(25.9–31.0)	23.2	27.3(23.2–29.8)	29.8(29.3–30.3)
Snout length	4.0	4.4(3.0–6.0)	4.2(3.4–5.0)	4.1	4.0(3.3–4.3)	5.0(5.0–5.0)
Eye diameter	9.7	10.8(9.7–11.8)	10.4(9.4–11.3)	11.2	10.2(9.1–11.2)	10.2(9.4–10.9)
Bony interorbital width	4.0	3.9(0.9–5.6)	3.8(2.7–4.6)	2.1	2.7(1.9–4.0)	2.6(2.4–2.8)
Least depth of caudal peduncle	10.5	9.4(7.4–10.7)	8.5(7.4–10.7)	12.2	10.6(9.8–12.2)	10.3(10.0–10.6)
Caudal peduncle length	21.0	21.5(17.8–25.4)	22.0(19.5–26.3)	23.4	22.2(18.3–23.5)	23.0(19.2–26.8)
Snout to origin of first dorsal fin	33.9	35.3(29.5–38.9)	35.9(33.3–38.2)	32.0	31.9(28.1–34.8)	34.5(33.3–35.6)
Snout to origin of second dorsal fin	52.4	53.5(50.0–61.8)	51.9(50.0–53.4)	56.2	56.3(51.1–56.2)	56.7(55.8–57.6)
Snout to origin of pelvic fin	29.0	30.9(26.8–35.3)	31.1(29.5–33.1)	28.3	31.1(28.3–34.1)	33.5(32.7–34.3)
Caudal fin length	24.2	23.3(17.9–27.1)	25.4(23.2–27.5)	—	18.5(17.2–20.0)	21.3(20.2–22.4)
Pelvic fin length	28.2	25.5(17.0–30.2)	25.6(22.5–27.5)	—	20.1(14.9–24.3)	24.7(20.2–29.1)
Pectoral fin length	16.1	18.0(13.4–21.7)	18.0(14.1–23.9)	—	23.9(20.2–27.0)	21.6(19.2–24.0)
First dorsal spine length	16.1	15.5(11.2–18.4)	17.0(15.2–18.3)	—	14.2(9.2–17.2)	13.8(13.4–14.2)
Second dorsal spine length	40.3	39.7(23.0 55.0)	43.7(38.2 51.8)	—	16.2(11.5 18.3)	18.3(17.4 19.2)
Third dorsal spine length	12.9	16.8(11.2–20.1)	18.3(15.2–20.6)	—	15.8(11.7–17.8)	17.5(17.1–17.9)
Fourth dorsal spine length	—	—	—		15.8(14.2 18.7)	13.3(11.6–14.9)
Fifth dorsal spine length	—	—	—		10.9(10.4–11.6)	11.5(10.8–12.1)

MATERIALS AND METHODS

All specimens were measured with dial calipers. Proportional measurements were made by micrometer in a dissecting microscope and with calipers. Proportions are expressed as percent of standard length (SL) in millimeters (Table 1). Fish were collected with the anesthetic quinaldine mixed with 95% isopropyl alcohol. Specimens of *T. taylori* were captured in a fine meshed net and immediately placed into vials to prevent damage. Color photographs were taken as records of live coloration. Fifty specimens have been deposited as representative types of the species.

Abbreviations of institutional names cited herein are as follows: AMS, Australian Museum, Sydney; BPBM, Bernice P. Bishop Museum, Honolulu; BMNH, British Museum of Natural History, London; CAS, California Academy of Sciences, San Francisco; MCZ, Museum of Comparative Zoology, Harvard University; USNM, National Museum of Natural History, Washington, D.C.

Comparative material examined: *Trimma caesiura*, holotype, USNM 51772; USNM 156727 to 156738 (25+ specimens); USNM 218362. *T. tevegae*, paratypes, USNM 203437 (9). *T. eviotops*, holotype, USNM 116169; paratypes, USNM 116170 (3); paratype, MCZ 37267 (1). X-ray photographs of these species are on file at the USNM and BPBM. I have also examined species of related genera deposited at the USNM, MCZ, AMS, and BPBM.

Trimma Taylori sp. nov.
Fig. 1; Table 1.

HOLOTYPE: BPBM 19919, 15.5 mm SL, taken in a cave at 44 meters depth off the leeward coast of Oahu, Hawaii, near Makaha Beach, July 12, 1975, P. S. Lobel.

PARATYPES: BPBM 19920, 15 mm SL, locality same as holotype, July 20, 1975, P. S. Lobel (specimen photographed in color and figure 1). MCZ 51685, 14 mm SL, collected with holotype. BPBM 19921, 2 specimens each 14 mm SL; collected with BPBM 19920 (cleared and stained). MCZ 51686, 2 specimens, 13 15 mm SL; collected with BPBM 19920. MCZ 51687, five specimens, 12–13.5 mm SL; collected with holotype. USNM 215323, 9 specimens, 6 13 mm SL; same location as holotype, Aug. 13, 1975, P. S. Lobel. AMS I18686–001, eight specimens, 6–13 mm SL; same location as

Figure 1. *Trimma taylori*, male 15 mm. s.l. Paratype BPBM 19920.

holotype, Aug. 13, 1975, P. S. Lobel. CAS 35450, six specimens, 11 13 mm SL; collected with BPBM 19920. BPBM 19922, eight specimens, 6 14.5 mm SL; same location as holotype, Aug. 13, 1975, P. S. Lobel. BMNH 1976.4.6.1–7, seven specimens, 6–13 mm SL; same location as holotype, Aug. 13, 1975, P. S. Lobel.

Diagnosis. This species can be easily distinguished from all other *Trimma* spp. by a combination of characters: Dorsal VI-I, 10, anal I, 10, and pectoral 14; second spine of the first dorsal fin filamentous, longest, extending past the midpoint of the second dorsal fin when depressed.

Description. Morphometric characters of specimens are presented in Table 1. Tooth shape and pattern are illustrated in Figure 2. Head length 25% of standard length. Eye diameter about 40% head length. First dorsal fin originates one third the standard length distance from snout. Mouth slanted about 45° upward, corner of mouth in line with midpoint between forward margin of eye and pupil. Eye to snout distance approximately one-half eye diameter. Body scaled except for head and operculum, but including nape. Scales in longitudinal series from opercule to hypural base, 22–23. Seven scales from the origin of the anal to the first dorsal. Middorsal area from first dorsal spine to head with three scales. Gill raker count of three specimens: 3–1–12, 3–1–13, and 3–1–14. Five lobes on

pseudobranch. Fin ray formulae: Dorsal VI–I, 10, anal I, 10, pelvic I5, and pectoral 14. Vertebral count 25, not including urostyle. Dorsal fins separate. Second spine of first dorsal fin elongated, extending over second dorsal fin. Posterior most ray of second dorsal fin and of anal fin split to base but counted as one. Pelvic fins connected at base but not united by frenum. Additional characters are the same as described for the genus (see Cohen and Davis 1969).

Color in life. Overall color pale straw yellow with darker yellow pigment spots bordering base of each scale. Immediately posterior to the eye, orange spot almost equal in area to eye. Dorsal portion of this orange spot speckled with small melanophores. Head dorsally speckled with numerous orange and black chromatophores. Dorsal and anal fins with broad deep orange band at base and with thin band of black pigmentation above it; fins overall light orange, with a diffuse dark edge. Caudal fin similar in color to dorsal and anal fins but without deep orange band. Pelvic and pectoral fins yellow-orange.

Figure 2. *Trimma taylori,* detail of mouth and teeth. S.E.M. photo by E. Seling.

MALE

FEMALE
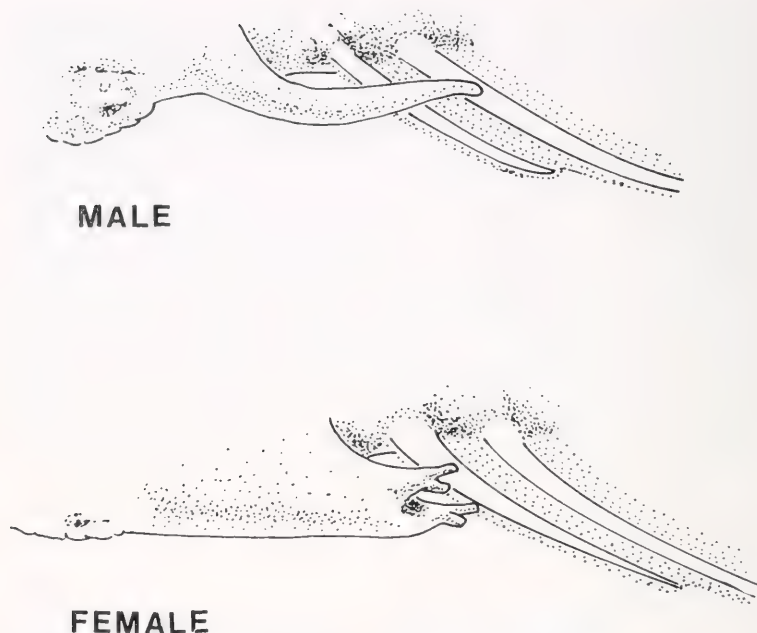
Figure 3. *Trimma taylori*, sexual dimorphism of genital papillae. Drawn from MCZ 51686. Paratypes by Karsten Hartel.

Color in alcohol. All colors vanish, body pale. Pigment spots on dorsum of head visible after one year but fade thereafter. Fins transparent.

Sexual dimorphism. Morphometric differences are not immediately apparent between the sexes; however, males and females may be distinguished on the basis of genital papillae (Fig. 3). The papilla of the male is slender, curved and tapers to a point posteriorly. The female's papilla is greater in diameter than that of the male and uniform in thickness, terminating in a round opening with a bilobed flap bilaterally; it is also directed posteriorly but it is not as long as that of the male. Immature gobies exhibit no sexual difference in the shape of the papilla (see also Egami 1960).

There are significant differences in both shape and size of male and female genitalia among *Trimma eviotops, T. taylori* and *T. caesiura*. The genitalia of *T. taylori* and *T. caesiura* are very similar in shape and structure but differ in relative length of the papilla of the male.

The relative lengths of male papillae (in percent of standard length) are: *T. taylori* 6%, *T. caesiura* 3.4%, and *T. eviotops* 2.2%. The papilla of *T. eviotops* is not curved as is that of *T. taylori* (Fig. 3), but extends straight posteriorly and is comparatively thinner and not tapering to a point, ending bluntly. A pigment line runs ventrally along the length of the male papilla of *T. eviotops*.

Arai (1964) illustrated the genital papillae of 25 goby species. Four are particularly relevant here: *Eviota abax* (Jordan and Snyder), *Quisquilius eugenius* (Jordan and Evermann), *Zonogobius semidoliatus* (Cuvier and Valenciennes) and *Fusigobius neophytus* (Günther) (Fig. 4 modified from Arai, 1964). The genitalia in both sexes of *T. taylori* and *T. caesiura* appear most like that of *Fusigobius neophytes*. The genital papilla of *T. eviotops* is more similar to those of *Zonogobius semidoliatus*. The genitalia of *Quisquilius* and *Zonogobius* are superficially more similar to each other than either is to those of *Fusigobius*. Such comparisons may become important when the phylogeny of these taxa is revised.
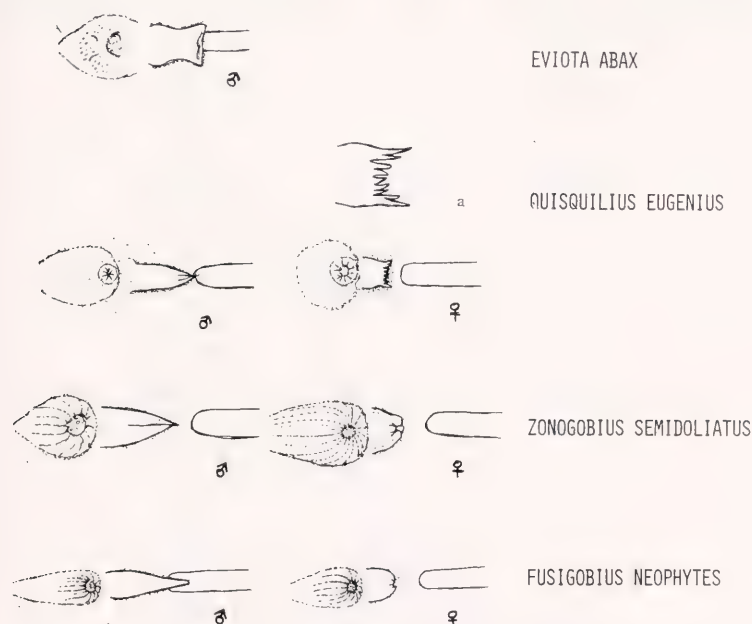
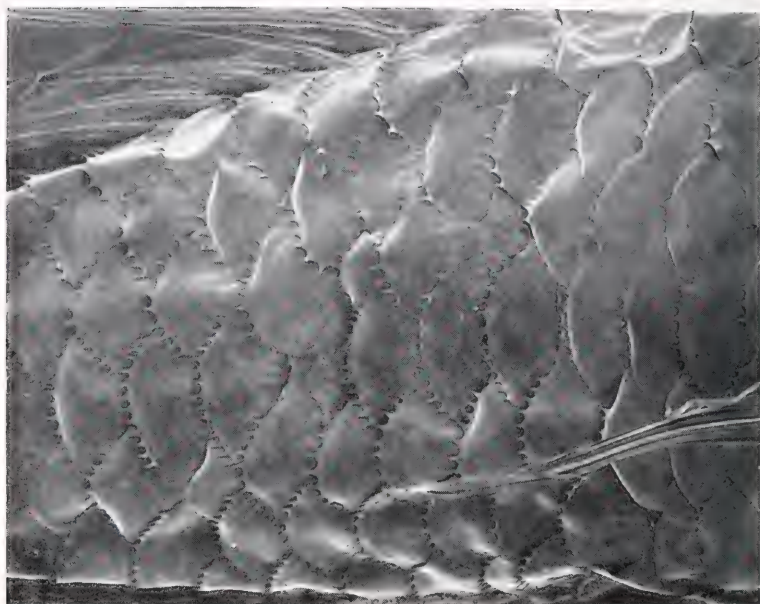Figure 4.   Genital papillae of some related Gobiids. Modified from Arai (1964).

Figure 5. *Trimma taylori,* detail of scales on flank. S.E.M. photo by E. Seling.

Scale Morphology.   The number of ctneii in a single row along the
posterior margin of the scale may differentiate species of *Trimma.*
The pattern and structure of scales of *T. taylori* (Fig. 5), and of *T.
caesiura* (Fig. 6), is characteristic for each species. *Trimma taylori*
possess fewer and larger scale ctenii (mean 10.9, range 8–14 per scale,
N = 12) than does *T. caesiura* (mean 31.6, range 28–36, per scale, N =
5). Comparison to other species was not possible due to the
unavailability of specimens. Consequently, the taxonomic value of
such scale morphology is uncertain.

Zoogeography.   *Trimma taylori* is known only from the island of
Oahu, Hawaiian archipelago. All other *Trimma* species occur in the
Indopacific oceanic region or in the Indian Ocean. None are
recognized from the Atlantic Ocean or within the temperate zones.
All *Trimma* spp. with known habits are reef dwellers.

Entymology.   *Trimma taylori* is named in honor of Dr. Leighton R.
Taylor, Jr. on the occasion of his appointment as director of the
Waikiki Aquarium. A tradition of the Waikiki Aquarium has been

that each of its directors have a uniquely Hawaiian fish as a namesake.

DISCUSSION

The nominal species of *Trimma*

The original description of the genus *Trimma* was not adequate and there has consequently been confusion in the generic assignment of the species. The genus *Trimma* was defined on the basis of *T. caesiura* by Jordan and Seale (1906). It was diagnosed as "near *Eviota* but the region before the dorsal is fully scaled. In texture the species is firmer and less translucent" (Jordan and Seale, 1906, p. 361). This description does not adequately define the genus with regard to some of the species that have since been included in it. Additional morphometric data of *T. caesiura* are listed in Table 1 with comparisons to *T. taylori*.

The species included in the genus *Trimma* which appear closely related to *T. caesiura* based on the original generic characters and other characters described below are *Trimma naudei* Smith (1956) and *T. tevegae* Cohen and Davis (1969). Other species placed in

Figure 6. *Trimma caesiura*, details of scales on flank. S.E.M. photo by E. Seling.

Trimma present an enigma. *Trimma eviotops* Schultz (1943) is presently considered a valid species but its placement in *Trimma* will soon be reconsidered (S. Karnella, pers. comm.). It clearly differs from *T. caesiura* in the lack of scales along the nape. *Trimma eviotops* does not fit comfortably in other closely related genera. For example, it differs from species of *Eviota* by lacking head pores, although this may not be taxonomically significant. Smith (1956) remarked that *T. eviotops* may well become the type of a new genus. Consequently, it is included here only provisionally. However, there is no difficulty in assigning *Trimma taylori* to the genus *Trimma*.

I follow Hoese's (pers. comm.) unpublished classification for species of *Trimma*. The species (as originally designated) are *Eviota macrophthalma* Tomiyama (1936), *Eviota grammistes* Tomiyama (1936), *Zonogobius flammeus* Smith (1959) and *Zonogobius corallinus* Smith (1959). These all differ from *Trimma caesiura* in lacking predorsal scales along the nape but resemble *Trimma eviotops* in that character. Until related species and genera are better known the decision to include these species in *Trimma* involves the fewest complications. However, if *T. eviotops* is removed from *Trimma*, then the generic placement of these other species should also be carefully reconsidered since some are more similar to *T. eviotops* than to *T. caesiura*, the species on which the genus is based. Meristic and color traits of the nominal species of *Trimma* are contrasted in Table 2.

There exists numerous problems with the classification of the genera and species of gobies. However, most of the conflicts cannot be solved until both more species are described and the characters defining the genera are delineated. The genus *Trimma* is no exception but since assignment of *Trimma taylori* into this genus offers no conflicts, discussion of other issues is postponed until more data are available.

Ecology. *Trimma taylori* appears to be an exclusively deep reef species that inhabits the recesses of caves and crevices. Its habits are somewhat like those described for *T. tevegae* (Cohen and Davis, 1969). During the daytime, swarms of 50 to 150 individuals hover near the ceiling, in about the midsection of a cave or pocket. The shallowest location at which adults have been observed is at a depth of 30 meters. A few juveniles have been seen somewhat shallower.

The cave habitat in which all specimens were collected was typically a small crevice (one to two meters deep) along a vertical wall of the deep reef, Oahu, Hawaii. Perhaps it is significant that these shallow pockets did not house holocentrids or priacanthids. Caves containing the latter were inspected for *Trimma taylori* but none were found. Sympatric cave inhabitants which were conspicuous included a prawn, *Stenopus* (an undescribed species) and the fishes *Pterois sphex* (Scorpaenidae), *Apogon maculiferus* (Apogonidae), *Gymnothorax* spp. (Muraenidae), an undescribed species of *Quisquilius* (Gobiidae), Scorpaenid sp., and *Pseudanthias* sp. (Serranidae-Anthiinae). Of these fishes, only *Pterois sphex*, *Gymnothorax* spp. and *Apogon maculiferus* seem likely potential predators of *T. taylori*.

Trimma taylori feeds on harpacticoid copepods. Eight specimens were examined for gut contents and three of these were empty.

KEY TO THE NOMINAL SPECIES OF TRIMMA

1. a. Predorsal scales on nape 2
   b. No scales on nape 5
2. a. Dorsal fin with 8 rays 3
   b. Dorsal fin with more than 8 rays 4
3. a. Gill raker on first arch 3+1+16 .... *T. caesiura*
   b. Gill raker on first arch 3+1+13 or 14 .... *T. naudei*
4. a. Dorsal fin VI–I10, Pectoral 14 .... *T. taylori*
   b. Dorsal fin VI–I9, Pectoral 13 .... *T. tevegae*
5. a. Pectoral fin with fewer than 19 rays 6
   b. Pectoral fin with 19 rays .... *T. coralinus*
6. a. Pectoral fin with 17 rays 7
   b. Pectoral fin with fewer than 17 rays 8
7. a. Body with eight dark bars or saddles .... *T. eviotops*
   b. Body without bars or saddles .... *T. flammeus*
8. a. Pectoral with 15 rays, 11 scales transverse series .... *T. grammistes*
   b. Pectoral with 16 rays, 9 scales transverse series .... *T. macrophthalma*

SUPPLEMENTARY KEY TO HAWAIIAN GOBIID FISHES

1. a. pelvic fins separate (no frenum) 2
   b. pelvic fins united to form a cup .... See Gosline and Brock 1960, p. 266
2. a. each scale with a dark crescent shaped mark, no spines on the preopercle
      3
   b. no markings on scales, head compressed, 3 to 5 spines on the preopercle ..
      .... *Asterropteryx semipunctatus*
3. a. no predorsal scales on nape .... *Eviota epiphanes*
   b. predorsal scales on nape present .... *Trimma taylori*

TABLE 2

Comparison of the Nominal species of *Trimma*

Nominal Species	Author	Dorsal fin	Anal fin	Pectoral fin	Pelvic fin	Longitudinal scales
T. caesiura[1]	Jordan and Seale 1906	VI–I,8	I,8	15	I,5	23–25
T. coralinus	(Smith 1959)	VI–I,10	I,9	19	—	30
T. eviotops	Schultz 1943	VI–I,9–10	I,8–9	17	I,5	26–27
T. flammeus	(Smith 1959)	VI–I,9–10	I,8–10	17	—	26–36
T. grammistes[2]	(Tomiyama 1936)	VI–I,10	I,9	15	I,5	30
T. macrophthalma[2]	(Tomiyama 1936)	VI,I,9	I,9	16	I,5	23
T. naudei	Smith 1956	VI–I,8	I,8	16	—	24–25
T. taylori	n.sp.	VI–I,10	I,10	14	I,5	22–23
T. tevegae	Cohen and Davis 1969	VI–I,9	I,9	13	I,5	28

[1] I examined 21 specimens for additional counts.
[2] Pectoral fin count from drawing with description.

TABLE 2

Comparison of the Nominal species of *Trimma*

Scale Transverse	Gillrakers on first arch	Vertebrae	Locality	Live Coloration
6–7	3–1–16	25	Samoa	Plain bright red with grey spots on back of tail and grey spots on many scales of back and head. Fins all bright red.
10–11	3+1+10	—	Seychelles	Body red with two silvery areas on back below first, and three below second dorsal fin. Orange spots on head and peduncle. Rays red with pink membrane.
8–9	3+1+11–12	25	Phoenix & Samoan Islands	Pale with eight vertical bars, saddles on head and body.
8–9	3+1+11–12	—	Australia & S. Africa·	Light orange with darker spots; edge of soft dorsal and caudal, dusky.
11	—	—	Japan	Longitudinal dark bands.
9	—	—	Japan	(not described)
8	3+1+13–14	—	Seychelles	Body and fins brilliant orange-scarlet, irregularly mottled with iridescent light areas; dorsal fin with two light pink bars between the orange.
7	3+1+12–14	25	Hawaii	All straw yellow with orange-red and dark pigment spots on head.
7	—	25	New Britain	(Live body color not described) Dark reddish spot at end of caudal peduncle.

NOTE: *Asterropteryx semipunctatus* and *Eviota epiphanes* were placed in the Eleotridae by Gosline and Brock (1960). However, the only eleotrid in Hawaii is *Eleotris sandvicensis*, which is restricted to freshwater. It can be easily distinguished from the gobies. *E. sandvicensis* possesses about 75 scales in longitudinal series whereas gobies generally have less than 30 longitudinal scales. In addition, eleotrids are primarily freshwater and have six branchiostegal rays; gobies are mostly marine and have five branchiostegal rays. There are 21 other gobies presently known in the Hawaiian Islands.

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B R E V I O R A

Museum of Comparative Zoology

TWO NEW SPECIES OF *ELEUTHERODACTYLUS* (AMPHIBIA: LEPTODACTYLIDAE) FROM THE LOWLANDS AND LOWER CLOUD FORESTS OF WESTERN ECUADOR

JOHN D. LYNCH[1] AND KENNETH MIYATA[2]

ABSTRACT: *Eleutherodactylus muricatus* sp. nov., an ally of the large, flare-snouted frogs of the *rubicundus* assembly, is named from lowland and lower cloud forest localities in Provincia Pichincha, Ecuador. The new species is smaller than its sympatric allies *E. crenunguis* and *E. latidiscus. Eleutherodactylus tenebrionis* sp. nov., is also found in primary lowland and lower cloud forests in west-central Ecuador. It is allied to a species found in the high cloud forests in western Ecuador but differs in color pattern and lacks a calcar and ulnar tubercles.

INTRODUCTION

Approximately 15 species of *Eleutherodactylus* inhabit the Pacific lowlands of Ecuador (Lynch, in press) and perhaps another 40 species are found in the cloud forests of the Pacific versant in the Ecuadorian Andes. Most of these frogs are small organisms (less than 35 mm SVL) but two members of the *rubicundus* assembly [*Eleutherodactylus crenunguis* Lynch and *E. latidiscus* (Boulenger)] are much larger species having long, slender limbs and digits and large emarginate (or notched) digital pads.

Our field work in western Ecuador over the past several years has revealed that *crenunguis* is a frog of the lower cloud forests (800–1500 m) and is not an altitudinal replacement for *latidiscus* (20–1500 m). In the course of this field work two additional species having notched or indented digital pads were found in sympatry

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with both of the larger species. In spite of sharing the notched pads, only one of these species seems allied to the *rubicundus* assembly as defined by Lynch (1979). The other species appears to be most closely allied to a species found in the high cloud forests of western Ecuador (Lynch and Trueb, in press).

The format of the descriptions follows Lynch's long-used style. Abbreviations employed below include the following: SVL — snout-vent length; HW — head width; IOD — interorbital distance; E-N — eye to nostril distance.

Eleutherodactylus muricatus sp. nov.

Holotype: MCZ 94469, an adult male collected at the Río Faisanes where it is crossed by Ecuador Highway 28 (the road from La Palma to Quito via Chiriboga), 14.4 km from the junction with Highway 30 (the Aloag to Santo Domingo de los Colorados road) at La Palma, Provincia Pichincha, Ecuador, 1380 m, on 12 November 1977 by Ken Miyata.

Paratypes. MCZ 92091, 92095, 92100–01, 94848, 97528–31, USNM 211172–74, topotypes; MCZ 97592, Centinela, 14.1 km SE Patricia Pilar by road, Provincia Pichincha, 570 m; MCZ 90337, 94456, 94460, Centro Cientifico Rio Palenque, 47 km S Santo Domingo de los Colorados, Provincia Pichincha, 220 m.

Diagnosis. 1) skin of dorsum smooth with numerous conical tubercles, that of venter feebly areolate; no dorsolateral folds; no anal sheath; 2) tympanum moderately distinct, its length ¼ eye length; 3) snout subacuminate in dorsal view, rounded in lateral profile; canthus rostralis moderately distinct; 4) upper eyelid much wider than IOD, bearing many conical warts: no cranial crests; 5) vomerine odontophores large, triangular in outline, narrowly separated; 6) males with vocal slits, subgular vocal sac; no nuptial pads; 7) first finger shorter than second; all digits bearing broad discs, pads on fingers II–IV, those of III and IV notched; 8) fingers bearing lateral keels; 9) 1–2 small ulnar tubercles; 10) one large conical tubercle on heel; low tubercles along outer edge of tarsus; short inner tarsal fold; 11) two metatarsal tubercles, inner elongate, 10 times size of round, subconical outer; supernumerary plantar tubercles at base of toes; 12) toes bearing lateral fringes, not webbed; toe

Figure 1. (A) *Eleutherodactylus muricatus*, MCZ 94456, 33.8 mm SVL; (B) *E. tenebrionis*, KU 146171, 36.9 mm SVL; (C) *E. tenebrionis*, KU 179224, 30.6 mm SVL; (D) *E. latidiscus*, KU 131612, 45.1 mm SVL.

pads notched, smaller than those of outer fingers; 13) dorsum brown with black spots; ventral surfaces brown with cream flecks; slightly darker brown chevrons on throat; posterior surfaces of thighs brown; 14) adults from type-locality moderate-sized, males 31.8– 40.7 (x̄= 36.0, n = 4) mm SVL, one female 46.3 mm SVL; two gravid females from the lowlands (Centinela and Rio Palenque) are only 33.8–36.0 mm SVL.

Eleutherodactylus muricatus is most similar to *E. crenunguis* but differs in coloration (no orange patch on the breast) and in having fewer, larger tubercles on the dorsum (Fig. 1). It is also smaller than *E. crenunguis* (Lynch 1976).

Description. Head as wide as or wider than body, wider than long: HW 37.1–39.9 (x̄ = 38.4, n = 7) per cent SVL; snout subacuminate in dorsal view, rounded in lateral profile; nostrils weakly protuberant, directed dorsolaterally; canthus rostralis relatively sharp (swollen), straight or weakly convex; loreal region concave, sloping gradually to lips; lips flared; E-N 80.7–100.0 per cent (x̄ = 89.4, n = 7) eye length; upper eyelid 100.0–132.3 per cent (x̄ = 119.7, n = 7) IOD, bearing many pungent tubercles; no cranial crests; supratympanic fold moderately distinct, obscuring upper edge of tympanum; tympanum not prominent, round, separated from eye by distance equal twice tympanum length; tympanum length 22.0–27.9 (x̄ = 25.1, n = 6) per cent eye length except in MCZ 94456 (small female from Rio Palenque has ratio of 37.5 per cent); postrictal tubercles present, not prominent; choanae round, not concealed by palatal shelf of maxillary arch; vomerine odontophores median and posterior to choanae, large, triangular in outline, separated on midline by distance less than 1/3 an odontophore width, each larger than a choana, bearing 5–12 teeth in a transverse row; tongue longer than wide, its posterior edge notched; posterior 1/3 not adherent to floor of mouth; males with vocal slits posterolateral to tongue, median subgular vocal sac.

Skin of dorsum smooth but bearing many warts, most numerous on lower back (where skin is tuberculate); many elongate, subconical warts on flanks; no dorsolateral folds; no anal sheath; skin posterior and posterolateral to anus areolate but also bearing conical warts; skin of throat areolate, that on other ventral surfaces smooth with very feeble areolations; discoidal folds well anteriad to groin; one or two small ulnar tubercles; palmar tubercle bifid, larger

than oval thenar tubercle; several prominent supernumerary palmar tubercles; subarticular tubercles round, pungent; fingers bear lateral keels; all digits with pads, that of thumb scarcely wider than digit below pad, on II twice as wide, on III–IV three times as wide (wider than tympanum); pads of fingers III–IV notched apically; discs on all pads broader than long; fingers long, first slightly shorter than second; thumb of male lacking nuptial pad or swelling.

Numerous tubercles on heel, one large conical tubercle (not a calcar); low tubercles along outer edge of tarsus; short fold at base of inner metatarsal tubercle which is three times as long as wide, 10 times size of round, subconical outer metatarsal tubercle; supernumerary plantar tubercles at bases of each toe; subarticular tubercles longer than wide, pungent; toes bearing distinct lateral fringes, broad discs, expanded pads; pads notched apically, smaller than those of outer fingers; heels of flexed hind limbs broadly overlap; shank 54.7–62.2 per cent ($\bar{x} = 58.4$, $n = 7$) SVL.

Brown above with black spots enclosing tubercles; bars evident on thighs but remainder of pattern (limbs, labial bars, canthal-supratympanic stripe, dorsal chevrons, etc.) only suggested by black spots; venter brown with cream flecks and small spots; inverted brown chevrons on chin and throat; undersides of limbs and groin brown with cream flecks; anterior and posterior surfaces of thighs brown with cream flecks. In small individuals, ground color gray and with evident shank bars (narrow and oblique), labial bars, and canthal-supratympanic stripe.

In life, *E. muricatus* from the type locality are pale to dark brown with black rings around large tubercles; flanks paler brown with yellowish wash; venter dark purplish-brown with yellow-brown mottling; iris gold flecked with black. Lowland specimens lack the black rings around the tubercles; the venter is a muddy yellow mottled with dark brown; the lower flanks, groin, and underside of the limbs have a purplish-brown wash; the iris is copper. The above color descriptions apply to daytime patterns; at night all individuals are much paler in dorsal coloration, ranging from pale buff to olive brown, but the various markings remain intact.

Measurements of holotype (in mm).   SVL 32.3; shank 20.1; HW 12.5; head length 11.6; upper eyelid 2.9; IOD 2.9; tympanum length 1.0; eye length 4.3; E-N 3.9.

Etymology. The specific epiphet is derived from the Latin, meaning spiny, in reference to the pungent tubercles on the dorsum and upper eyelid.

Variation. The two adult females from low elevations (MCZ 94456 from Río Palenque, 220 m, and MCZ 97592 from Centinela, 570 m) are much smaller than the only adult female from the type-locality. They are also peculiar (Fig. 1) in having prominent vertebral stripes which are yellow-cream to buffy orange in life. All of the material from the lower elevations has venters more pale than the topotypic material; in life the ventral surfaces of the topotypic population are predominantly brown with some yellowish mottling while those of the low elevation populations are predominantly yellowish with brown mottling. The lowland populations also have more prominent tubercles on the eyelids and dorsum. All of these differences are rather minor and probably represent slight geographical or altitudinal variation. We are taking a conservative approach in assigning all of these specimens to the same taxon; further work may well prove we have confused two species.

Remarks. Adults of *E. crenunguis* and *E. latidiscus* are seldom encountered. No adult females of *E. crenunguis* have been found, although juvenile females to 41.3 mm have been examined, and adult males range in size from 35.0 to 49.2 mm SVL. Very few adults of *E. latidiscus* are available even though juveniles are often quite common. Three males with vocal slits are 43.9–50.0 mm SVL and four females having convoluted oviducts are 49.7–64.5 mm SVL. Both of these frogs are considerably larger than the sympatric *E. muricatus.*

Natural History. *Eleutherodactylus muricatus* from the type-locality have been collected on streamside vegetation within 1.5 m of the water surface. Several specimens were taken on logs just above water level, but the majority were perched on large leaves adjacent to the stream. For a description of the type-locality see Miyata (in press). Individuals are found in low density on most nights at this locality.

The lowland specimens have all been taken from primary forest or, in the case of the Centinela specimen, from very recently eut primary forest. The Río Palenque specimens were taken from low vegetation in forest with a dense canopy on rainless nights.

Eleutherodactylus muricatus appears to have a spotty distribu-
tion, somewhat analogous to that seen in other anurans in this
region (Lynch 1977). *E. muricatus* has not been collected at the Río
Orito, a locality very close to the type locality, despite several visits
by field parties from the University of Kansas. More field work is
needed to confirm the spottiness of the distribution.

Eleutherodactylus tenebrionis

Holotype: MCZ 90326, an adult male collected at the Hotel
Tinalandia, 16 km E Santo Domingo de los Colorados by road,
Provincia Pichincha, Ecuador, 800 m, on 6 August 1975 by Ken
Miyata.
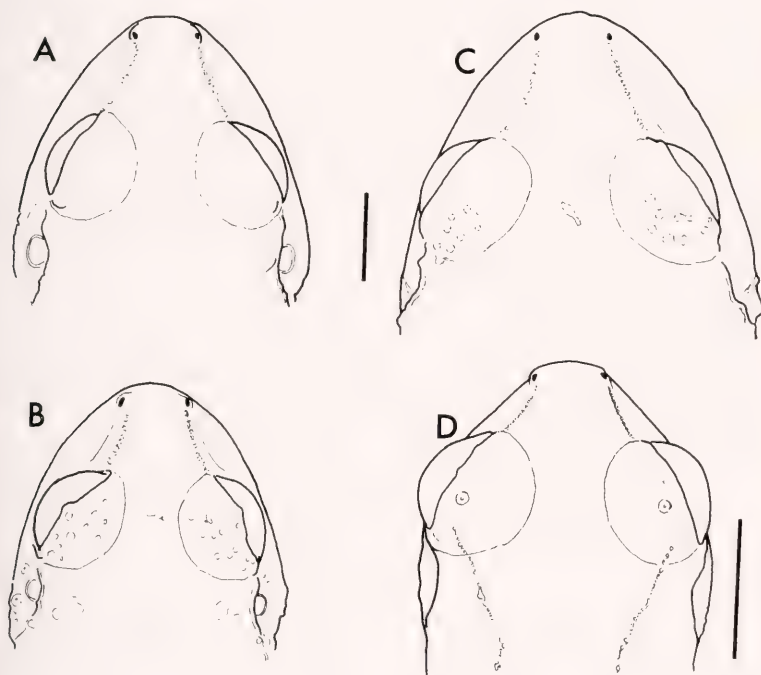
Figure 2. Outlines of heads of western Ecuador *Eleutherodactylus*. (A) *E.
crenunguis*, MCZ 92099; (B) *E. muricatus*, MCZ 92095; (C) *E. latidiscus*, cotype,
BM 98.4.28.109; (D) *E. tenebrionis*, MCZ 92081. Scale for A–C is between figs.
A and C; that for D is to its right. Scales equal 5 mm.

Paratypes: MCZ 88890, 90325, 90327–29, 92079–81, 94712, top-
otypes; KU 179224–27, Santo Domingo de los Colorados, Provincia
Pichincha, 580 m; KU 179228–30, 2 km E, 1 km S Santo Domingo
de los Colorados, Provincia Pichincha, 600 m; MCZ 97596–97,
USNM 211176, Centinela, 14.1 km SE Patricia Pilar by road, Pro-
vincia Pichincha, 570–600 m; KU 146171, 165874–77, MCZ 94864–
65, 94867, 98164–66, USNM 211175, Centro Cientifico Río
Palenque, 47 km S Santo Domingo de los Colorados by road,
Provincia Pichincha, 170–220 m.

Diagnosis. 1) Skin of dorsum smooth with occasional tubercles,
that of venter areolate; no dorsolateral folds; no anal sheath; 2)
tympanum distinct, round, its length 1/4–2/5 eye length; 3) snout
round in dorsal view, truncate in lateral profile; canthus rostralis
distinct; 4) interorbital space narrower than upper eyelid; low cra-
nial crests in females; small tubercle on upper eyelid; 5) vomerine
odontophores elevated, triangular in outline, narrowly separated; 6)
males with vocal slits; males lack nuptial pads on thumb; 7) first
finger shorter than second; all digits bearing broad discs on
expanded pads, pads of fingers III–IV largest, emarginate, those of
I–II smaller, rounded apically; 8) fingers lack lateral fringes; 9) no
ulnar tubercles; 10) small tubercles on heel, none on knee or tarsus;
11) two metatarsal tubercles, inner oval, 4 times size of flat outer;
low supernumerary tubercles at bases of toes II–IV; 12) toes lack
lateral fringes; discs broader than long on weakly emarginate pads,
pads smaller than those on fingers; 13) brown above with little
indication of pattern (Fig. 1); venter cream with extensive brown
reticulation; undersides of limbs brown with cream flecks; anterior
and posterior surfaces of thighs brown with small cream flecks; in
life, iris blue; 14) adults moderate-sized, males 20.8–26.8 ($\bar{x} = 23.8$
$\pm$ 0.9, n = 16) mm SVL, females 30.6–36.9 ($\bar{x} = 33.8 \pm 1.6$, n = 7)
mm SVL.

Eleutherodactylus tenebrionis has no close relatives known to us
except for an undescribed species from the upper cloud forests
(2000–2700 m) in Provincias Imbabura and Pichincha, Ecuador
(Lynch and Trueb, in press) which differs from *E. tenebrionis* in
having prominent conical tubercles on the forearm, tarsus, and
upper eyelid and a calcar on the heel.

Description. Head as wide as or wider than body, wider than

long; HW 37.0–41.4 per cent ($\bar{x}$ = 39.3, n = 23) SVL; snout round in dorsal view, truncate in lateral profile; E-N in males 72.0 84.8 per cent ($\bar{x}$ = 77.9, n = 16) eye length, in females 75.9–87.0 ($\bar{x}$ = 82.9, n = 7); nostrils protuberant, directed laterally; canthus rostralis distinct, weakly concave; loreal region concave, sloping abruptly in males and gradually in females to lips; lips not flared (Fig. 2); upper eyelid 110.3–165.7 per cent ($\bar{x}$ = 125.8, n = 23) IOD, bearing 1–2 small conical tubercles; adult females have low cranial crests (not evident in smaller frogs); lower 3 4 of tympanum distinct, upper edge hidden by diffuse supratympanic fold; tympanum separated from eye by almost its length; tympanum length in males 25.0–35.0 per cent ($\bar{x}$ = 29.4, n = 16) eye length, in females 29.6–38.5 (x = 32.9, n = 7); small postrictal tubercles present; skin on rest of head smooth; choanae longer than wide, not concealed by palatal shelf of maxillary arch; vomerine odontophores median and posterior to choanae, pungent, triangular in outline, bearing 5–7 teeth in a transverse row, separated on midline by a space equal to 1/3–1/2 of odontophore width; odontophores nearly as large as a choana; tongue longer than wide, its posterior border notched, posterior 1 5 not adherent to floor of mouth; male with vocal slits.

Skin of dorsum essentially smooth but some small, low, flat warts on lower back (in a few examples these warts are pungent) and a few tiny warts scattered on back; no dorsolateral folds; flanks become areolate, areolation continuing onto venter; throat smooth; discoidal folds present; no anal sheath; no ulnar tubercles; palmar tubercles bifid (outer lobe the smaller), as large as or smaller than oval thenar tubercle; if present, supernumerary palmar tubercles flat, indistinct; subarticular tubercles relatively low, round; fingers lacking lateral fringe or keel; all fingers bearing broader than long discs; pad smallest on I, intermediate on II, largest on III and IV; pad of III as large as tympanum; pads on III and IV feebly emarginate; II longer than I; males lack nuptial pads.

No tubercles on knee or tarsus; 1 2 small tubercles on heel; inner metatarsal tubercle twice as long as wide, outer 1 4 (or less) size of inner, flat; supernumerary plantar tubercles low, at bases of toes II IV; subarticular tubercles longer than wide, not conical; toes lack lateral fringes, bearing broad discs on expanded, feebly emarginate pads (toe pads smaller than those on outer fingers); heels of flexed hind legs overlap; shank of males 52.8–62.5 ($\bar{x}$ = 57.9, n = 16) per cent SVL, of females 52.2–59.7 ($\bar{x}$ = 56.1, n = 7).

Brown above with diffuse dark brown or black scapular "W", supratympanic stripe, interorbital bar, and indefinite sacral chevron; canthal stripe, labial bars, anal triangle brown, not distinct; limb bars brown, nearly transverse on shanks, about as wide as interspaces; flanks pale brown (cream invasion of brown); venter cream with dense fine brown reticulation; some cream flecks on limbs, fewest on underside of shank; throat and breast heavily stippled with brown (relative to venter); anterior and posterior surfaces of thighs (and groin) brown with small cream flecks.

In life, *E. tenebrionis* is burnt umber with black and dull golden flecks above; the venter is gray with gray-brown mottling. The iris is gray-blue. At night they tend to be a much paler yellowish-tan dorsally with prominent black spots in the shoulder region.

Measurements of Holotype (in mm). SVL 26.4; shank 15.0; HW 10.8; head length 10.4; upper eyelid 3.0; IOD 2.6; tympanum length 1.4; eye length 4.4; E-N 3.3.

Etymology. The specific epithet is derived from the Latin, meaning a lover of darkness, in reference to the restriction of *E. tenebrionis* to primary forest.

Natural History. *Eleutherodactylus tenebrionis* is restricted to primary forest, where it is most frequently found at night on low vegetation along stream courses. The lowland rain forests in western Ecuador which this species inhabits are characterized by full canopies and relatively sparse understories. Epiphytes are especially prominent in these wet forests, and some of the lowland forests appear superficially like cloud forest. Much of this region is covered with clouds during the dry season which encourages this lush growth even though annual rainfall is only moderately heavy (Dodson and Gentry 1978).

The preference of *E. tenebrionis* for streamside vegetation appears to be real and not a sampling bias. One of us (KM) has spent considerable time working study plots in primary forest at Rio Palenque located on top of a plateau and lacking any streams and has never encountered *E. tenebrionis* there. Along the small creeks elsewhere in the Rio Palenque forest they are encountered regularly, if not commonly. The specimens from Centinela likewise all came from along a small forest stream rather than from the primary ridgetop forest or the recently cleared hillside forest. At Tinalandia

occasional individuals were found perched on low vegetation within 2 m of the ground along a hillside about 30 m above stream level, but this area at 800 m elevation is more mesic than the lower localities.

DISCUSSION

The flared lips and long snouts of *E. crenunguis, E. latidiscus, E. muricatus,* and *E. rubicundus* are in marked contrast to the condition seen in *E. tenebrionis* (Fig. 2). All of these species share the narrow IOD, a relatively uncommon trait among *Eleutherodactylus* (Fig. 2). Low cranial crests are present in most of these species (except *E. muricatus*) but are generally evident only in adult females. These traits are also exhibited by *E. cruentus* (Peters), a species sometimes confused with *E. latidiscus* which may be allied to *E. crenunguis* and *E. latidiscus* (Lynch 1976). As noted by Lynch (in press) only *E. crenunguis, E. latidiscus,* and *E. rubicundus* of the *rubicundus* assembly have emarginate digital pads. We can now add *E. muricatus* to this list but we are not convinced that these four species are more closely related to one another than any is to the other two known species of the assembly. The weakly emarginate digital pads of *E. tenebrionis* are not convincing evidence of its relationship with the *rubicundus* assembly; its snout physiognomy suggests that it is allied elsewhere.

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B R E V I O R A

Museum of Comparative Zoology

A NEW SPECIES OF *ATELOPUS* (ANURA:BUFONIDAE) FROM THE CLOUD FORESTS OF NORTHWESTERN ECUADOR

KENNETH MIYATA[1]

ABSTRACT: *Atelopus coynei* is described from the Rio Faisanes in Pichincha Province, Ecuador. It appears to have an extremely restricted distribution and may be in danger of extinction as its habitat is altered by man. The new species is most closely to *Atelopus mindoensis*

INTRODUCTION

The western slope of the Andes in northern Ecuador has a rich anuran fauna, much of which has been described only within the past decade. Until recently access to this area has been difficult due to its precipitous terrain and dense blanket of montane forest. Many species appear to have restricted distributions and it is not surprising that they were missed by early collectors. Within this forested zone, which extends up to at least 3000 m elevation, there are several distinct asemblages of frogs. Maximum species diversity apparently occurs between 1000 and 1600 m. Many of these species are very restricted in distribution; few are known from outside Ecuador. My field work in this region revealed the presence of an apparently new species of frog of the genus *Atelopus* that seems to exhibit an exceptionally restricted distribution even in comparison with other elements of this fauna. Despite extensive collecting efforts in the cloud forests of western Ecuador by myself and field parties from the Museum of Natural History of the University of Kansas, this new species remains known from only two localities within a few kilome-

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ters of each other. Given the rather precarious status of these habi-
tats as human development encroaches, I take the opportunity here
to describe this species before the populations become extinct.

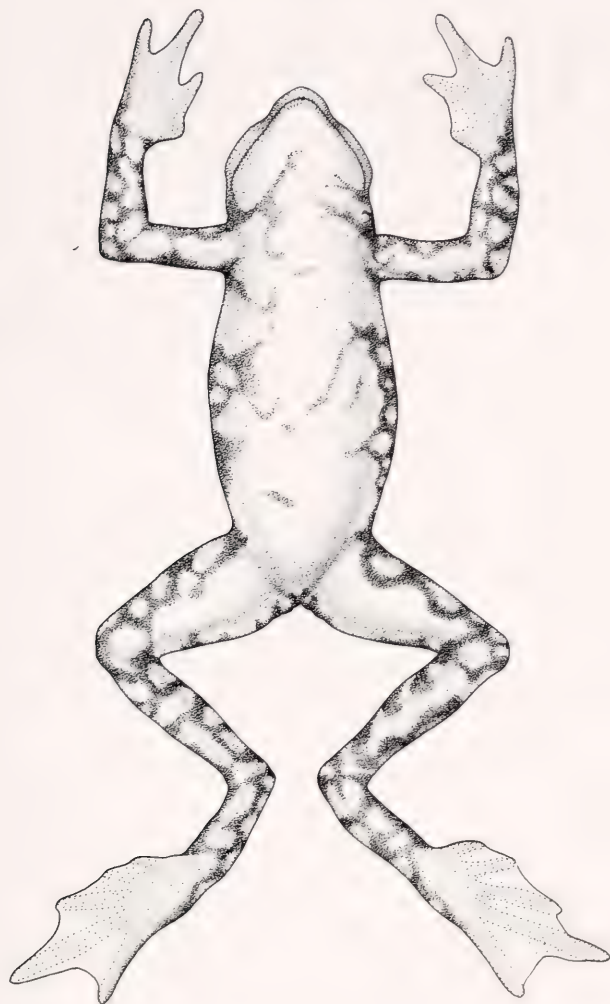Figure 1.   Dorsal view of holotype of *Atelopus coynei* (MCZ 91444).

Figure 2.   Ventral view of holotype of *Atelopus coynei* (MCZ 91444).

Atelopus coynei sp. nov.

Holotype: MCZ 91444, an adult male, one of a series collected on the banks of the Rio Faisanes where it crosses Ecuador Highway 28 (the road from La Palma to Quito via Chiriboga), 14.4 km from the junction with Highway 30 (the Aloag to Santo Domingo de los

Colorados road) at La Palma, Pichincha Province, Ecuador, 1380 m, on 11 July 1976 by Godfrey Guynn, Kay Harker, Steven Kaal, Ken Miyata, David Paul, and Harrison Weed.

Paratypes. Topotypes: MCZ 91445-91449, 96775-96756, collected with the holotype; MCZ 91450, collected on 7 August 1976 by Jerry Coyne and Ken Miyata; MCZ 95411, collected on 8 January 1978 by Lauren Cardullo, Andrea Dion, Ken Miyata, Hugh Torbert, and Lisa Schwadron; MCZ 95676, collected on 30 April 1978 by Paul Greenfield and Ken Miyata; MCZ 96754, collected on 12 November 1977 by Ken Miyata; USNM 211171, collected on 17 February 1979 by Roy McDiarmid. From 4 km E Dos Rios, Pichincha Province, Ecuador, 1140 m: KU 164744, collected on 2 April 1975 by William Duellman.

Diagnosis. A small *Atelopus* (males to 23 mm, females to 32 mm) distinguished from all other known species by the following combination of characters: 1.) Hind limbs relatively long, the heels overlapping slightly when held parallel to femora at right angles to the body and reaching or just falling short of the orbit when adpressed. 2.) First finger almost entirely buried in a thick, rather fleshy webbing. 3.) Ventral pattern consisting of a sparse network of fine dark reticulations on a light opaque background.

Description. Head narrower than body, somewhat longer than wide. Snout projecting past tip of lower jaw, rounded from above. Projecting snout forming fairly sharp right angle above and in front of nostril in lateral profile. Nostrils opening laterally about 2/3 of way from anterior margin of orbit to tip of snout, directly above or slightly behind tip of lower jaw. From above, canthi diverging slightly from behind nostrils to a point just anterior of orbits where they diverge outward more abruptly. Canthus rostralis rounded with slight depression in loreal region. Interorbital space wider than upper eyelid. Tympanum hidden. Skin on head generally smooth with some very sparse and fine granulation.

Dorsum finely shagreened, dorsolateral folds absent. Venter and sides with numerous plate-like folds, smallest and most distinct on throat and neck, becoming larger and less distinct on sides and towards cloaca. Pair of narrow low ridges on dorsum in parotoid region.

Forearm slightly thicker than upper arm. Forefeet fleshy with thick webbing. First finger almost buried in fleshy webbing with only the tip free. Other fingers basally webbed with lateral fringes

extending past distal subarticular tubercles. Subarticular tubercles indistinct; palmar tubercle prominent, oval in shape. Males with cornified pad on inner margin of first finger.

Heels overlap slightly when tibiofibulae held parallel to femora at right angles to body. Adpressed heels reach to, or fall just short of, posterior margin of orbit. Tarsal fold absent. Hind feet fleshy with extensive thick webbing to tips of all toes except the fourth which is free distally. Subarticular tubercles indistinct; outer metatarsal tubercle small and rounded.

Measurements.   Mean standard length for adult males is 22.6 mm, the single known adult female is 32.1 mm. The holotype is 22.4 mm. Table 1 summarizes the measurements and ratios used by Peters (1973) in his review of Ecuadorian *Atelopus.*

Color in life.   The dorsum of males varies from green with dark brown reticulations to dark brown with green spots and blotches. In all specimens the dorsal green becomes turquoise blue laterally. The single adult female (MCZ 96754) was bright green with sparse dark brown dorsal reticulations and no trace of turquoise blue on the sides. The ventral surfaces of the males were opaque white, occasionally with a yellowish wash, with a sparse network of dark brown or black reticulations (Fig. 2). The female was a bright opaque yellow ventrally with dark brown reticulations and a reddish-orange wash on the palms and soles. This same reddish-orange wash on the palms and soles was seen on one male as well (MCZ 94511), but it was not as prominent as on the female. The iris varies from golden yellow to orange-copper.

Color in preservative.   The parts of the dorsum which were green in life are pale lavender. The dark brown parts of the dorsal pattern remain brown, but are somewhat paler and have a reddish wash. The venter remains white in the males, but all traces of the yellow wash are lost. The female retains some of the yellow ventral color after 20 months in preservative. The ventral reticulations range from pale to medium brown.

Etymology.   The specific epiphet is a patronym for Dr. Jerry Coyne, whose timely financial assistance helped stave off the wolves on several occasions and allowed me to complete the description.

NATURAL HISTORY

The Río Faisanes is a small mountain stream flowing through a narrow forested canyon where it crosses Ecuador Highway 28, 14.4

km from the village of La Palma on the road to Quito. The elevation of the stream where it crosses the road is given as 1380 m on a topographical map of the area prepared by the Instituto Geografico Militar of Ecuador in 1969 (Alluriquin quadrat, CT-NIII-A3, 3893-111). This falls into the "bosque muy humedo Pre Montano" ecological zone (Instituto Geografico Militar 1977), and the forest is characterized by a relatively low canopy height with an extremely heavy epiphyte growth. The Río Faisanes is rarely more than 5 m in width and few places are more than 0.5 m deep. The bottom consists of pea-sized gravel and the bed sometimes flows over or against large rocks. The water normally runs clear and in most places the canopy completely overhangs the water (see below). The other known locality where *coynei* has been collected (4 km E Dos Rios, 1140 m) is along the Río Orito and is located about 1.3 km NSW of the type locality. According to the topographical map, the elevation is 1280 m. The two small rivers flow into the Río El Tránsito, which then flows into the Río Pilaton a few kilometers to the SW.

All of the specimens taken on 11 July 1976 were collected along the banks of the Río Faisanes. Individuals were captured in the late afternoon while they were active on the rocky banks of the river during a light rain. At night additional specimens were collected sleeping on streamside vegetation, usually within 1 m of the ground and frequently on leaves overhanging the water. A total of 41 specimens was collected that day in approximately 18 person-hours of collecting along a 250 m stretch of the river. Most of these specimens were used for biochemical analysis of possible skin toxins by Harrison Weed and were not available for this description.

Subsequent visits to the Río Faisanes in July and August of 1976, May and November of 1977, January and April of 1978, and February of 1979 resulted in the collection of very few additional specimens. All of these later visits were made at night and hence no more active individuals were found. All of these specimens were sleeping on the tops of leaves within 1 m of the ground. These specimens were not taken along the Río Faisanes proper, but were found on the banks of a small tributary creek which crosses the road about 50 m SW of the Río Faisanes bridge.

Since the first visit to the type locality in July of 1976 the Río Faisanes seems to have become more silted as a result of small-scale logging operations and the canopy has been opened to a considerable degree in places. On the first visit the river was running clear despite the fact that it was high from the rains. On later visits the

Table 1. Measurements and ratios of *Atelopus coynei* (as in Peters 1973).

	Males (N=7)	Female (N=1)
Standard distance	22.6 mm	32.1 mm
Knee-knee	20.3	29.2
Tibofibula	10.6	15.5
Head width	6.6	8.7
Head length	7.8	10.5
Knee-knee/standard distance	87.7	91.0
Tibiofibula/standard distance	47.1	48.3
Head length/standard distance	34.4	32.7
Head width/head length	84.5	82.9
Tibiofibula/head length	137.1	147.6
Tibiofibula/knee-knee	52.5	53.1

water was often cloudy and turbid even though the level was low and there had been no recent rains. The scarcity of frogs after the first visit may be due partly to the increase in human activity along the stream which may have rendered it unsuitable for larval development. An increase in suspended silt in the water due to this human encroachment may cause the scraping of the algae off the surface of the rocks before the tadpoles can get to it.

Only a single female *coynei* has been found out of a total of 47 specimens (including the ones used for biochemical work). This is not necessarily indicative of a skewed sex ratio. All of the collections have been made along stream banks and McDiarmid (1971) has suggested that male *Atelopus* may spend considerably more time along the creeks than females. The large number of males taken on the first visit to the type locality is indicative of a breeding concentration and it is likely that the females had not yet arrived. Since then, individuals have been found in low concentrations and the bulk of the population may have dispersed into the forest. The apparent absence of *coynei* on recent visits may also be due in part to an absence of breeding concentrations.

Other anurans collected syntopically and synchronously with active *Atelopus coynei* include *Atelopus longirostris*, *Bufo chanchanensis*, *Eleutherodactylus achatinus*, *E. necerus*, and *Colostethus* sp.

COMPARISONS AND DISCUSSION

The relatively long hind limbs and the extensively webbed thumbs distingush *A. coynei* from all but a few species of *Atelopus*. Of these species, the hind limbs of *A. elegans, A. longibranchius, A. palmatus,*

and *A. rugulosus* are very long and the adpressed heel reaches beyond the anterior margin of the orbit, rather than just reaching or falling short of the posterior margin. In *A. cruciger* from Venezuela and *A. flavescens* from French Guiana the adpressed heels reach to near the posterior margin of the orbit, but they lack webbing between the second and third fingers and are larger than *A. coynei* (male *A. cruciger* to 29 mm, male *A. flavescens* to 32 mm).

Atelopus coynei most closely resembles *A. mindoensis*. The most striking difference between these two species is ventral pattern, with *A. mindoensis* lacking the reticulations which are characteristic of *A. coynei*. There are a number of other differences as well (Table 2) and there is little doubt that the taxa are distinct.

The description of a new species of *Atelopus* based on external morphology from two neighboring populations may seem unwise given the known degree of variation in such characters in some members of the genus (Peters 1973, Savage 1972). The close similarity of *A. coynei* to *A. mindoensis* may make it seem particularly suspect. Although *A. coynei* and *A. mindoensis* are almost certainly closely related, the differences outlined in Table 2 are consistent enough to warrant their recognition.

Although color pattern can be quite variable both within and between populations of some species of *Atelopus*, the ventral pattern of *A. coynei* is unique and allows the immediate recognition of

Table 2. *Atelopus coynei* and *mindoensis* compared

ATELOPUS COYNEI	ATELOPUS MINDOENSIS
Venter white to yellow with brown reticulations.	Venter reddish brown with yellow spots.
Ventral skin with numerous small scale-like folds anteriorly.	Ventral skin smooth or with small folds on throat.
Ventral skin completely opaque.	Ventral skin translucent to transparent.
Eggs not visible through skin in one gravid female known.	Eggs clearly visible through skin in gravid females.
No tubercles or enamelled pustules on back or sides.	Small tubercles and enamelled pustules on back and sides
Snout more rounded from above and coming to sharp angle from side.	Snout more pointed from above and coming to more rounded angle from side
No evidence of throat pouch in adult males.	Adult males with loose skin on throat.
Larger size; adult males average 22.6 mm, adult female 32.1 mm.	Smaller size; adult males average 18.7 mm (N=37), adult females 24.9 mm (N=22).

this species. I have examined the holdings of *Atelopus* in the MCZ collection and made a literature survey of all of the 40 presently recognized species (those listed by McDiarmid 1971 and subsequently described species; descriptions consulted in lieu of specimens include Bokermann 1962, Boulenger 1902, 1903, Cochran and Goin 1970, Donoso-Barros 1969, McDiarmid 1973, Noble 1921, Peters, 1973, Ruiz-Carranza and Hernandez-Camacho 1978, Savage 1972) and the only species that exhibit a reticulate ventral pattern are *A. chiriquiensis*, *A. longirostris*, *A. pachydermus*, *A. pulcher*, *A. tricolor*, and *A. varius*. In each of these species the reticulate pattern, when present (some species are variable in this character), is very bold and consists of thick lines mixed with blotches and spots. In contrast, the ventral reticulations of *A. coynei* are thin and sparsely distributed. Although the degree of this ventral marbling in *A. coynei* is variable, it is immediately recognizable in all of the specimens I have examined.

Although the 40 known species of *Atelopus* make it a relatively large assemblage of frogs, all of which are Neotropical, the species are distributed with remarkably little geographical overlap. Extensive sympatry between species of *Atelopus* is unusual, a situation which is in striking contrast to that seen in other Neotropical anuran genera of similar diversity. The rather specialized breeding requirements of *Atelopus* may somehow inhibit overlap. In areas where two species of *Atelopus* occur in sympatry they are usually of quite different habitus. To date, *A. coynei* has been collected with the larger and more gracile *A. longirostris* but has not been found with the similar *A. mindoensis*. Although *A. mindoensis* is known from elevations between 20 m and 2100 m, the lower records are from the drainage of the Río Cachabi in Esmeraldas Province. On the Río Toachi drainage in Pichincha Province *A. mindoensis* appears to be restricted to elevations above 1500 m and does not come into contact with either *A. coynei* or *A. longirostris*. Since *A. mindoensis* and *A. longirostris* do come into contact in the Río Guayllabamba drainage just to the north of the Toachi, it appears that *A. coynei* may be limited to the relictual populations described here.

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B R E V I O R A

Museum of Comparative Zoology

A NEW SPECIES OF *DENDROBATES* (ANURA: DENDROBATIDAE) FROM THE LOWLAND RAIN FORESTS OF WESTERN ECUADOR

GREGORY O. VIGLE[1] AND KENNETH MIYATA[2]

ABSTRACT: *Dendrobates erythromos* sp. nov. is described from the lowlands of western Ecuador. The new species is tentatively assigned to the genus *Dendrobates* on morphological grounds and appears to be most closely allied to the Colombian *D. ingeri*. This species may have specific microhabitat requirements which result in a spotty distribution.

INTRODUCTION

In January of 1978 several specimens of an apparently unde-scribed species of dendrobatid frog were collected at the Centro Científico Río Palenque in the Pacific lowlands of Ecuador. Prepa-ration of an account of the herpetofauna of the region requires that a name be assigned to this population, and here we describe the species on the basis of material in the Museum of Comparative Zoology (MCZ) and the National Museum of Natural History (USNM).

The generic partitioning of dendrobatid frogs is in a state of flux and the characters which have traditionally been used to define the genera are being supplanted by new ones. Following the criteria of Savage (1968) and Silverstone (1976) this new species would be assigned to *Phyllobates*. However, this genus has recently been defined as a monophyletic group (in the cladistic sense) on the basis of a biochemical synapomorphy by Myers et al. (1978) and consists of only four of the species recognized by Silverstone plus one newly

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described species. All of the remaining species of *Phyllobates* recognized by Silverstone (the *femoralis, pictus,* and *trivittatus* groups) were reassigned to *Dendrobates.* The new species most closely resembles those in Silverstone's *pictus* group on the basis of size, coloration, and the absence of toe webbing and we tentatively assign it to the genus *Dendrobates.*

Dendrobates erythromos sp. nov.

Holotype: MCZ 96384, an adult female collected at the Centro Científico Río Palenque, 47 km S of Santo Domingo de los Colorados, Provincia Pichincha, Ecuador, 170 m, on 17 January 1978 by Gregory O. Vigle.

Paratypes. All are topotypes: MCZ 96381–83, 96385, 94896 (lot of 3 tadpoles from back of 96385), USNM 211169–70.

Diagnosis. A dendrobatid frog with the following combination of characters: 1.) Teeth present. 2.) Omosternum present. 3). First

Figure 1. Paratype of *Dendrobates erythromos* (MCZ 96381). The slightly paler area on the dorsal surface of the forearm is the bright orange flash mark.

finger longer than second. 4.) Toe webbing absent. 5.) Muscle tissue flecked with black pigment. 6.) In life, the dorsum is dark brown and the venter is black with pale blue marbling. 7.) A bright reddish-orange flash mark on the posterodorsal surface of the upper arm in life. 8.) Size medium, to 23.5 mm snout-vent length (SVL).

The above combination of morphological characters, combined with the lack of any dorsal or dorsolateral striping and the bright orange flash marks distinguish *Dendrobates erythromos* from all other known dendrobatid frogs.

Description. Snout-vent length to 23.4 mm; four adult females 21.5-23.4 mm; two adult males 20.4 22.6 mm; one immature female 18.6 mm.

Skin smooth to very finely pitted dorsally, slightly rugose laterally and on posterior surface of thighs; smooth on venter and limbs. Head as wide as body or slightly wider, widest at jaw articulations. Eyes prominent, diameter about one and one-half times the length of the snout; width of upper eyelid less than interorbital width. Snout short, truncate in dorsal and lateral aspect. Canthus rostralis rounded; loreal region flat to slightly concave. Tympanum round, about one-half diameter of orbit; posterodorsal portion concealed.

Relative lengths of appressed fingers 3>4>2>1, each having a distinct disc expanded about 1.5 times the width of the distal end of the adjacent phalanx. First finger longer than second if not ap-pressed. A large outer metacarpal tubercle and a smaller, less promi-nent inner metacarpal tubercle at the base of the palm. One slightly prominent subarticular tubercle on fingers one and two and two slightly less prominent tubercles on fingers three and four; all are low with rounded surfaces. Relative lengths of appressed toes 4>5>3>2>1. Toes have distinct discs approximately 1.5 times the width of the distal end of the adjacent phalanx. A small elongated outer metatarsal tubercle and a smaller, round inner metatarsal tubercle at the base of the foot. Indistinct subarticular tubercles on toes; one on toes one and two, two on toes three and five, and three on toe four. A slightly prominent curved tarsal fold on the inner side with a weakly developed tubercle at the proximal end. Palms and soles flattened on bottom and slightly fleshy. Digits lacking lateral fringes (or with very narrow ones on toes), webbing, and supernu-merary tubercles.

Palatine bones absent. Maxillary and premaxillary teeth present. Omosternum present. Muscle tissue flecked with black pigment. Paired vocal slits in adult males; single subgular vocal sac.

Measurements of holotype. The undissected holotype is the largest individual in the type series. The following measurements are to the nearest 0.1 mm as measured on dial calipers. Snout to vent 23.4; tibia from heel to fold of skin on knee 9.6; greatest width of body 8.4; greatest width of head 8.5; head length from tip of snout to angle of jaws 7.6; length of snout from anterior edge of orbit to tip of snout 2.4; diameter of orbit 3.6; diameter of tympanum 1.9; length from proximal edge of large palmar tubercle to tip of third finger 5.7; width of disc of third finger 0.6; width of distal end of adjacent phalanx 0.4.

Color in Life. Dorsum dark brown, appearing almost black in some specimens. The sides are black or very dark gray. Bright reddish-orange flash marks on the posterodorsal surfaces of the upper arms, extending from the axilla to the elbow and sometimes slightly beyond to the forearm. Anterior surface of arms and hands dark brown. The dorsal surfaces of the hind limbs are banded dark brown and black. The throat and ventral surface of the body are black with pale blue marbling which extends slightly up the sides. The iris is brown.

Color in Preservative. The dorsal and lateral surfaces are black to very dark brown. The banding on the dorsal surface of the hind limbs is obscure. The flash marks on the upper arm are white. The ventral surface is black with dull gray marbling.

Tadpoles. The following description is based on the paratypic lot of tadpoles (MCZ 94896) taken from the back of an adult male (MCZ 96385) on 18 January 1978. Only two of the three tadpoles are in good condition and these are the ones used for the description.

The tadpoles are in stage 25 (Gosner 1963) and measure 9.04–9.60 mm total length (measurements taken with ocular micrometer). The head and body measure 3.20–3.68 mm and constitute 35–38% of the total length. The body is somewhat flattened with the width about 1.25 times the depth of the body. The eyes and nostrils are directed dorsolaterally. The spiracle is sinistral and the anus is dextral.

The tail has a relatively low fin and is as deep as the body or slightly deeper posteriorly; the dorsal fin extends forward slightly past the level of the anus.

There is one row of pigmented teeth on the anterior labium. The beak is keratinized, the upper jaw slightly convex anteriorly and the lower jaw in a strong "V" shape. The oral disc is laterally indented. There is a single row of small, blunt papillae which occur continuously along the lateral and posterior edges of the oral disc and are absent from the anterior edge.

The ground color is pale buff, heavily speckled with brown on the dorsal surface of the body. The venter is lightly pigmented anteriorly and heavily speckled posteriorly with brown. The brown speckling on the tail is restricted to the dorsal aspect and the fins are unmarked.

Etymology.   The specific epiphet is derived from the Greek *erythros,* meaning red, and *omos,* meaning upper arm, in reference to the distinctive reddish-orange flash marks on the posterodorsal surface of the upper arm.

Natural History.   *Dendrobates erythromos* is known only from the Centro Científico Río Palenque. The forest there is considered to be tropical wet forest in the sense of Holdrige (1967) although available clmatic data do not seem to match this physiognomy (Dodson and Gentry 1978). The frogs are apparently restricted to a single creek system within this patch of forest. All of the specimens have come from along the banks of Lodo and Sherd Creeks above trail 3a (see Dodson and Gentry 1978:ix for map of station). The forest along these creeks has a somewhat broken canopy with significant amounts of bamboo and other second-growth vegetation mixed in with the tall trees. The relief is rather steep and much of the openness of the canopy appears to be due to tree falls, although there has been some cutting in this area. The creeks flow over rocky or sandy beds and parts of them become dry during the end of the dry season. *Dendrobates erythromos* has been taken along these stream beds in January, when water levels were still low prior to the onset of the rainy season. Several specimens were collected along a dry portion of the bed of Lodo Creek although the majority were taken near flowing water. The frogs were never observed in the water but came from areas near the stream with good deposits of leaf litter and fairly heavy understory vegetation. They seemed to

prefer those areas with relatively closed canopies, avoiding the numerous light gaps along the streams.

All of the frogs of this species were taken during the day as they were active on the surface of the litter and ground. They were quite wary and difficult to approach and when pursued they sought shelter under the litter and in dense thickets of understory vegetation. Calls tentatively associated with this species were soft repetitive chirps.

Three other species of dendrobatids are known from the Centro Científico Río Palenque. They are *Dendrobates espinosai, D. histrionicus,* and *Colostethus infraguttatus.* Only the much smaller *D. espinosai* has been found syntopically with *d. erythromos,* although *D. histrionicus* is common in the adjacent forest away from the creeks.

DISCUSSION

Dendrobates erythromos most closely resembles *D. ingeri,* a species known only from a single locality in Amazonian Colombia. The two species are very similar morphologically, both sharing maxillary and premaxillary teeth and a light spot in the axilla and upper arm and both lacking lateral stripes. The dorsum of *D. ingeri* is very granular and it has a light calf spot and is easily distinguished from *D. erythromos.* The two species are probably closely allied; Silverstone (1976) placed *D. ingeri* closest to *D. pictus* within his *pictus* group. Although *D. pictus* does have lateral stripes and some specimens lack premaxillary and maxillary teeth, this arrangement does seem to have validity. The tadpoles of *D. erythromos* resemble those of *D. pictus* rather closely; those of *D. ingeri* are unknown. A fourth species, *D. parvulus,* was also associated with *D. pictus* by Silverstone, but it seems to be somewhat more distantly allied with the other three species. Silverstone believed that his *pictus* group might not be a natural group and recognized three different assemblages within it. The three species he associated with *D. pictus,* along with *D. erythromos,* do seem to constitute a group of similar organisms, but further information regarding calls and skin toxins will be necessary before the relationships can be worked out.

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B R E V I O R A

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ON THE EVOLUTION OF THE JAW ADDUCTOR MUSCULATURE IN PRIMITIVE GNATHOSTOME FISHES

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ABSTRACT. The primitive condition of the adductor mandibulae musculature in gnathostomes is a large unsubdivided, fan-shaped muscle mass originating from the palatoquadrate and inserting on the lateral aspect of the mandible. Unspecialized suborbital fibers extend posteriorly from the palatoquadrate to insert laterally on the lower jaw, and an intramandibular adductor division is absent. The Actinopterygii, Actinistia, Dipnoi, and Choanata primitively possess three distinct components of the adductor mandibulae: a suborbital division, a medial division, and a posterolateral division, as well as medial intramandibular adductor fibers. The suborbital division of the adductor mandibulae has been lost in teleosts and, independently, in coelacanths and living lungfishes. Devonian lungfishes and early choanates possessed both the suborbital and intramandibular adductor muscle components.

INTRODUCTION

Towards the end of the nineteenth and in the first half of the twentieth century, a large number of investigators were concerned with the homologies of the jaw musculature between the different vertebrate classes (Allis, 1897, 1917, 1923; Edgeworth, 1935; Kesteven, 1942, 1943, 1944; Lightoller, 1939; Luther, 1913; Souché, 1932; Vetter, 1874). The musculature of the mandibular arch was the subject of special attention and several attempts were made to precisely link each branchial arch muscle with its serial homologue on the mandibular arch [see Lightoller (1939) for an example of this procedure carried to an extreme]. In recent years, little work has been done on the evolution of the musculature in primitive gnathostomes, despite the discovery of significant new fossil material that allows more accurate reconstruction of the musculature in extinct taxa.

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Lauder (1980) has proposed that the primitive condition of the jaw musculature in the Actinopterygii (ray-finned fishes) is a tripartite division into distinct components: an anterior or suborbital division, a medial division, and a posterolateral division. In this paper, the consideration of adductor muscle components, including the intramandibular division, is extended to other primitive gnathostome taxa to elucidate the evolution and homologies of the gnathostome jaw adductor musculature.

COMPARATIVE ANATOMY

Elasmobranchiomorphi

The adductor musculature in the primitive living selachian *Chlamydoselachus anguineus* has been described by Allis (1923) and Smith (1937). Based on their descriptions and on the comparative anatomy of the adductor mandibulae in other living sharks, the adductor musculature in the primitive Devonian selachian *Cladodus* has been reconstructed (Fig. 1A).

In living selachians, the adductor musculature is divided into two main components. The adductor mandibulae proper [= quadrato-mandibularis of Kesteven (1942) and Lightoller (1939)] is a single unsubdivided muscle mass having a fan-shaped origin on the palatoquadrate. The fibers converge to a tendinous inscription before fanning out ventrally to insert on the lower jaw. The adductor insertion is on the lateral aspect of the mandible and no intramandibularis division is present.

A suborbitalis muscle [= pterygoideus of Kesteven (1942), adductor β of Vetter (1874), levator labii superioris of Allis (1923), preorbitalis of Luther (1913)] originates tendinously from the "ectethmoidal process" (Allis, 1923) of the cranium anteriorly and inserts onto the upper labial cartilage and the skin of the lip. In *Cladodus* this muscle is represented as distinct suborbital fibers of the adductor mandibulae originating from the palatoquadrate (Fig. 1A: SO). Some fibers may also have originated from the nasal capsule, as in living sharks, and inserted onto the labial cartilages, when present.
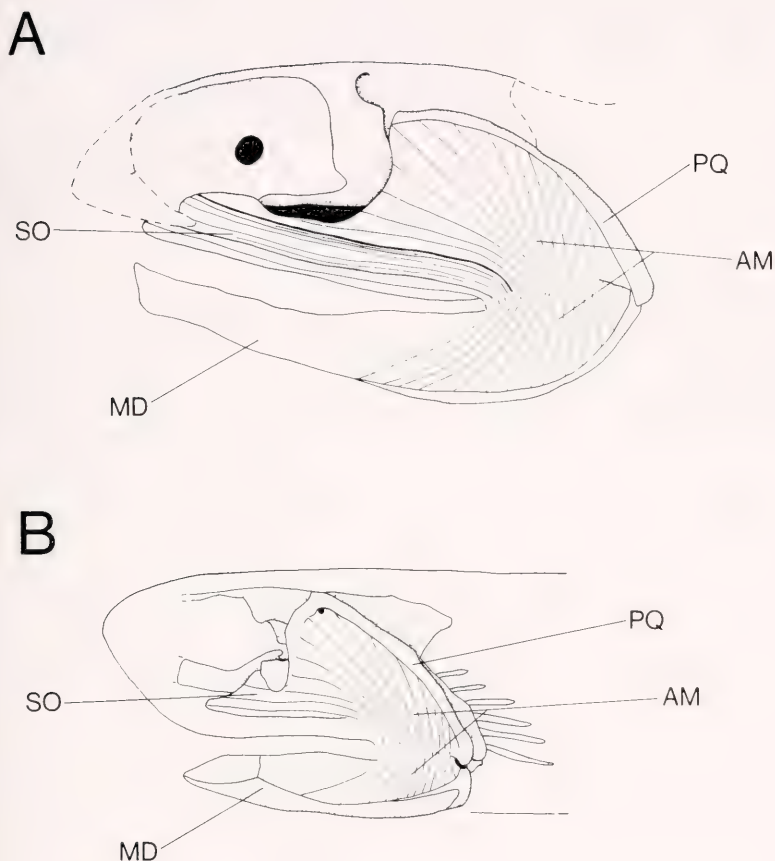
Figure 1. A: Reconstruction of the adductor mandibulae musculature in a primitive shark (*Cladodus*). Osteological features after Gross (1938). B. Reconstruction of adductor mandibulae musculature in an acanthodian (*Acanthodes*). Osteological features after Jarvik (1977) and Miles (1973). Abbreviations: AM, adductor mandibulae; MD, mandible; PQ, palatoquadrate; SO, suborbital fibers of the adductor mandibulae (separated into a distinct muscle in *Cladodus*).

In many living sharks, but not in *Chlamydoselachus*, a small superficial muscle overlies part of the adductor mandibulae. This muscle, the adductor mandibulae superficialis of Edgeworth (1935), adductor γ of Smith (1937), Vetter (1874), and Allis (1923), originates from the skin overlying the adductor mandibulae and inserts onto the posterior aspect of the palatoquadrate and mandible. There is currently no evidence to indicate whether the lack of this muscle in *Chlamydoselachus* is a specialization or if the primitive elasmobranchiomorph condition (absence of this muscle) has simply been retained. This muscle represents a small superficial component of the main adductor muscle, and I have reconstructed *Cladodus* (Fig. 1) with an unsubdivided adductor.

Acanthodii

The structure of the adductor mandibulae in acanthodians appears to have been very similar to that hypothesized to be primitive for elasmobranchiomorphs (Fig. 1). The large adductor mandibulae had a fan-shaped origin from the palatoquadrate and a lateral insertion on the mandible. An intramandibular division is hypothesized to have been absent since the "adductor fossa" is located on the lateral aspect of the mandible and the medial surface is convex in shape (Jarvik, 1977; Miles, 1973).

The adductor mandibulae is proposed to have extended anteriorly ventral to the orbit (Fig. 1B: SO); the suborbital fibers originating from the palatoquadrate and extending posteriorly to join the other adductor fibers at a tendinous inscription before inserting on the mandible.

Actinopterygii

In ray-finned fishes, the adductor mandibulae complex may be divided into three separate divisions each inserting on the lower jaw, and an intramandibular adductor component (Fig. 2; Lauder, 1980). Suborbital adductor fibers are present in *Amia, Lepisosteus,* and *Polyodon.* In *Amia,* these suborbital fibers have been called the levator maxillae superioris by Allis (1897) while the homologous adductor component in *Lepisosteus* is the palatomandibularis minor and major. *Polyodon* possesses a large separate anterior adductor

division originating on the palatoquadrate (Danforth, 1913). The suborbitalis adductor component has been lost in all teleosts (Fig. 2: character 6; also see Winterbottom, 1974).

In palaeoniscoid actinopterygians, the suborbital fibers were enclosed in the anterior part of the maxillary—palatoquadrate chamber (Schaeffer and Rosen, 1961) and extended posteroventrally to insert in the mandibular fossa.

The medial adductor division represents one of two components of the primitive unsubdivided postorbital adductor fibers. Homologies of the medial division in actinopterygians are given in Lauder (1980). The medial adductor fibers in *Polypterus* are called the "pterygoideus" and "temporalis" muscles by Allis (1922). The "pterygoideus" of Allis (1922) is not homologous to the "pterygoideus" of Kesteven (1942), which represents the suborbital division.

A distinct posterolateral adductor component is also hypothesized to be primitive for actinopterygians (Lauder, 1980). This muscle represents the superficial lateral adductor fibers which run dorsoventrally from the palatoquadrate to insert in the adductor fossa.

An intramandibular adductor division is present in most teleosts and in *Amia, Polypterus, Polyodon,* and palaeoniscoids (as inferred by the presence of an adductor fossa). The presence of intramandibular fibers is thus proposed to be a primitive actinopterygian character (Fig. 2: character 4).

Actinistia

Millot and Anthony (1958) describe three adductor muscles in *Latimeria.* A superficial adductor arises posteroinferiorly from the quadrate and inserts on the mandible in the mandibular fossa. This muscle appears to represent the posterolateral adductor division.

The two remaining adductors arise from the ethmosphenoid portion of the cranium posterior to the orbit. Millot and Anthony (1958) note that these muscles appear to correspond to the "pterygoideus" and "temporalis" adductors of *Polypterus,* and thus are both comparable to the medial adductor complex in primitive actinopterygians. No anterior (suborbital) division is present in *Latimeria;* all jaw adductors extend dorsoventrally behind the orbit.

A large intramandibular adductor occurs in *Latimeria* (Millot and Anthony, 1958: Fig. 19).
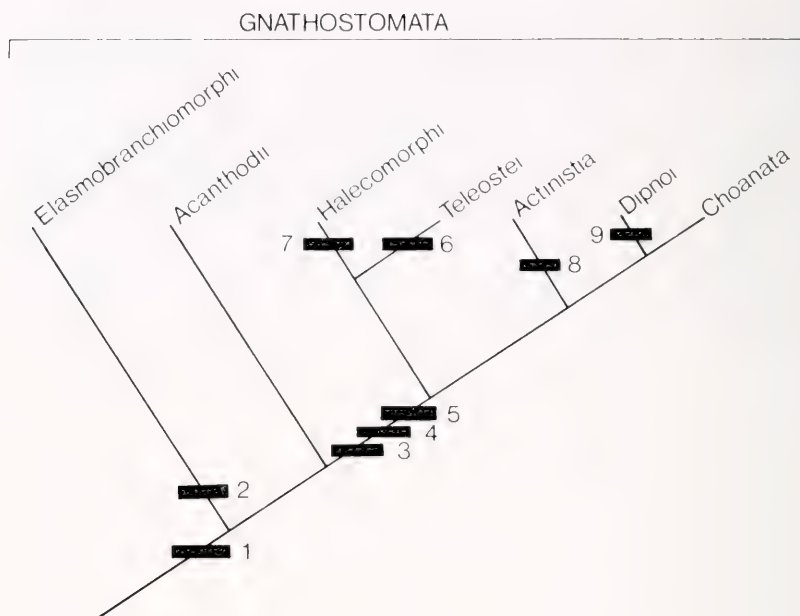
GNATHOSTOMATA

Figure 2. The distribution of various character states of the adductor mandibulae musculature in gnathostomes superimposed on one hypothesis of gnathostome phylogeny. For other characters supporting this phylogeny see Liem and Lauder (in press). Character 1: fan-shaped adductor mandibulae with unspecialized suborbital and postorbital fibers and a lateral insertion on the mandible; 2: suborbitalis muscle differentiated from suborbital fibers; 3: medial insertion of the adductor mandibulae on the mandible; 4: intramandibular adductor division present; 5: postorbital adductor component divided into medial and posterolateral divisions; 6: loss of suborbital adductor component; 7: specialization of suborbital fibers into the levator maxillae superioris 3 and 4 muscles (see Allis, 1897); 8: loss of the suborbital adductor component; 9: loss of suborbital component in living forms.

Dipnoi

While extant dipnoans lack both intramandibular and suborbital adductor divisions, Devonian lungfishes appear to have possessed both. A space between the infraorbital bones laterally and the palatoquadrate medially may have housed the anterior adductor (suborbital) division, and an adductor fossa for the intramandibular adductor is found on the medial surface of the lower jaw (see Miles, 1977).

The main adductor mass in living lungfishes is divisible into posterolateral and medial components. The adductor mandibulae posterior (Edgeworth, 1935; = retractor anguli oris of Luther, 1913), corresponds to the posterolateral adductor division, and lies lateral to the ramus maxillaris and mandibularis V. The adductor mandibulae anterior (Edgeworth, 1935; = temporalis of Luther, 1913) is located anteromedially to the posterior adductor. In adult lungfishes the adductor mandibulae anterior is a large muscle with a broad postorbital origin from the skull. In larval lungfishes (Edgeworth, 1935), the anterior adductor is nearly equal in mass to the posterior adductor and lies medial to it, and lateral to the trabeculae.

Choanata

Olson (1961) and Thomson (1967) both provide partial reconstructions of the adductor mandibulae complex in primitive choanates. A suborbital component of the adductor mandibulae was located anteriorly and presumably had its origin from the palatoquadrate. This division was housed in a chamber formed between the palatoquadrate medially and the dermal skull bones laterally. Postorbitally, the lateral wall of the suborbital adductor chamber was formed by the postorbital and jugal bones; while anteriorly the prefrontal, jugal, and maxilla enclosed the suborbital adductor. The posterolateral and medial adductor divisions both appear to have been present (Thomson, 1967) and thus the configuration of the adductor mandibulae in primitive choanates closely resembles that of palaeoniscoid actinopterygians. An intramandibular adductor division is inferred to have been present by the occurrence of an adductor fossa in the lower jaw (see Romer, 1966).

DISCUSSION

In figure 2, the various configurations of the adductor mandibulae complex are superimposed on one hypothesis of gnathostome phylogeny. Other characters supporting this hypothesis may be found in Liem and Lauder (in press). The primitive configuration of the adductor mandibulae in gnathostomes is hypothesized to be a single unsubdivided fan-shaped muscle mass with unspecialized suborbital fibers originating anteriorly from the palatoquadrate (Fig. 2: character 1). Elasmobranchiomorphs retain the fan-shaped adductor configuration but possess specialized suborbital fibers (Fig. 2:

character 2); these fibers originate, in most cases, from the nasal capsule. A fan-shaped adductor muscle is also hypothesized for acanthodians (Fig. 1B), and the main postorbital adductor mass is reconstructed as being unsubdivided.

One notable aspect of the adductor mandibulae in elasmobranchiomorphs and acanthodians is its lateral insertion on the lower jaw. This condition contrasts sharply with the medial adductor insertion in actinopterygians, actinists, dipnoans, and choanates (Fig. 2: character 3). The medial insertion correlates with the presence of an intramandibularis adductor division (Fig. 2: character 4) and the occurrence of an adductor fossa on the medial surface of the lower jaw, in contrast to the lateral fossa of elasmobranchiomorphs and acanthodians.

In the Actinopterygii, Actinistia, Dipnoi, and Choanata, an hypothesis of a tripartite division of the adductor mandibulae into suborbital, medial, and posterolateral components best fits the embryological data and morphological relationships of the musculature in the adult (Fig. 2: character 5). Although among living taxa, *Polypterus* lacks the suborbital adductor fibers and *Lepisosteus* the intramandibular division, other primitive actinopterygians (including palaeoniscoids) possess or show evidence of three extramandibular adductor components.

Teleost fishes have lost the suborbital adductor division (Fig. 2: character 6) but halecomorphs (*Amia*) retain specialized derivatives of the suborbital musculature, the levator maxillae superioris 3 and 4 of Allis (1897) (Fig. 2: character 7). The cylindrically-shaped suborbital muscles of *Amia* are not morphologically homologous to the similarly shaped and located suborbitalis muscle of elasmobranchiomorphs. Both muscles, however, are derived from the same geographical area of the adductor anlagen, and are thus homologous as suborbital fibers of the adductor mandibulae.

Coelacanths retain both the medial and posterolateral adductor components but have lost all suborbital fibers (Fig. 2: character 8).

The primitive condition for dipnoans and choanates is the presence of well-developed suborbital, medial, and posterolateral adductor divisions as well as an intramandibular section. Devonian dipnoans and early choanates appear to possess a very primitive configuration of the jaw adductor musculature, similar in all essential features to that of palaeoniscoids. Living lungfishes have lost all suborbital adductor fibers (Fig. 2: character 9).

Based on this analysis, the following classification of jaw adductor muscle states is proposed. The primitive gnathostome condition consisted of a jaw adductor composed of unspecialized suborbital and postorbital components. The presence of both suborbital and postorbital fibers defines the "fan-shaped" condition. Suborbital fibers occur in elasmobranchiomorphs as a distinct suborbitalis muscle while the postorbital component is divided into two divisions in actinopterygians, dipnoans, and choanates. The mandibular component represents the third adductor component. It lies lateral to the mandible in elasmobranchiomorphs and acanthodiáns, and medial to it in all other groups (Fig. 2).

ACKNOWLEDGEMENTS

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GEOGRAPHIC VARIATION IN
ANOLIS BREVIROSTRIS
(SAURIA: IGUANIDAE) IN HISPANIOLA

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ABSTRACT. The nominal Hispaniolan anole species, *Anolis brevirostris* Bocourt, is considered to be comprised of four distinct parapatric sibling species: *A. brevirostris, A. caudalis, A. websteri,* and *A. marron.* These species and the subspecies of *A. brevirostris* are described.

INTRODUCTION

Anolis brevirostris Bocourt is a rather small and stocky anoline lizard that occurs within an irregular range in xeric habitats on Hispaniola and associated islets. In 1870 Bocourt named *Anolis brevirostris* from Haiti. The name fell into disuse and obscurity, with specimens of *A. brevirostris* generally being included with *A. dominicensis* Reinhardt and Lütken. Cochran (1941) described and named two satellite island subspecies of *A. dominicensis: wetmorei* from Isla Beata, Dominican Republic; and *caudalis* Ile de la Gonâve, Haiti. Barbour (1937) first combined *A. dominicensis* with *A. distichus* Cope. This combination was followed by Mertens (1939) who resurrected *brevirostris* as a subspecies of *A. distichus* from the vicinity of Barahona in southwestern Dominican Republic. Ernest E. Williams, at the Museum of Comparative Zoology at Harvard University, recognized that some of the forms in Haiti and the Dominican Republic associated with *A. distichus* actually pertain to another similar species, *A. brevirostris* (the differential characters were reported in Schwartz, 1968). Named forms correctly associated with *A. brevirostris* are *caudalis* Cochran and *wetmorei* Cochran. Webster and Burns (1973) used electrophoretic observa-

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tions on several proteins to assign mainland Haitian populations of
"*A. brevirostris*" to three unnamed sibling species. Webster (1978a)
later expanded his electrophoretic studies to include most of the
remaining distribution of *A. brevirostris*. His accidental death left
behind two near-final-form manuscripts on *A. brevirostris* which
lack the tables, figures, and numerical data he would have prepared
to give his statements full documentation. These manuscripts subse-
quently became available in the Third *Anolis* Newsletter (Williams,
editor, 1977). Thus, as understood by Webster, the *brevirostris* com-
plex consisted of three unnamed sibling species referred to as A, B,
and C, and two named satellite island subspecies. Williams (1976)
referred the mainland Haitian species B to *caudalis* Cochran and
regarded species C as nominate *brevirostris*.

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METHODS

I have not considered it worthwhile to study all the available collected specimens of the *brevirostris* complex since many of the older specimens are long-preserved and now much faded and since coloration and pattern play such a major role in differentiation of the various species and subspecies. I have attempted to examine all the material which might be assignable to new taxa proposed herein and have examined all specimens designated as holotypes, syntypes, and paratypes.

The *brevirostris* complex needs fine sampling to be understood (Webster, *in litt.*, 1972); therefore I have restricted the type-locality of *A. brevirostris*. Lists of associated specimens, not from the type-locality itself, include localities and museum numbers which I have assigned to certain taxa on the basis of my examination. A list of referred specimens in Appendix 1 includes localities and museum numbers which I have assigned to taxa on the basis of provenance; specimens so listed have not been examined by myself. The probability is high that almost all lizards listed as referred specimens are correctly designated specifically and subspecifically, since they are delimited by fresh material that I have examined. Exceptional cases or uncertain allocations are noted in the text.

Various scale counts and relationships were used by Oliver (1948) to describe Bahamian populations of *A. distichus*. Schwartz (1968) applied the same counts to non-Bahamian populations. Hoping that an application of these counts to *A. brevirostris* complex members might reveal differences other than coloration and pattern between various sibling species and their subspecies, I have followed the techniques of Oliver and of Schwartz and applied them to the material I have examined. The following data were recorded on each specimen:

1) Snout-vent length, in millimeters.

2) Number of scales across the snout at the level of the second canthal scale, reckoned from the anterior border of the orbit.

3) Number of horizontal rows of loreal scales.

4) Minimum number of scales between the supraorbital semi-circles.

5) Number of rows of scales between the interparietal scale and the supraorbital semicircles on each side [this datum written as a fraction] (e.g., 1/1 = one row of scales on each side).

6) Number of scales bordering the postfrontal laterally (see Oliver, 1948:16, for drawings showing these scales in *A. distichus*). In a small number of specimens of *A. brevirostris,* the postfrontals may extend so far laterally as to make contact with one or two of the canthals. In such instances, I have not included the canthal as a scale in contact with the postfrontal, since the condition is anomalous.

7) Number of median (usually azygous) scales posterior to the posterior-most paramedian pair of snout scales, usually restricted to the midline from the anterior border of the postfrontals posteriorly to the anterior border of supraorbital semicircle contact, thus excluding the highly variable preoccipital region. (This count differs from those of Oliver and Schwartz but is made comparable by subtracting 1 from their counts — the nearly-always present preoccipital of *A. distichus*.)

8) Number of supraorbital semicircle scales in contact with the interparietal scale. This count is partly correlated with (5), the number of rows of scales between the semicircles and the interparietals; for instance, if the latter count is 1/1, the number of supraorbital scales in contact with the interparietal will of necessity be 0/0. However, if the count of (5) is 0/0 (i.e., there are no scales between the semicircles and the interparietal) then (8) may have a fairly wide fluctuation.

9) Number of postmental scales.

10) Condition of the preoccipital region categorized as: preoccipital present (+); series of small scales bordering interparietal anteriorly which may be incomplete (ss); preoccipital present but separated from interparietal by a series of small scales (ps); multiple small scales in preoccipital region (ms); preoccipital present, but tiny (t); and preoccipital absent (−), supraorbital semicircles in contact with anterior border of interparietal.

11) Condition of nuchal patch, categorized as large, medium, reduced, or absent; dark or faint; with or without white border. A medium-sized nuchal patch is reckoned to approximate the size of the external ear opening.

The above counts and notations were taken on 770 specimens from Haiti and the Dominican Republic. Test counts taken on the number of subdigital lamellae on phalanges II and III of the fourth toe of the hind foot and the number of scales in tail verticils were discontinued as no significant variation was observed. Complete

scale counts for each specific and subspecific samples are given in Table 1, where frequencies and modes are also shown. The reader is referred to this table for details of scutellar variation.

A few scale counts as modes, not as absolute counts, have proven to be useful in defining the species and subspecies. The degree of overlap between various counts for different samples is generally extensive, so that it is impossible to identify the species and subspecies of a particular specimen solely on the basis of any set of counts. Therefore reliance must be placed on such features as dewlap pattern and coloration, nuchal patch pattern, and coloration and pattern of the head and body in general. These additional data were taken from series having field notes on coloration. (As mentioned above, museum specimens as such have very limited utility.) The colors of many dewlaps were noted in the field with reference to Maerz and Paul (1950).

THE *ANOLIS BREVIROSTRIS* COMPLEX

As noted in the Introduction, the *brevirostris* complex is presently understood to consist of three sibling species. The material on which the name *A. brevirostris* was based had its provenance merely as "Haiti". I have examined the three syntypes loaned by the Muséum National d'Histoire Naturelle in Paris and find that two are *A. distichus*. The remaining one is *A. brevirostris* and has similarities to those lizards which are currently called "Species C". With the recognition of new species within the *brevirostris* complex, it is appropriate to restrict the type-locality of *A. brevirostris* in order to clarify my concept of the species; I hereby designate the vicinity of Fond Parisien, Département de l'Ouest, Haiti, as the type-locality of *A. brevirostris*. It is not unlikely that the original specimens, collected by M. Braconnier, actually came from the vicinity of Port-au-Prince, for the Haitian capital has long been a prominent Caribbean seaport. No *brevirostris* complex anoles have been collected recently from Port-au-Prince, yet sibling species A, B, and C have all been collected within 20 km airline of that city. Therefore I have chosen to designate the type-locality of *A. brevirostris* in the known distribution of Species C. Henceforth in this paper, *A. brevirostris* will refer only to Species C and "*A. brevirostris*" will refer to the complex in general.

Table 1. Meristic data for eight scale counts of six populations of anoles of the *Anolis brevirostris* complex. N=number of specimens examined. The first vertical column indicates the variation in each character, with the frequencies indicated thereafter in the following vertical columns. Modes are set in italics, and the percentage of the sample having the modal condition (or bi- or tri-modes) is indicated in parentheses. Means (x) are indicated only for number of postmental scales.

		A. b. brevirostris	*A. b.* deserticola	*A. b.* wetmorei	*A.* caudalis	*A.* marron	*A.* websteri
N		146	179	232	131	31	51
Scales across snout	3	—	—	—	1	—	—
	4	*79 (54%)*	*137 (77%)*	*100 (43%)*	34	*19 (61%)*	*33 (65%)*
	5	35	24	61	42	6	8
	6	26	16	50	*48 (37%)*	6	10
	7	4	1	5	3	—	
	8	1		5	3	—	
Loreal rows	3	5	—	1	1	—	—
	4	*89 (61%)*	73	92	*82 (63%)*	13	*27 (53%)*
	5	51	*100 (56%)*	*127 (55%)*	44	*16 (52%)*	24
	6		5	12	3	2	—
	7		—	—	1	—	
Scales between semicircles and interparietal	0/0	26	*88 (49%)*	51	43	*13 (42%)*	7
	0/1	17	19	26	18	4	2
	1/1	*71 (49%)*	65	*121 (52%)*	*54 (41%)*	11	*32 (63%)*
	1/2	15	2	15	9	2	7
	2/2	14	4	18	6	1	3
	2/3	—			1	—	—
	0/2	1	—	—	—	—	—

Table 1 (continued)

Scales in contact with interparietal	0/0	100 (69%)	72 (40%)	156 (57%)	70 (53%)	14 (45%)	42 (82%)
	0/1	18	17	25	18	4	2
	1/1	17	37	29	32	5	7
	1/2	5	24	10	7	6	—
	2/2	2	21	11	4	1	—
	2/3	1	5	1	—	1	—
Lateral postfrontal contact	1/2	2	—	—	—	—	—
	2/2	10	133 (75%)	80 (35%)	88 (68%)	18 (56%)	21 (41%)
	2/3	31	21	45	24	6	9
	3/3	79 (54%)	17	80 (35%)	12	5	14
	3/4	16	2	15	5	1	5
	4/4	5	2	2	—	1	—
	2/4	2	1	7	2	—	1
	2/5	—	1	—	—	—	—
	4/5	—	—	1	—	—	1
Median head scales	0	32 (43%)	33 (39%)	53	17	7	5
	1	63 (43%)	69 (39%)	100 (43%)	35	10 (32%)	18 (35%)
	2	31	69 (39%)	58	44 (34%)	10 (32%)	14
	3	16	5	16	27	2	11
	4	3	2	5	7	2	1
	5	—	—	—	1	—	2

Table 1 (continued)

		A. b. brevirostris	A. b. deserticola	A. b. wetmorei	A. caudalis	A. marron	A. websteri
Postmentals	2	—	2	—	2	—	1
	3	2	—	5	4	1	4
	4	68 (47%)	30	60	52 (40%)	5	12 (24%)
	5	44	46 (26%)	82 (35%)	44	9 (29%)	12 (24%)
	6	24	46 (26%)	52	23	9 (29%)	12 (24%)
	7	6	33	24	4	5	7
	8	—	16	6	1	2	2
	9	—	5	1	—	—	1
	x	4.7	5.8	5.2	4.7	5.6	5.3
Condition of preoccipital region	—	6	49	15	4	2	2
	t	—	11	6	4	2	2
	s	75 (52%)	75 (42%)	128 (55%)	35	17 (55%)	34 (67%)
	ms	23	6	15	13	1	6
	ps	6	7	12	13	2	5
	+	34	31	56	67 (46%)	7	2

"*ANOLIS BREVIROSTRIS*" NATURAL HISTORY

Anoles of the *brevirostris* complex and *A. distichus* are usually allotopic, but broadly sympatric. However, in certain localities where the generally xeric habitat of "*A. brevirostris*" intergrades with the generally mesic habitat of *A. distichus,* the two are precisely syntopic. In these situations hybridization is known to occur, to varying degrees, producing in the analyzed cases sterile offspring (Webster, 1978b).

"*A. brevirostris*" is cryptic. A generalized, composite head and dorsal pattern for the entire complex consists of: barred limbs and tail, two longitudinal dorsolateral stripes, an interocular bar, inter-parietal U, interocular V, and a series of five to seven dorsomedian chevrons pointed posteriorly. The first chevron is an internuchal patch. The upper longitudinal stripe extends from the angle of the jaw posteriorly to the level of the scapulae. Localized emphasis of this stripe forms the nuchal patch and scapular stripe. The lower longitudinal stripe extends from beneath the jaw across the shoulder to the hindlimbs. The pigmentation for the median dorsal stripe with chevrons is darker than the region below the upper dorsolateral stripe. All the markings are in general, faint with poor contrast, and interrupted outlines.

The largest specimens of "*A. brevirostris*" are from inland north-ern Haiti. In the Vallée de l'Artibonite in the vicinity of Dessalines and Pont Sondé, males reach a snout-vent length of 51 mm and females 47 mm. In general, females of all populations reach a maxi-mum size about 4 to 8 mm less than do males. The smallest speci-mens are from Isla Beata off the coast of the Península de Barahona, where males reach a snout-vent length of only 43 mm and females 38 mm.

"*A. brevirostris*" has an extensive but narrow distribution on Hispaniola. It occupies situations varying from mesic moderate ele-vations (Sierra Martín García, 915 m) to extreme xeric regions (Cul de Sac-Valle de Neiba plain, at or below sea level). Typically an inhabitant of xeric habitats, "*A. brevirostris*" prefers the larger trees of xeric woods and flourishes in the proximity of springs and in the conspicuously taller *Acacia* around villages. It is present through much of the low (often dense) *Acacia* scrub between the more favor-able habitats.

In the mesic regions along the east coast of the Península de Barahona, "*A. brevirostris*" is frequently observed on fenceposts in variegated sun and shade situations as well as on trees. In addition, "*A. brevirostris*" has been collected on vines, shrubs, trees, and on a cliff face 90 m above the ocean. In the extreme xeric region of the Cul de Sac-Valle de Neiba plain it is more frequently associated with *Cocos*, being found diurnally on the ground under palm logs, stacks of palm fronds, in coconut piles, and in *Cocos* trash. It is possible that in this region "*A. brevirostris*" resorts to such situations for nocturnal retreats. Generally, when it is found asleep it is one to three m above the ground on vines, shrubs, or particularly *Acacia*.

SYSTEMATIC ACCOUNT
Anolis brevirostris brevirostris Bocourt

Anolis brevirostris Bocourt, 1870, Nouv. Arch. Mus. Hist., Paris 6:11.

Lectotype. MNHP 2467B, an immature female collected by M. Braconnier.

Type-locality. "Haiti"; restricted here to within 5 km of Fond Parisien, Dépt. de l'Ouest, Haiti.

Associated specimens. Haiti, Dépt. de l'Ouest, Léogâne (MCZ 13781); Fond Michelle, 549 m (ASFS V37159); 7.4 km W. Thomazeau (ASFS V8156); Terre Rouge (ASFS V24266-94); La Source, Fond Parisien on edge of Etang Saumâtre (ASFS V8129-31); Source Fond Parisien, 1.6 km NE Fond Parisien (ASFS V36921-58); 3.2 km NW Fond Parisien (ASFS V36980-81); *Dominican Republic, Independencia Province,* Tierra Nueva (ASFS V42367-88); 10.4 km NE Jimaní (ASFS X9506); 5 km N Jimaní (ASFS V35476-77); Boca de Cachón (ASFS V4379, ASFS V39719-41); Las Baitoas (ASFS V14310-22); 6 km NW Duvergé (ASFS V17142-46); 5 km NNW Duvergé (ASFS X9937); just E Duvergé (ASFS V23274); Los Saladillos (ASFS V41744-45).

Definition. A sibling species of the *A. brevirostris* complex characterized by: moderate size (males to 48 mm, females to 45 mm snout-vent length); dorsum dark gray to medium gray and brown; dewlap pale, monochromatic, shades of orange, peach, yellow, gray, olive, and brown; nuchal patch variable, from reduced but dark, with no white border to medium and dark, with a white border; modally 1/1 scales between the supraorbital semicircles and the

interparietal; modally 0/0 supraorbitals in contact with the interparietal; modally a single row of small scales bordering interparietal anteriorly; modally 3/3 scales in contact laterally with the postfrontals (Species C of Webster and Burns, 1973).

Distribution. Hispaniola: in the Dominican Republic from Independencia Province (Las Salinas), the Valle de Neiba, west into the Haitian Cul de Sac Plain, Dépt. de l'Ouest (Daspinasse) and an isolated population on the Cap de Léogâne, Dept. de l'Ouest (Léogâne).

Description of lectotype. The lectotype has the following measurements and scale counts: snout-vent length 34 mm, tail 55 mm, four scales across snout, four loreal rows, semicircles in contact, 1/1 scales between supraorbital semicircles and the interparietal, 0/0 supraorbitals in contact with the interparietal, a single row of small scales bordering interparietal anteriorly, 2/2 scales in lateral contact with postfrontals, one median azygous head scale, six postmentals. Syntypes MHNP 2467 and 2467A are both *A. distichus.*

Variation. Scale counts for the series of 146 specimens of *A. b. brevirostris* are shown in Table 1.

The dorsum and markings of *A. b. brevirostris* vary clinally. In the east (Duvergé), the dorsum is medium gray-brown. The interocular bar is present. The interparietal U and interocular V are often present. Dorsomedian chevrons are occasionally found. Both dorsolateral stripes are present in reduced form. The upper remains as a scapular stripe and a nuchal patch is medium and dark, with a white border. The lower dorsolateral stripe is irregularly interrupted. The limbs and tail are barred. The more western the population, the more vague are the head and body markings, and the darker and more uniform gray the dorsum. At the western extreme the interparietal U and the dorsomedian chevrons are absent. The tail and limbs are vaguely barred. The upper dorsolateral stripe is reduced, often to a scapular spot and a reduced, dark, borderless nuchal patch.

Three geographical regions of dewlap variation in *A. b. brevirostris* are discernible. At the western extreme (Daspinasse to Thomazeau) dewlaps are pale, monochromatic in hues of gray, brown, yellow, yellow-gray, cream, peach, and rarely white. In the southern Cul de Sac Plain and Valle de Neiba the dewlaps are predominately pale orange and peach. Dark and bright orange dewlaps have been noted in the vicinity of Fond Parisien and Duvergé. Bicolored dewlaps, pale orange with a thin pale yellow margin, are found within

this region from Las Salinas to 10 km west of Duvergé. A third region, the northern Valle de Neiba between Etang Saumâtre and Lac Enriquillo, has predominately pale yellow and yellow-brown dewlaps. Hues noted for *A. b. brevirostris* are: Pl. 9I6, Pl. 9K5, Pl. 14Cl, and Pl. 14H5.

The isolated population on the Cap de Léogâne is represented by a single specimen (MCZ 13781) collected by G. M. Allen, August 1919. The dorsum is a medium to dark brown with a dark colored and medium sized nuchal patch with a white border. The limbs and tail are barred. The scapular stripe is present, but other markings are obscured by the dark dorsum. Scale counts for the Léogâne *A. b. brevirostris* are: six scales across the snout, four loreal rows, supraorbital semicircles in contact, 1/1 scales between semicircles and interparietal, 0/0 supraorbitals in contact with interparietal, 4/3 scales in lateral contact with postfrontals, four median head scales, four postmentals, and preoccipital present but separated from interparietal by a row of small scales.

Anolis brevirostris deserticola, new subspecies

Holotype. MCZ 132391, an adult male.

Type-locality. 2.1 km S San José de Ocoa, Peravia Province, Dominican Republic one of a series taken 19 November 1971, collected by natives. Original number ASFS V34034.

Paratypes (all from *Peravia Province, Dominican Republic*). ASFS V34031-33, ASFS V34035-67, same data as holotype; ASFS V724-25, 1.8 km S San José de Ocoa, 24 August 1963, A. Schwartz; ASFS V15615-25, San José de Ocoa, 3 August, 1968, native collectors.

Associated specimens. Dominican Republic, *La Estrelleta Prov.*, 2.5 km NW El Llano, 365 m (ASFS V31510-12); *San Juan Prov.*, 6.8 km NW Juan Herrera, 490 m (ASFS V31401); 1.7 km NW Sabaneta, 670 m (ASFS V31394); 10.2 km S Las Matas de Farfán, 550 m (ASFS V31327, ASFS V31468); 7.8 km NW Vallejuelo, 732 m (ASFS V31312); 1 km W Sabana Alta (MCZ 125547-48); SE Sabana Alta (MCZ 125554-55); 3 km W Guanito (MCZ 128236-47); 15 km SE San Juan (ASFS V412, ASFS V470-86); *Azua Prov.*, Padre las Casas (MCZ 58474-76); Sierra Martín García, Mt. Busú, 610 854 m (ASFS V31214-24); Sierra Martín García, above Barreras, *ca.* 915 m (ASFS V21174-202); Barreras, 10 km SW Puerto Viejo (ASFS V21110-16); *Peravia Prov.*, 3-5 km S San José de

Ocoa (ASFS V21396-97); 14.2 km S San José de Ocoa, 396 m (ASFS V715); 16.2 km S San José de Ocoa, 396 m (ASFS V712); 10 km S Los Ranchitos (ASFS V15627); 19 km NW Baní (ASFS V15632); Limonal (ASFS V14921-28); *Barahona Prov.*, west side Punta Martín García (ASFS V111-16); 3.2 km NE Fondo Negro (ASFS X9688); 4 km SE Canoa (ASFS V40785); 15 km ESE Canoa (ASFS V40796); 0.8 km NE Cachón, 122 m (ASFS V30749); 7.5 km E Cabral (ASFS X9604-05); *ca.* 3 km E Cabral (ASFS V20540-41); 11.8 km S Cabral, 701 m (ASFS X9849-53); 12.3 km S Cabral, 640 m (ASFS X9834-37).

Definition. A subspecies of *A. brevirostris* characterized by: moderate size (males to 48 mm, females to 45 mm snout-vent length); dorsum medium gray-brown to medium brown; venter white; dewlap bicolor, red-orange basal spot, margin cream or pale yellow to pale, or monochromatic, peach, salmon, or yellow; nuchal patch large and dark, with white border; modally 0/0 scales between the supraorbital semicircles and interparietal; modally 0/0 supraorbitals in contact with the interparietal; modally one or more rows of small scales bordering interparietal anteriorly; modally 2/2 scales in contact laterally with the postfrontals.

Distribution. Dominican Republic Valle de San Juan (El Llano, La Estrelleta Prov.), east onto the southern slopes of the Sierra de Ocoa and to the Llanos de Azua (Limonal, Peravia Prov.) and south onto the northern slopes of the Sierra de Baoruco (south of Cabral, Barahona Prov.).

Description of holotype. The holotype has the following measurements and scale counts: snout-vent length 45mm, tail (broken) 48mm, four scales across snout, four loreal rows, semicircles in contact, 0/0 scales between supraorbital semicircles and interparietal, 1/1 supraorbitals in contact with interparietal, preoccipital absent, 2/2 scales in lateral contact with postfrontals, one median azygous head scale, seven postmentals.

Variation. Scale counts for the series of 179 *A. b. deserticola* are shown in Table 1.

The dorsum of *A. b. deserticola* is medium gray-brown to medium brown. The head markings are distinct and generally include the interocular bar, parietal U, and interocular V. Dorsomedian chevrons are absent, except for the internuchal chevron which is rare. The lower dorsolateral stripe is absent. The upper is present and extends from the scapula to the hindlimbs in an interrupted

pattern. The nuchal patch is large and dark, with a white border. The limbs and tail are barred. The venter is white to pale yellow with pale yellow on the underside of the tail. The dewlap is uniformly pale yellow, peach, or salmon to bicolor peach or red-orange with a pale yellow or cream margin; hues noted for the dewlap are: Pl. 10D8, Pl. 18F1, Pl. 17E1, with centers of Pl. 5B12 and Pl. 6B11.

The dorsum is a darker gray and the markings most distinct in specimens from the Sierra Martín García and from the southern slopes of the Sierra de Ocoa. The browner dorsum and least distinct markings characterize specimens from the eastern Valle de San Juan (San Juan).

Seven specimens collected west of San Juan are noteworthy. The samples are small (one to three each) and were collected in ravines peripheral to the Valle de San Juan. The preoccipital is present in 71% of the specimens—significantly different from all other *A. b. deserticola*. The nuchal patch is reduced to absent.

Scale counts for specimens from the moderate elevations between Lago de Rincón and the Bahía de Neiba and along the northern slopes of the Sierra de Baoruco are intermediate between those of *A. b. deserticola* to the north and *A. b wetmorei* to the south. The scale counts and dewlap more closely favor *A. b. deserticola* and have thus been included with them.

Anolis brevirostris wetmorei Cochran

Anolis dominicensis wetmorei Cochran, 1931, Proc. Biol. Soc. Washington 44:89.

Anolis brevirostris wetmorei: Schwartz, 1968, Bull. Mus. Comp. Zool. 137(2): 257.

Holotype. USNM 83881, an adult male, 13 May 1931, collected by A. Wetmore and F. C. Lincoln.

Type-locality. Isla Beata, Dominican Republic.

Associated specimens. Dominican Republic, Barahona Prov., Barahona (ASFS X9530-60, ASFS V14017-38, ASFS X9456-58); 5 km S Barahona (ASFS V20545-48); 6 km SE Barahona (ASFS V40787-88); 6.6 km SW Barahona, 137 m (ASFS V30240-43, V30418-19); 15 km SW Barahona (ASFS V40781-83); 5.3 km NE La Ciénaga (ASFS X9379-81); 6.4 km SW La Ciénaga, 46 m (ASFS V39858); 9 km SW La Ciénaga, 91 m (ASFS V42710); 2 km NW Paraíso (ASFS V17-24); 1 km NE Paraíso, Río Nizaito (ASFS

V40762-71); 1 km W Paraíso (ASFS V40772-80); 7.7 km W Paraíso, 152 m (ASFS V30928-31); 17.9 km NE Caletón (ASFS V30790-802); Los Patos (ASFS V16926); 6 km N Enriquillo, 427 m (ASFS V42190-209); 2.2 km NE Enriquillo (ASFS V14078-80); *Pedernales Prov.*, 21 km SW Enriquillo (ASFS X9416); 8 km NE Oviedo (viejo) (ASFS X9964-65); 7 km N Oviedo (viejo) (ASFS V23121); 5 km NE Oviedo (viejo) (ASFS V14073-75); 3 km NW Oviedo (nuevo) (ASFS V40678-87, ASFS V40471-82); 7 km N, thence 20 km SE Cabo Rojo, 183 m (ASFS V29769-70); 7 km N, thence 17.6 km SE Cabo Rojo, 152 m (ASFS V30088-89); 2 km E turn to Cabo Rojo (MCZ 128257); behind Cabo Rojo police station (MCZ 143407-08); 21 km NE Cabo Rojo, 396 m (ASFS V16782-85); 21.2 km N Cabo Rojo on Alcoa mine road, 440 m (MCZ 143403-04); L'Eglise, near La Mercedes (ASFS V21510); 10 km N Pedernales, 244 m (ASFS V30115-17); 4 km SE Pedernales (ASFS V16729-30); south center of Pedernales (ASFS V29846); Pedernales (ASFS V2505-06, ASFS V2919); *Isla Beata* (ASFS V2670-71, UF/FSM 36969-70, MCZ 37520, MCZ 58695-702, AMNH 41414, AMNH 41416-18, AMNH 44854-58); just E Punta Beata (ASFS V17220); *Haiti, Dépt. de l'Ouest*, near Saltrou (MCZ 49274-79); 4 km NNE Marigot, 61 m (ASFS V37372-77).

Definition. A subspecies of *A. brevirostris* characterized by: large size (males to 50 mm, females to 45 mm snout-vent length); dorsum pale grayish tan to gray to tan to brown to mottled greenish tan; venter white to yellow; dewlap color very variable from locality to locality (see below); nuchal patch reduced and gray to brown with no white border to large and dark with white border; modally 1/1 scales between supraorbital semicircles and interparietal; modally 0/0 supraorbitals in contact with interparietal; modally a single row of small scales bordering the interparietal anteriorly; bimodally 2/2 or 3/3 scales in contact laterally with postfrontals.

Description of holotype. The holotype has the following measurements and scale counts: snout-vent length 43 mm, tail (broken) 62 mm, five scales across snout, four loreal rows, semicircles in contact, 1/1 scales between supraorbital semicircles and interparietal, 0/0 supraorbitals in contact with interparietal, a single row of small scales bordering interparietal anteriorly, 3/3 scales in lateral contact with postfrontals, three median head scales, five postmentals.

Variation. Scale counts for the series of 232 *A. b. wetmorei* are shown in Table 1.

Distribution. Hispaniola: in Haiti from the Dépt. de l'Ouest (Marigot), the southern coast of the Tiburon Peninsula east across the southern portion of the Dominican Península de Barahona (Enriquillo), Isla Beata, and north along the eastern coast of the Península de Barahona to the city of Barahona.

A. b. wetmorei varies geographically. On Isla Beata, whence *wetmorei* was first described, the dorsum is nearly uniform tan or light gray. In general the head and body markings are faint to absent. The interocular bar is faint and the interocular V is reduced to a short postocular stripe. The dorsomedian chevrons and dorsolateral stripes are absent. The nuchal patch is present and varies from large and dark to reduced and gray, but always with a white border. The limbs and tail are faintly barred. The venter is whitish and the dewlap is pale yellow.

On mainland Hispaniola *wetmorei* dewlaps vary from pale yellow to bicolored yellow with an orange central spot to deep orange or red-orange. However, regionally the variation is less extreme, favoring either the deep orange, red-orange, and bicolored orange with a thin pale margin (Enriquillo to la Ciénaga and Pedernales to Cañada la Cerca) or the pale yellow to yellow with orange blush basally characteristic of the remainder of the extensive *wetmorei* distribution. The full range of variation has been observed at the northeastern distribution extreme, Barahona, and at the regional interfaces at Pedernales, La Ciénaga, and south of Enriquillo.

The eastern orange-dewlap *wetmorei* have a dorsum that is pale greenish tan to tan. The markings of the head and body are cryptic to the point that the dorsum has a woodgrain pattern. The interocular bar is regularly present. The interparietal U is wide and dark. Mediandorsal chevrons are occasionally present, although most often they are reduced to dorsomedian spots or are absent. The upper and lower dorsolateral stripes are interrupted to absent. The legs and tail are lightly barred. The nuchal patch is reduced and faint, often gray, tan, or reddish brown, and with no white border. Hues noted for the dewlap in this series are: Pl. 10I7, Pl. 10G11, Pl. 3F12, Pl. 4B11, and Pl. 11J8.

The western orange-dewlap *wetmorei* are similar to the eastern, but there are no reports of any green in the dorsal color. The markings have greater contrast. The scapular stripe is long and there are remnants of the lower dorsolateral stripe. Pl. 10C10 is the only hue noted for the dewlap.

The yellow-dewlap *wetmorei* are in general more conspicuously marked, except in the vicinity of Oviedo where the dorsum is a darker and grayer version of *wetmorei* on Isla Beata. The nuchal patch for these populations is highly variable, from large and dark with a white border to reduced and faint with no white border. Additional hues noted for the dewlaps are: Pl. 10F1, Pl. 11F3, Pl. 11E1, with Pl. 11B10 and Pl. 11O7 centrally.

Anolis caudalis Cochran

Anolis dominicensis caudalis Cochran, 1932, Proc. Biol. Soc. Washington 45:185.

Anolis brevirostris caudalis: Schwartz, 1968, Bull. Mus. Comp. Zool. 137(2):257.

Holotype. USNM 76801, an immature male, March 1929, collected by A. J. Poole and W. M. Perrygo.

Type-locality. Nan Café, Ile de la Gonâve, Haiti.

Paratypes. Haiti, Ile de la Gonave, USNM 76799-800, same data as holotype; USNM 77080-82, Pointe à Raquettes, "1927", W. J. Eyerdam; USNM 80388-89, 8.3–16.7 km inland Anse-à-Galets, 23 March 1930, L. H. Parish and W. M. Perrygo; Ile de la Petite Gonâve, USNM 80390, 23 March 1930, L. H. Parish and W. M. Perrygo.

Associated specimens. Haiti, Dépt. de l'Ouest, Trou Forban (ASFS X1939, ASFS V8204-14); 3.5 km E Trou Forban (ASFS X4001-03); 0.3 km NE Carries, Ouanga Bay Hotel (ASFS V36876-82); 4 km N Arcahaie (MCZ 125008-18); 3 km SE Arcahaie (ASFS V43778-81); 6 km N Duvalierville (MCZ 125022-37); 1.4 km SE Duvalierville (ASFS V36872-74); 6 km SE Duvalierville (ASFS V9834-36); Ile à Cabrit, 6 km airline SE Duvalierville (ASFS V9853-56, ASFS V44806-25); Source Matelas (MCZ 125019-21); *Dépt. du Sud,* Presqu'ile de Baraderes, vicinity of Grand Boucan (ASFS V26342-48); 4.2km W Jérémie (USNM 59255-56); *Ile de la Gonâve,* Source Picmi, above Picmi (ASFS V26610-15, ASFS V26652); Anse-à-Galets (ASFS V22413-22); Etroits (ASFS X2410-15).

Definition. A sibling species of the *A. brevirostris* complex characterized by: moderate size (males to 48 mm, females to 44 mm snout-vent length); dorsum medium brown to light gray-tan to light gray; venter pale yellow; dewlap highly variable from uniformly

white, yellow or yellow-gray to bicolor yellow with red or orange centers to bicolor gray-green with rusty centers; nuchal patch medium, dark with white border; modally 1/1 scales between the supraorbital semicircles and the interparietal; modally 0/0 supraorbitals in contact with the interparietal; modally preoccipital present; modally 2/2 scales in contact laterally with the postfrontals (Species B of Webster and Burns, 1973).

Distribution. Haiti: Dépt. de l'Ouest, from Trou Forban south along the coast of the Canal de St. Marc to the Baie de Port-au-Prince (Source Matelas); Ile de la Gonâve; Ile de la Petite Gonâve; and two isolated populations on the northern shore of the Tiburon Peninsula (Dépt. du Sud: Presqu'île de Baraderes and Jérémie).

Description of holotype. The holotype has the following measurements and scale counts: snout-vent length 42 mm, tail broken, six scales across snout, four loreal rows, semicircles in contact, 0/0 scales between supraorbital semicircles and interparietal, 1/1 supraorbitals in contact with interparietal, preoccipital region with five small scales with an incomplete row of small scales bordering interparietal anteriorly, 2/2 scales in lateral contact with postfrontals, one median azygous head scale, five postmentals.

Variation. Scale counts for the series of 131 *A. caudalis* are shown in Table 1.

The dorsum of *A. caudalis* is medium brown to light gray; the lightest specimens examined are from Anse-à-Galets, Ile de la Gonâve. The head markings are generally absent. Dorsomedian chevrons are absent. The nuchal patch is large and dark with a white border. The scapular stripe is short but distinct. The remainder of the dorsolateral stripes are reduced, interrupted, and vague to absent. The limbs and tail are weakly barred. The venter is pale yellow. The dewlap color is highly variable from uniformly white, yellow, yellow-gray, or gray-green, to bicolored white or yellow with variable orange centrally to bicolored yellow-green or gray-green with yellow, mustard, rusty, or darker gray-green centers. Hues noted for the dewlap color are: Pl. 12E1, Pl. 10C1, and Pl. 6K10 centrally with Pl. 10I1 and Pl. 17G1 peripherally.

At the northern mainland extreme of *A. caudalis* (Trou Forban) the dewlap is uniformly white or pale yellow to bicolored with a small orange basal spot. There is a clinal increase in the size and intensity of the orange spot the farther south along the coast (Webster and Burns, 1973). However, the extent of the orange, even at the

southern mainland extreme (Source Matelas), is not so great as that of *A. websteri*. Two exceptions to this general cline are recorded. At Trou Forban, one series (ASFS V8204-14) had dewlaps gray to greenish gray with mustard or darker gray-green centers. On the Ile à Cabrit in the Baie de Port-au-Prince the dewlaps are gray-green.

On Ile de la Gonâve no such cline exists, and the dewlap color is variable and includes all dewlap colors described above for *A. caudalis*.

The two disjunct populations of *A. caudalis* are of particular interest. Jérémie *caudalis* is represented by only two specimens (USNM 59255-56) collected by Henderson and Bartsch, 10 April 1917. The dorsum is a faded gray-tan, with a dorsomedian stripe and short scapular stripe. The nuchal patch is large and dark with a white border. The limbs and tail are barred. The head has a faint interocular bar, short ocular stripe, and a broad and dark interparietal U. Scale counts for these two *caudalis* are: six scales across snout, four loreal rows, supraorbital semicircles in contact, 0/0 and 1/1 scales between semicircles and interparietal, 0/0 and 1/1 supraorbitals in contact with interparietal, 2/2 scales in lateral contact with postfrontals, no median head scales, and preoccipital present.

The other disjunct population, Grand Boucan *caudalis*, is represented by seven specimens (ASFS V26342-48) collected by Richard Thomas and natives, 4 August 1971. Of the three known disjunct populations of "*A. brevirostris*" on the Tiburon Peninsula, only Grand Boucan *caudalis* have dewlap color notes. The dewlaps are colored "pale (greenish) with faint basal dull yellow smudge". The dorsum is medium to dark brown with a scapular stripe. The lower dorsolateral stripe is discernible. The interparietal U and interocular bar and V are present. The limbs and tail are barred. The nuchal patch is large and dark with a white border. Grand Boucan *caudalis* differ from mainland and Gonâve *caudalis* in two modal scale counts: five scales across the snout and three median head scales. The preoccipital, although present, is fragmented into multiple scales in three of seven specimens.

Anolis marron, new species

Holotype. MCZ 124732, an adult male.

Type-locality. Jacmel, Département de l'Ouest, one of a series taken 15 June 1970, collected by T. P. Webster.

Paratypes. MCZ 124730-31, MCZ 124733-36, same data as holotype.

Associated specimens. Haiti, Dépt. de l'Ouest, Marigot (MCZ 124723-29); 3.2 km W Marigot (ASFS V9771-78); 4.8 km E Cayes Jacmel (ASFS V9711-16); 8 km W Jacmel (ASFS V9696-97); Terre Noire, 19.2 km SW Jacmel (ASFS V37509).

Definition. A sibling species of the *A. brevirostris* complex characterized by: moderate size (males to 50 mm, females to 42 mm snout-vent length); dorsum pale gray and tan to medium brown; venter pale yellow to off-white; dewlap uniformly olive-gray to bicolor tan with reddish center; nuchal patch large and dark with faint white border; modally 0/0 scales between supraorbital semicircles and the interparietal; modally 0/0 supraorbitals in contact with the interparietal; modally one or more rows of small scales bordering interparietal anteriorly; modally 2/2 scales in contact laterally with postfrontals.

Distribution. Haiti; the southern coast of the Tiburon Peninsula, from Marigot west to Terre Noire.

Description of holotype. The holotype has the following measurements and scale counts: snout-vent length 47 mm, tail 62 mm, four scales across snout, four loreal rows, semicircles in contact, 0/0 scales between supraorbital semicircles and the interparietal, 2/1 supraorbitals in contact with the interparietal, a series of small scales bordering interparietal anteriorly, 2/2 scales in lateral contact with postfrontals, one median azygous head scale, five postmentals.

Variation. Scale counts for the series of 31 *A. marron* are shown in table 1.

The dorsum of *A. marron* is pale gray and brown to medium brown. A thin interocular bar is regularly present, but other head markings are vague or absent. The dorsomedian chevrons are reduced to small dorsal spots or are absent in all but the darkest specimens. The thin, dark scapular stripe broadens and becomes less distinct posteriorly. The lower dorsolateral stripe is interrupted and vague. The nuchal patch is large and dark with a white border. The limbs and tail are barred. The venter is pale yellow to off-white. The dewlap is either uniformly dark olive-gray or bicolored tan with a reddish center; hues noted for the dewlap are: Pl. 15H5, Pl. 6B10, and Pl. 6C10.

Anolis websteri, new species

Holotype. MCZ 132390, an adult male.

Type-locality. 7.4 km NW Dessalines, Département de l'Artibonite, Haiti, one of a series taken 8 July 1974, collected by natives. Original number ASFS V39323.

Paratypes. ASFS V39322, ASFS V39324-37, same data as holotype.

Associated specimens. Haiti, Dépt. *de Nord Ouest.* Môle St. Nicholas (MCZ 63143-53); Dépt. de l'Artibonite, 6.7 km NW Gonaïves (ASFS V39295-302); 1 km NE Pont Sondé (ASFS V39342-50); Bains de Amani-y (ASFS V36900-03, ASFS V43742); 2.6 km NW Montrouis (ASFS V36888-89).

Definition. A sibling species of the *A. brevirostris* complex characterized by: large size (males to 51 mm, females to 47 mm snout-vent length); dorsum medium to dark gray and brown; venter bright yellow to yellow-orange; dewlap orange with a thin pale yellow edge; nuchal patch large and dark with no white border; modally 1/1 scales between the supraorbital semicircles and the interparietal; modally 0/0 supraorbitals in contact with interparietal; modally a single row of small scales bordering interparietal anteriorly; modally 2/2 scales in contact laterally with postfrontals. (Species A of Webster and Burns, 1973).

Distribution. Haiti; from the Dépt. de Nord Ouest (Môle St. Nicholas) and northwestern Dépt. de l'Artibonite (Marché aux Poteux; between Gonaïves and Ennery), south into the Vallée de l'Artibonite (Dessaliens and Pont Sondé) and along the coast of the Golfe de la Gonâve to Pointe de Montrouis (Montrouis).

Description of holotype. The holotype has the following measurements and scale counts: snout-vent length 47 mm, tail 70 mm, five scales across snout, four loreal rows, semicircles in contact, 1/1 scales between supraorbital semicircles and interparietal, 0/0 supraorbitals in contact with interparietal, a single row of small scales bordering interparietal anteriorly, 3/3 scales in lateral contact with postfrontals, one median azygous head scale, four postmentals.

Variation. Scale counts for the series of 51 *A. websteri* are shown in Table 1.

The dorsum of *A. websteri* is moderate to dark gray or brown. Head and body markings, if present, are generally dark and diffuse,

often disrupted. The nuchal patch is large and dark, with no white
border. The scapular stripe is dark and short. The interocular bar is
present in the lighter colored specimens, as is sometimes the case
with the interparietal U and interocular V. Dorsal chevrons are
always absent. The dorsolateral stripes are disrupted and diffuse.
The limbs and tail are vaguely barred. The interparietal is yellow,
but appears as a copper flake in preserved specimens. The venters
are bright yellow to yellow-orange. The dewlap is uniformly orange
or orange with a narrow yellow margin; hues noted for the dewlap
are: Pl. 9L7, Pl. 9L8, Pl. 9L10, Pl. 10L8, and Pl. 11K10.

A series of eight *A. websteri* from Pont Sondé is notable in the
variation in dewlap color and modal scale counts. The dewlaps vary
from orange (Pl. 10L8) to mustard (Pl. 12L7) to pale yellow (Pl.
11L4). The venters are not so bright as other *websteri*. Modal scale
counts differences for the series are: six scales across the snout; five
loreal rows; and 3/3 scales in contact laterally with postfrontals.

Well outside its normal distribution, *A. websteri* was found in
abundance 3.5 km NW Bon Repos, Dépt. de l'Ouest, in young
native mahogany (*Swietenia mahagoni* Jacq.). Electrophoretic evi-
dence indicates that it is slightly more similar to northern *A. web-
steri* than to southern specimens of that species. Presumably, *A.
websteri* in this location was a recent introduction by man to an
artificial habitat. Recent road improvement has led to the total
destruction of the localized habitat (Webster, 1978a). No specimens
were preserved.

DISCUSSION

INTERACTION OF THE "*ANOLIS BREVIROSTRIS*"—
ANOLIS DISTICHUS COMPLEXES

Species of the "*A. brevirostris*"—*A. distichus* group often present
contrasting dewlap colors in areas of contact or proximity. Such
differences suggest that dewlap color may be important for species
identification and reproductive isolation (Webster and Burns, 1973).
Both body size and color appear to be important in *Anolis* species
identification, especially in simple (e.g., two species) faunas (Will-
iams and Rand, 1977).

The *A. brevirostris* complex is closely associated with four sub-
species of *A. distichus: dominicensis, ravitergum, favillarum,* and
suppar. In areas of sympatry "*A. brevirostris*" and *distichus* gener-

ally vary in body size, body color, and dewlap color. In brief, the associated subspecies have the following characteristics: *dominicensis*, males to 58 mm, females to 48 mm snout-vent length, dorsum bright marbled green to rich chocolate brown, dewlap usually pale yellow; *ravitergum*, males to 56 mm, females to 45 mm snout-vent length, dorsum ashy gray to dark tan to pale greenish, dewlap pale yellow to bicolored with an orange basal spot; *favillarum*, males to 54 mm, females to 47 mm snout-vent length, dorsum dark green, dewlap vivid orange centrally with narrow pale yellow edge; *suppar*, males to 54 mm, females to 44 mm snout-vent length, dorsum pale green, dewlap pale yellow to yellow-green, at times with a dull yellow-orange basal smudge. For more detailed descriptions, see Schwartz (1968) and Webster (1978b). In general, *A. distichus* is larger than *"A. brevirostris"* and the green and brown unmarked dorsa of *distichus* contrast with the gray and marked dorsa of *"brevirostris"*.

A. *caudalis* is the only species within the *brevirostris* complex which is not extensively sympatric with *A. d. dominicensis*. Quite to the contrary, both mainland and Gonave *caudalis* appear to exclude *dominicensis*, except for two specimens, one from Trou Forban and another from nearby Ste. Philomène. At the disjunct populations on the Tiburon Peninsula, Grand Boucan *caudalis* also appear to exclude *dominicensis* and the Jérémie population is sympatric with another subspecies, *A. d. suppar*. No color notes exist for the Jérémie *caudalis*, nor can any be assumed. *A. caudalis* here is the smaller lizard and has two prominent markings. The nuchal patch is large and faint with a white border and the interparietal U is broad and dark.

A. d. *dominicensis* is broadly sympatric with *A. websteri* and *A. marron* throughout the latters' respective ranges. Locally *dominicensis* is precisely syntopic with *websteri*. *A. websteri* has the largest snout-vent length for the *brevirostris* complex and at this region of syntopy is larger than *dominicensis*. The reduced, borderless nuchal patch and generally vague and diffuse markings of gray-brown *websteri* probably indicate an increased reliance on dewlap color for species recognition and reproductive isolation. The orange dewlap of *websteri* sharply contrast with the typical pale yellow of *dominicensis* and white to gray-yellow with greenish basally of *A. caudalis*. The isolation is incomplete, for Webster (1978b) reports a low inci-

dence of hybridization at Montrouis with *dominicensis*; and (in litt.) some hybridization and introgression (two of five proteins, only one way, only a short distance) with *caudalis* at Trou Forban.

Though populations of *A. marron* are never far from those of *A. d. dominicensis*, no areas of syntopy are known. The dark olive-gray or bicolored tan with reddish center dewlap contrast with the pale yellow of *dominicensis*. The dark scapular stripe and large, dark, white bordered nuchal patch of *marron* are more prominent dorsal markings than those of *A. websteri* and may provide additional cues for species recognition and reproductive isolation. *A. marron* and *A. b. wetmorei* come in contact near Marigot. The bicolored pale yellow with orange basal spot of *A. b. wetmorei* contrasts with the *marron* dewlap.

In the eastern Cul de Sac Plain (Thomazeau; Manneville), *A. b. brevirostris* is sympatric (but apparently not syntopic) with *A. d. dominicensis*. Of the two species in the area, *A. b. brevirostris* is distinctly the inhabitant of the xeric scrub and *A. d. dominicensis* the inhabitant of more mesic situations (oases and cultivated areas). *A. b. brevirostris* is the widespread lizard in open areas, whereas *A. d. dominicensis* is restricted to certain less rigorous habitats and is in effect surrounded by *A. b. brevirostris*. Here, the dewlap color of *A. d. dominicensis* is atypically a deep orange (Pl. 4C11, Pl. 4G10, and Pl. 4G11), at times with a faintly brown cast (Schwartz, 1968). This contrasts strongly with the dewlap of *A. b. brevirostris*, which locally is dully pigmented with no conspicuous pattern in white to pale shades of yellow, gray-yellow, and gray-brown.

There is a clinal decrease in the amount of orange in the dewlap of *A. d. dominicensis* away from *A. brevirostris*, until at the southern edge of the Cul de Sac and Valle de Neiba plain, pale yellow is again the typical color of *A. d. dominicensis* dewlaps. It is important to note that in this area (Fond Parisien to Duvergé) *A. b. brevirostris* dewlaps are predominantly pale orange, dull orange, to bright orange.

Another subspecies, *A. d. ravitergum*, is sympatric with *A. b. brevirostris* at the latter's eastern distribution. Webster (1978b) reports hybridization locally at Balneario la Zurza, 5 km WNW Duvergé. Here the dewlaps of *A. d. ravitergum* range from uniformly light yellow-orange to strongly bicolored with an orange basal spot. Dewlaps of *A. b. brevirostris* are all monochromatic

orange in varying degrees of intensity. Dewlaps do not appear consistently to differentiate these populations despite the strong dewlap color contrast.

A. b. wetmorei, like *A. caudalis,* appears to exclude *A. distichus* but is locally sympatric with two subspecies of *A. distichus* at three localities. *A. d. dominicensis* and *A. b. wetmorei* are sympatric at Belle Anse (=Saltrou), Dépt. de l'Ouest, and Las Mercedes, Pedernales Province. Here, *wetmorei* is bicolored with an orange basal spot and a yellow or cream outer margin. *A. d. dominicensis* dewlap is typically pale yellow but occasional specimens in the Sierra de Baoruco in Pedernales Province have the dewlap very pale yellow to practically white.

A. d. favillarum and *A. b. wetmorei* are sympatric at Hermann's finca, near Paraíso, Barahona Province. No color notes exist for the single specimen of *wetmorei* taken from this locality. (These are, however, old records and may not imply real sympatry.)

At all three of these widely separated localities, *wetmorei* is generally the lizard of the lower elevations with *distichus* occupying the moderate to higher elevations (300–1250 m) of the Massif de la Selle and Sierra de Baoruco.

A. b. deserticola is sympatric with one of three subspecies of *A. distichus* throughout most of its range. *A. d. dominicensis* and *A. b. deserticola* are widely sympatric in the Valle de San Juan from 7 km NW Vallejuelo and 15 km SE San Juan westward to the Dominico-Haitian border. The dewlaps of both are pale yellow except at Vallejuelo where *deserticola* is bicolored with a pale orange blush. *A. d. ravitergum* is sympatric throughout most of the remaining range of *deserticola* and in local situations is even syntopic (0.5 and 2.5 km E Cachón). Webster (1978b) notes the similarity in dewlaps. Both are bicolored, with a pale margin surrounding a darker or brighter spot of variable size. Corresponding to this high degree of similarity is a higher incidence of hybridization at these localities.

A. b. deserticola extends onto the northern slopes of the Sierra de Baoruco, where in the intermediate altitudes and transitional vegetation it is sympatric and locally syntopic with *A. d. favillarum*. The dewlaps are here identical; both are dark orange, but the nuchal patch and gray dorsum of *deserticola* contrast strongly with the green dorsum of *favillarum*. The incidence of hybridization here has not been investigated.

The sample examined in this study represents the known distribution of the "*A. brevirostris*" complex. Three of the six populations recognized by scale counts correspond to the informal siblings A, B, and C of Webster and Burns (1973). *A. brevirostris* is restricted to Species C and the name *A. caudalis* is assigned to Species B as suggested by Williams (1976). The distribution of *A. b. wetmorei* of Isla Beata is expanded to include the Península de Barahona and part of the southern coast of the Tiburon Peninsula. Species A (*A. websteri*), a new sibling species (*A. marron*), and a new subspecies (*A. b. deserticola*) are described. Scale counts were taken as supplementary evidence of geographic variation along with that in dewlap color within the *brevirostris* complex, and to provide a basis for the formal description of parapatric siblings.

A. caudalis and each of the three subspecies of *A. brevirostris* overlap in dewlap color variation. Dewlaps bicolored yellow with orange centers and/or uniformly pale yellow are found to varying degrees in the distribution of each species. *A. caudalis* is, by modalities of scale counts, the most readily distinguishable of these species and of the entire *brevirostris* complex. Modally, has six scales across the snout (all others four), preoccipital present (all others a single row of small scales bordering the interparietal anteriorly), and two median scales (all others modally one or bimodally one and two).

Webster (1978a) noted the presence of shared alleles of *A. caudalis* with *A. marron* and *A. b. deserticola*. The scale counts of the latter two populations differ from the former not only by the unique modalities of *caudalis* noted above, but further by the modes shared by *marron* and *deserticola:* scales between interparietal and supraorbital semicircles 0/0 (all others 1/1); postmentals, bimodes five and six, with the highest mean values *deserticola* 5.8 and *marron* 5.6 (others, mode four or five, or trimode four, five, and six; means 4.7 to 5.3). Despite the wide geographic separation (*ca.* 120 km airline across the Sierra de Baoruco and Massif de la Selle at the closest points), these two populations have essentially the same scale counts. The modalities for the scale counts taken are the same, the percentages of the modalities are within three to 17% of each other, and the distribution of the non-modal counts is similar. Further, these are two of the three populations that are extensively sympatric with *A. distichus*. *A. marron* differs from *A. b. wetmorei* and the

entire *brevirostris* complex by its unique dewlap color (dark olive-gray to tan with reddish center).

A. b. brevirostris differs from other populations in the "*A. brevirostris*" complex by the unique modes of 3/3 scales in contact with postfrontals laterally (all others modally 2/2 or bimodally 2/2 and 3/3) and four postmentals, with 4.7 the lowest mean value (others modally five, bimodally five and six or trimodally four, five, and six; means 4.7 to 5.8).

A. b. wetmorei differs from other populations in the *brevirostris* complex by the unique bimode of 2/2 and 3/3 scales in contact with postfrontals laterally. *A. b. wetmorei* differs from the other subspecies of *A. brevirostris* in having modally five postmentals (*brevirostris* modally four and *deserticola* bimodally five and six), but share this characteristic with *A. caudalis*. Variation in scale counts and dorsum occur within *A. b. wetmorei*. At Enriquillo there is a dramatic change in vegetation and geography from the mesic slopes of the Sierra do Baoruco in the north to the arid plain that forms the southern tip of the Península de Barahona. This change appears to effectively inhibit genetic exchange between *A. b. wetmorei* populations demonstrated by Webster's observation of different frequencies for variants of three proteins and the modal shift in loreal rows and the dorsum coloration differences for the two regions documented by the present study. On the eastern coast of the Península de Barahona (Barahona to Enriquillo) *wetmorei* modally has five loreal rows and a greenish tan dorsum in association with the orange, red-orange, and bicolored orange with a thin yellow margin dewlap color. To the south and west (Oviedo to Marigot) *wetmorei* modally has four loreal rows and no greenish dorsa have been recorded.

A. websteri differs from other populations in the *brevirostris* complex by the unique trimode of four, five, and six postmentals (others modally four or five, or bimodally five and six). *A. websteri* and each of the three subspecies of *A. brevirostris* overlap in dewlap color variation. Dewlaps uniformly orange and bicolored orange with a thin yellow margin are found to varying degrees in the distribution of each species. The subspecies of *A. brevirostris* are further distinguishable from *A. websteri* by their unique modal scale counts noted above.

The distribution presented in this paper follows closely that of Webster and Burns (1973), but varies from that of Webster (1978a). Webster noted electrophoretic similarities between *A. caudalis* and the Jacmel-Marigot populations and between *A. caudalis* and the San Juan-San José de Ocoa populations. He implied that the Jacmel-Marigot populations be referred to *caudalis*. Here the southwestern Tiburon populations are designated as a new species, *A. marron*. For the *brevirostris* complex, *marron* varies greatly from *caudalis* in modal scale counts, dewlap color, and in relationships to *A. distichus*. Modal scale count variations are: scales across snout (four versus five), loreal rows (five versus four), scales betwen supraorbital semicircles and interparietal (0/0 versus 1/1), median head scales (bimodes one and two versus mode two), postmentals (bimodes five and six versus mode five), and preoccipital condition (modally a series of small scales bordering interparietal anteriorly versus preoccipital modally present). The dark olive-gray to tan with reddish centered dewlap of *marron* distinguishes it not only from *caudalis* but is unique in the whole *brevirostris* complex. *A. caudalis* excludes *A. distichus dominicensis* where *A. marron* and *A. distichus* are sympatric. Webster also noted shared alleles of *marron* with *A. b. wetmorei* at Bell Anse.

The northern Dominican populations having electrophoretic similarities to *A. caudalis* are designated as a new subspecies, *A. b. deserticola*. *A. b. deserticola* and *A. marron* have the same scale count modes, and thus the same substantial difference from *caudalis*. Webster (1978b) noted variation in hybridization of *A. distichus* with *A. b. brevirostris* from that with *A. b. deserticola*. However, neither this variation nor the electrophoretic similarities discouraged Webster from associating *deserticola* with *brevirostris*.

A. marron would then appear to be an extension of "*A. brevirostris*" from the Península de Barahona, a pattern found in other reptilian species (*Ameiva leberi, Ameiva lineolata privigna, Ameiva taeniura vulcanalis*).

APPENDIX   1

1) *Anolis brevirostris brevirostris*: *Haiti*, Dépt. de l-Ouest, Source Trou Caiman (MCZ 124737-49); Thomazeau (MCZ 13769-70, MCZ 59388-89, MCZ 124705); between Thomazeau and Manneville (MCZ 59381); Manneville (MCZ 59382-87, MCZ 63154-58,

MCZ 121777-78, MCZ 123125-55) Eaux Gaillées (MCZ 59943-48, MCZ 63159-71, MCZ 118790-92, MCZ 121096-101); Ganthier (MCZ 124706-22); *Dominican Republic, Independencia Prov.*, Las Lajas (AMNH 41456, AMNH 41458-59, AMNH 41461); La Descubierta (AMNH 41433, AMNH 41437-38); Las Baitoas (AMNH 50149-50, AMNH 50199, AMNH 50210-16); 8.8 km W Duvergé (MCZ 125541); 2 km SW Duvergé (UF/FSM 42738).

2) *Anolis brevirostris deserticola: Dominican Republic, Azua Prov.*, 4 km SW Sabana Yegua, 420 m (UF FSM 42739); *Barahona Prov.*, Cabral (MCZ 58511-25, MCZ 58526-36); 5 km S Cabral (MCZ 58509-10); La Cueva (MCZ 58425, MCZ 58429, MCZ 58432, MCZ 58436); lower part of road to Polo (MCZ 125551-53, MCZ 128219-25); 7.5 km N Canoa (MCZ 125549-50); Sierra Martín García, 1540 m (UF FSM 36971); *Peravia Prov.*, 2 km N San José de Ocoa (MCZ 107079-80); 1 km N San José de Ocoa (MCZ 128255-56); 1 km S San José de Ocoa (MCZ 126012-44); 2 km S San José de Ocoa (MCZ 128248-54); Río Limón, 8 km S San José de Ocoa (MCZ 107081-82); 5 km N Baní, 110 m (UF/FSM 36972).

3) *Anolis brevirostris wetmorei: Dominican Republic, Barahona Prov.*, Barahona (AMNH 41307-15, AMNH 41317, AMNH 41322, AMNH 51430, AMNH 51446, AMNH 51533, MCZ 58694, MCZ 93106, UF/FSM 42733-35, USNM Field No RIC 040037-43); aviation field, Barahona (AMNH 51508-22, AMNH 51525, AMNH 51527); Hotel Guarocuya, Barahona (MCZ 107083-86); 1.7 km S Barahona (MCZ 9311); SW Barahona (AMNH 51535-40); Paraiso (AMNH 51630-31); Hermann's finca, near Paraíso (AMNH 516145); Los Patos (MCZ 58559-60); *Pedernales Prov.*, Oviedo (viejo) (MCZ 58537-38); 2 km E turn to Cabo Rojo (MCZ 128215-18, MCZ 128258-59); 1 km SW Las Mercedes, 380 m (UF FSM 42736); 2 km E Las Mercedes, 250 m (UF/FSM 42737); *Haiti, Dépt. de l'Ouest* Lan Banane, near Saltrou (MCZ 68685-90).

4) *Anolis caudalis: Haiti, Dépt. de l'Ouest*, 6.3 km N Duvalierville (MCZ 123072-99); Ste. Philomène (USNM 123351-56); *Ile de la Gonâve*, no other locality (MCZ 13783-89); Anse-à-Galets (MCZ 29046-50, MCZ 37507-16, MCZ 85299-309); Nan Café (MCZ 85225-45, UF/FSM 12286-1-9, UF/FSM 12287-1-9, UF, FSM 12288, UF FSM 12290); Pointe à Raquettes (MCZ 25509-18, MCZ 80613-38, UF/FSM 12291-1-2); vicinity of Pointe à Raquettes (MCZ 80581-86); Ti Roche, 9.5 km Pointe à Raquettes (MCZ 80587-612); Nan Palmiste, 4 km from Pointe à Raquettes (MCZ
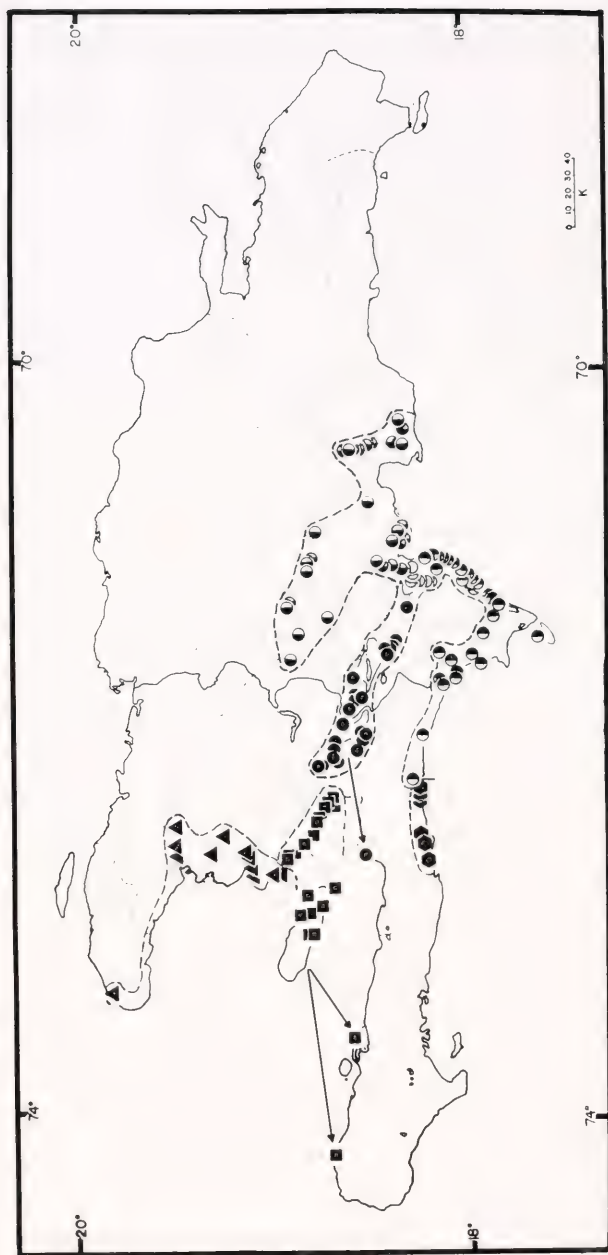
Figure 1. Map of Hispaniola, showing the distribution of the four members of the *Anolis brevirostris* group. Symbols for species are: *brevirostris*, circles; *caudalis*, squares; *marron*, hexagons; *websteri*, triangles. The three subspecies of *A. brevirostris* are indicated as: *A. b. brevirostris*—solid circles; *A. b. deserticola*—circles with left half blackened; *A. b. wetmorei*—circles with right half blackened. Note also the two arrows to the distal portion of the Tiburon Peninsula showing localities for *A. caudalis* at Jérémie and Grand Boucan, and the arrows showing the occurrence of *A. b. brevirostris* at Léogâne. The open circles between Barahona and Lago de Rincón, and including the northern slopes of the Sierra de Baoruco south of Cabral represent specimens that are intermediate between *A. b. wetmorei* and *A. b. deserticola*, but are closer to the latter.

80639-58); Nan Saline (MCZ 85169-74, MCZ 85175-81); Tête Source (MCZ 85182-205); Platon Yéyé (MCZ 85206-24); Lan Coupe (MCZ 85281-98); *Ile de la Petite Gonâve* (AMNH 49745, AMNH 49747-48).

5) *Anolis websteri: Haiti, Dépt. de l'Artibonite*, Marché aux Poteaux (MCZ 125117-25); Passe Reine, between Gonaïves and Ennery (MCZ 63141-42); Pont de l-Estère (MCZ 63135-40); bridge over Rivière de l'Artibonite, St. Marc road (MCZ 59355-80); Lafond (MCZ 118783-89, MCZ 123101-24, MCZ 125110-16); St. Marc (AMNH 42593, AMNH 49696, AMNH 49699-700, AMNH 49702-04, AMNH 49708-09, AMNH 49711-12, AMNH 77566, USNM 59219); Montrouis (MCZ 125126-69).

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B R E V I O R A

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ELEUTHERODACTYLUS EREMITUS, A NEW TRANS-ANDEAN SPECIES OF THE *LACRIMOSUS* ASSEMBLY FROM ECUADOR (AMPHIBIA: LEPTODACTYLIDAE)

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Abstract: Eleutherodactylus eremitus is named from cloud forests along the Ríos Mindo, Pilatón, and Saloya, in Provincia Pichincha, Ecuador, between 1540 and 2100 m. The new frog is most closely related to *E. bromeliaceus* from the Amazonian versant of the Andes in southern Ecuador.

Lynch and Duellman (1980) included the following four species (all cis-Andean) in the *lacrimosus* assembly of the *unistrigatus* group of *Eleutherodactylus* –E. *bromeliaceus* Lynch, *E. lacrimosus* (Jiménez de la Espada), *E. mendax* Duellman, and *E. petersi* Lynch and Duellman. *Eleutherodactylus lacrimosus* is distributed below 1000m from eastern Ecuador east to the mouth of the Amazon river (Lynch and Schwartz, 1972; Lynch, 1979), whereas the other three species occur on the eastern slopes of the Andes—*E. petersi,* from the headwaters of the Río Magdalena (Colombia) south to the val-ley of the Río Pastaza (Ecuador); *E. bromeliaceus,* south of the Pastaza Trench to the Cordillera de Zamora in southern Ecuador; and *E. mendax,* from central Perú (Huánuco) south into adjacent Bolivia.

In 1970 while collecting on the Pacific slopes in Andean Ecuador, I found a small, green frog in a bromeliad. Subsequent study of the collections of the late James A. Peters provided two additional examples from nearby localities. Additional specimens were obtained by William E. Duellman, Kenneth Miyata, and myself in the course of field work between 1975 and 1978. Sufficient material is now available to provide a description of the first trans-Andean representative of the *lacrimosus* assembly.

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Eleutherodactylus eremitus sp. nov.

Holotype: MCZ 92103, a gravid female, taken on the La Palma-Chiriboga road (hwy 28), 25.7 km above (NE) La Palma, Prov. Pichincha, Ecuador, 1820 m, on 12 July 1976 by Kenneth Miyata.

Paratypes (all from Prov. Pichincha, Ecuador). Topotype, MCZ 92104; 2 km W Campamento Silante (La Palma-Aloag road), 2100m, KU 140878; 5 km ESE Chiriboga, Quebrada Zapadores, 2010m, KU 179085–86, 180248; km 58, ± 8 km W Chiriboga, USNM 211209; 3.5 km NE Mindo, 1540m, KU 165884; 6.2 km E Tandapi, 1750m, MCZ 92105; Tandayapa, USNM 211208.

Diagnosis. 1) skin of dorsum finely areolate, that of venter coarsely areolate; no dorsolateral folds; no anal sheath; 2) tympanum partially visible, round, its length 2/5–1/2 eye length; 3) snout subacuminate in dorsal view, rounded or weakly protruding in lateral profile (papilla at tip); canthus rostralis moderately distinct; 4) upper eyelid bearing a conical tubercle, narrower than IOD; no cranial crests; 5) vomerine odontophores oval in outline, elevated; 6) males with vocal slits, vocal sac, and non-spinous nuptial pads; 7) first finger shorter than second; all fingers with broad discs, pads on II–IV expanded; numerous supernumerary palmar tubercles; 8) fingers bear lateral fringes; 9) 2–3 small, subconical ulnar tubercles; 10) small tubercles on knee, heel, outer edges of tarsus; 11) two metatarsal tubercles, inner oval, 4 times size pungent outer; numerous supernumerary plantar tubercles; 12) toes bear lateral fringes, broad discs, dilated pads; pads smaller than those of fingers; 13) cream with faint brown stippling; vague canthal-supratympanic and flank stripe; colorless areas in groin and on posterior surfaces of thighs; 14) adults small, males 17.2–20.0 (x̄=18.9, N=6) mm, one adult female 27.6 mm SVL.

Eleutherodactylus eremitus most closely resembles *E. mendax* but differs in having areolate skin on the dorsum and more prominent vomerine odontophores (odontophores absent or indistinct in *E. mendax*). Both have larger tympana than do *E. bromeliaceus, E. lacrimosus,* and *E. petersi.*

Description. Head broader than body (except in gravid female), wider than long; HW 35.1–38.4 (x̄=36.4, N=8) per cent SVL; snout subacuminate in dorsal view with conical papilla at tip, in profile rounded or truncate but with papilla, sometimes protruding; snout moderately long, E–N in males 81.5–88.5 (x̄=85.4, N=4) per cent

eye length, in females 86.4–100.0 (x̄=95.6, N=4) per cent; nostrils weakly protuberant, directed dorsolaterally; canthus rostralis moderately distinct, straight; loreal region weakly concave, sloping gradually to lips, lips not flared; upper eyelid width 70.4–93.4 (x̄=81.5, N=8) per cent IOD, bearing one conical tubercle in center (Fig. 1a–b) and several low warts (areolations) posterolaterally; no cranial crests; tympanum moderately distinct, annulus visible through thin skin, directed dorsolaterally, round, its length 42.3–50.0 (x̄= 47.2, N=8) per cent eye length, separated from eye by distance equal to tympanum length; supratympanic fold indistinct amidst areolations; large, subconical, postrictal tubercles posterolateral to tympanum.

Choanae round, large, not concealed by palatal shelf of maxillary arch; vomerine odontophores elevated, median and posterior to choanae, oval in outline, separated on midline by distance equal to 1–1/2 odontophore widths, each bearing transverse row of 4–5 teeth; tongue longer than wide, bearing a shallow notch along posterior border or not, posterior 2/5 not adherent to floor of mouth; males with vocal slits posterolateral to tongue; vocal sac median, subgular, external.

Skin of dorsum finely areolate (most obvious paravertebrally and on upper flanks), venter coarsely areolate; throat areolate in females, no dorsolateral folds or anal sheath; larger warts posterior and posterolateral to vent; discoidal fold well anteriad to groin.

Three to four small, subconical ulnar tubercles; palmar tubercle bifid, much larger than oval thenar tubercle; palm areolate, but 1–2 more pungent supernumerary tubercles evident at base of each finger; subarticular tubercles pungent, round (or slightly broader than long); KU 179086 has a bifid basal subarticular tubercle on finger III; fingers bear prominent lateral fringes; similar fringe on outer edge of IV continuing along most of palm (Fig. 1); fingers bear broad discs, pads (except on thumb) moderately large, apically rounded; first finger shorter than second; thumbs of males swollen, bearing white, non-spinous nuptial pads.

Small (but prominent), subconical tubercles on knee, heel, outer edge of tarsus; less distinct tubercle on inner edge of tarsus; inner metatarsal tubercle twice as long as wide, relatively flat; outer subconical, 1/4 size of inner; numerous supernumerary plantar tubercles (some more prominent than others, in rows); subarticular tubercles round to slightly longer than wide; toes bear prominent
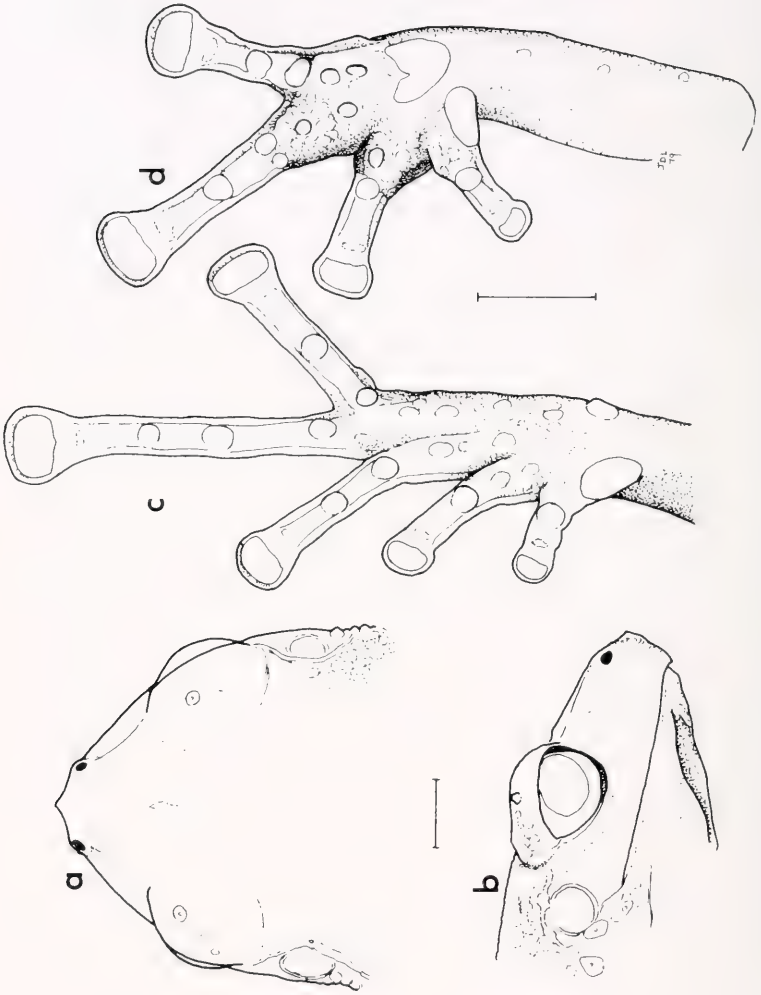
Figure 1. *Eleutherodactylus eremitus* (A–B) head, MCZ 92103; (C–D) hand and foot, KU 179086. Lines equal 2 mm.

lateral fringes, no webbing; toe pads smaller than those of fingers, apically rounded, bearing broad discs; heels of flexed hind limbs overlap; shank 47.1–55.0 ($\bar{x}$=51.9, N=8) per cent SVL.

Most individuals are cream with diffuse brown stippling above and less below; pigmentless areas in groin and on posterior surfaces of thighs (bordered by more dense brown stippling); no labial or limb bars; indefinite canthal-supratympanic stripes, continuing as a diffuse band onto anterior flanks. KU 140878 and 179086 have dark brown dorsolateral stripes continuous with canthal-supratympanic stripe (Fig. 2). KU 179085 is golden brown above with a brown blotch in the center of the back and prominent canthal-supratympanic stripes.

In life, *E. eremitus* is green above with a brown to reddish brown head and white below (throat stippled with brown). The groin and posterior surfaces of the thighs are pale yellow. The iris is bright copper with brown flecks.

Measurements of holotype in mm. SVL 27.6; shank 13.0; HW 9.7; head length 8.5; upper eyelid width 2.8; IOD 3.0; tympanum length 1.5; eye length 3.1; E–N 3.1.

Etymology. Latin, meaning lonely or solitary, in allusion to its relatives which are all cis-Andean.

Natural history. KU 140878 was found during the day in a large terrestrial bromeliad beside hwy 30, before the habitat was severely altered by road construction. Specimens from the Quebrada Zapadores were collected at night as they sat on broad leaves in the forest beside the streams. *Eleutherodactylus eremitus* is either quite uncommon or several collectors have failed to discover its preferred micro-
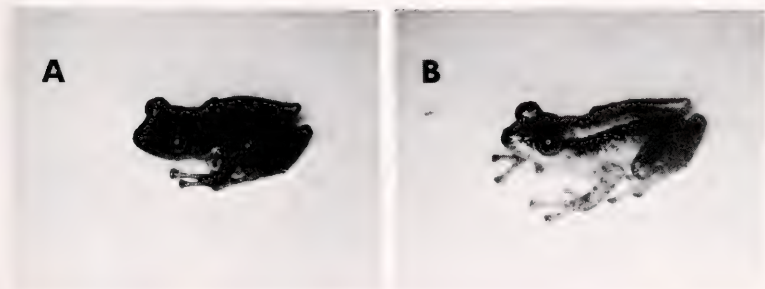
Figure 2. *Eleutherodactylus eremitus.* (A) KU 179085, male, 19.8 SVL; (B) KU 179086, juvenile female, 23.0 mm SVL.

habitat in the cloud forests (on only one occasion has more than one specimen been found [Miyata secured two on a single night in the type-locality]).

Remarks. Frogs of the *lacrimosus* assembly have been discovered slowly. *Eleutherodactylus lacrimosus* was named in 1875 but not reported again until 1952 (Lutz and Kloss, 1952). Duellman (1978), Lynch (1979), and Lynch and Duellman (1980) each named species found on the Amazonian slopes of the Andes from Colombia to Bolivia, but the first specimens of these were not obtained until the late 1950's or early 1960's. In eastern Ecuador, these small frogs are especially common in arboreal bromeliads. In July 1977 at Mera (Prov. Pastaza), at least a dozen examples of *E. lacrimosus* and *E. petersi* were found in one bromeliad in remaining patches of forest along the Río Pastaza. The bromeliad microhabitat is occupied by a variety of frogs on the Pacific versant. At the base of the Andes, *E. subsigillatus* (Boulenger) normally is found only in arboreal bromeliads. In high cloud forests, *E. celator* Lynch, *E. phoxocephalus* Lynch, and *E. thymelopsoides* Lynch are found almost exclusively in bromeliads. I suspect *E. eremitus* is actually more abundant on the Pacific versant between 1500 and 2100 m than is suggested by the ten specimens now available. Too infrequently I have failed to exploit the bromeliad microhabitat betwen 800 and 2400 m, in part because frogs were abundant at night and I collected infrequently by day. Inspection of only three bromeliads in July 1977 at Tandapi (Prov. Pichincha) yielded one example each of *E. crucifer* (Boulenger) and *E. parvillus* Lynch.

Eleutherodactylus bromeliaceus seems to be the closest known relative of *E. eremitus,* with *E. mendax* being less closely related. *Eleutherodactylus lacrimosus* and *E. petersi* are considered more closely allied to one another than either is to the other three species.

ACKNOWLEDGMENTS

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JAW MUSCULATURE OF THE WEST INDIAN SNAKE *ALSOPHIS CANTHERIGERUS BROOKSI* (COLUBRIDAE, REPTILIA).

KENNETH V. KARDONG[1]

ABSTRACT

The West Indian colubrid snake *Alsophis cantherigerus brooksi* is presently assigned to the subfamily Xenodontinae (*sensu* Maglio, 1970). It is a member of an assemblage of related snakes from continental stocks that have spread to and diversified within this Caribbean archipelago. The head myology proves to be representative of other xenodontine snakes of the West Indies and thus is a convenient reference for comparison to other subspecies and may be useful in later comparisons to other species' assemblages of the region. Its jaw musculature conforms basically to that of other generalized colubrid snakes. Special attention is given to the internal fascicular bundles within each muscle.

The adductor mandibulae externus superficialis passes posteroventrally from its origin on the skull, inserting mostly by a broad aponeurosis except, for a rostral slip that forms its anterior edge and inserts directly on the mandible. The adductor mandibulae externus profundus consists of anterior and posterior wedges of muscle delineated by a vertical suture between them. Adductor mandibulae externus medialis is separable into superficial and deep slips. One significant difference in general muscle anatomy from some other colubrids concerns the protractor quadrati. This muscle inserts on the retroarticular process of the mandible which differs from the genus *Opheodrys* in which it is reported to insert on the quadrate.

Lateral jaw musculature proves to be very similar within the subspecies of *Alsophis cantherigerus*. The only detectable difference occurs in the deep division of the depressor mandibulae. In most subspecies (*adspersus, brooksi, cantherigerus, caymanus, schwartzi*), this deep division is a single slip of the depressor arising from a single site. However, in *fuscicauda, pepei,* and *ruttyi* it splits lengthwise so as to arise from two sites of origin. One instance of individual asymmetry was identified in *adspersus* wherein the insertion of the superficialis differs on left and right sides.

The conformity of lateral jaw musculature among subspecies related to *brooksi* emphasizes the uniform nature of this group. Other authors also found this uniformity in features of the integument, skull osteology, and hemipenial characteristics.

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INTRODUCTION

Examination of the West Indian colubrid snakes of the subfamily Xenodontinae by Maglio (1970) served to emphasize the special island biogeographic features of these species. Compared to continental species, West Indian insular members of this subfamily have well delineated distributions and their probable origin, namely from mainland genera, seems better established. Routes of initial colonization by and diversification within the different species assemblages through this Caribbean archipelago were proposed by Maglio as well. With a view to testing this and related proposals on the phylogeny of this group, I examined the jaw musculature of members from the various assemblages, following any changes through the various species on the different islands. This work and its implications will be the subject of later reports. The present paper is restricted to the species *Alsophis cantherigerus* and, in particular, the subspecies *A. c. brooksi.*

This subspecies is found only on the Swan Islands, located almost 200 kilometers north of Honduras. It deserves special attention for several reasons. It is part of the assemblage of closely related populations that spread to and diversified over the islands. Its jaw musculature is representative of the condition in other West Indian xenodontine species. Its jaw anatomy can thus serve as a central point of reference in later analysis of these island snake species. It is also a rare subspecies even in museum collections.

MATERIALS AND METHODS

All descriptions of the head anatomy of *Alosphis cantherigerus brooksi* are based on a single alcohol preserved female specimen from the Museum of Comparative Zoology (MCZ) 11979. The specimen, taken on Swan Islands and donated to the collection in 1916, measured 85.5 cm snout-vent length. The tail, missing its severed tip, measured 23.4 cm. The cranial musculature was exposed initially by cutting through the integument along the lips and reflecting the skin backwards. This revealed that the specimen had sustained a deep cut in the neck musculature that also severed the vertebral column through the fourth cervical vertebra and consequently limited the description of structures in the immediate vicinity. This study centered upon the jaw musculature and therefore often required the disruption of nerves to first confirm muscle at-

tachments with certainty. As a result, some of the peripheral distributions of the nerves were lost before they could be traced with confidence. The blood vessels proved impractical to follow for the same reasons. Consequently, only those pathways and distributions of nerves and blood vessels that could later be confirmed are included in the descriptions. No bilateral asymmetry in jaw musculature was detected. Muscle and ligament terminology follows Haas (1973), Kardong (1973, 1974), and Pregill (1977); interpretation of cranial nerves relies upon Auen and Langebartel (1977); and cephalic gland nomenclature is based on Taub (1966). One departure in nomenclature concerns the muscle running between the neck and dorsal end of the quadrate, which is often referred to as *M. retractor quadrati* especially in descriptions of venomous snakes (e.g. Dullemeijer, 1956). Others employ this same term for a quite different muscle (e.g. Kochva, 1962). To avoid confusion herein, the term *M. cervicoquadratus* is used instead.

The other subspecies of *Alsophis cantherigerus* examined include: *adspersus* (MCZ 68727), *cantherigerus* (MCZ 13288), *caymanus* (MCZ 44886), *fuscicauda* (MCZ 44875), *pepei* (MCZ 13289), *ruttyi* (MCZ 44877), and *schwartzi* (MCZ 56430).

GENERAL DESCRIPTION

Cephalic Glands

The **nasal glands**, like other lateral cephalic glands, are bilaterally paired. Each rests in an anterior depression on the anteromedial face of the prefrontal and is bounded medially by a dorsal process of the respective septomaxilla and by the nasal capsule. The **Harderian gland** (Figs. 2, 3a, 4b) is found ventral to and extends behind the eye. Beneath the eye the gland lies within the orbit and is compressed between eyeball and the ligamentum orbitale interioris (septum interorbitale of Dullemeijer, 1956) which forms the ventral floor of the orbit. Passing posteriorly out of the orbit it enlarges, occupying the space lateral to the levator pterygoidei muscle and medial to the postorbital bone and the adductor mandibulae externus superficialis muscle. The **infralabial glands** (Fig. 4c) extend posteriorly along the lateral aspect of the dentary and compound bones to approximately the level of the anterior insertion of the adductor mandibulae externus superficialis muscle. The **supralabial glands**

extend posteriorly slightly farther. However, they lie along the upper lips and pass lateral to the superficialis muscles and maxillae. Pressed into the side of each supralabial gland and residing behind the eye is the large **Duvernoy's gland** (Fig. 4c), which in the preserved state appears lighter in color and more distinctly lobed. The small, unpaired **premaxillary gland** lies beneath the upper lip on the superficial face of the premaxillary bone.

In the chin, the **sublingual gland** (Fig. 6a, b) is represented by three parts, a single medial and paired lateral glands. The medial sublingual gland is stationed along the ventroanterior end of the tongue and anchored to its connective tissue sheath. The lateral sublingual glands insert into the oral epithelium and serve as attachment sites for the pars glandularis of the transversus branchialis and the protractor larygeus muscles.

Ligaments

A number of small, unnamed ligaments link the cranial elements together, but only the prominent or most commonly cited in the literature are discussed here. Two primary ligaments serve to check the motion of the supratemporal relative to the braincase. One is the **parieto-supratemporal ligament** that runs from the dorsal edge of the supratemporal to the dorsal surface of the exoccipital. It also serves as the site of origin for parts of the adductor mandibulae externus medialis and depressor mandibulae muscles. The other is the **prooto-supratemporal ligament** that attaches to the ventral edge of the supratemporal and to the adjacent region of the braincase. Rotation of the prefrontal is controlled in part by the **fronto-prefrontal ligament** (Fig. 2) from the ventromedial corner of the prefrontal to the adjacent parasphenoid.

Several prominent ligaments are associated with the palato-maxillary arch (pterygoid, ectopterygoid, maxilla, and palatine). Within the arch, the **intramaxillary ligament** (Fig. 2) reaches from the medial ectopterygoid process of the maxilla forward to attach jointly on the palatine process of the maxilla and maxillary process of the palatine. The short, fan-shaped **quadrato-pterygoid ligament** runs from the narrow posterior end of the pterygoid to a wider medial attachment site along the mandible that includes the retroarticular process and extends below the articular notch. The strong, cord-like **maxillo-postorbital ligament** (Fig. 4) reaches from the

downward directed tip of the postorbital to the lateral side of the maxilla just anterior to its articulation with the ectopterygoid. The **quadrato-maxillary ligament** (Fig. 4) begins along the laterodorsal edge of the retroarticular process, passes forward above the lateral condyle of the quadrate, and divides. The smaller division attaches to the nearby dermis beneath the most posterior supralabial scale, whereas the larger division continues forward to attach to the posterolateral region of the maxilla.

Cranial Nerves
Figs. 2, 3a–d, 4a–c

Trigeminal Nerve (V). The trigeminal is one of three major nerves supplying the jaw musculature. Trigeminal branches that supply the jaw musculature exit from the cranium through two openings in the prootic bone, the maxillary and mandibular foramina. Five branches could be found passing through the maxillary foramen. The largest, the maxillary division (V_2), passes lateral to the pseudotemporalis then bends forward continuing in an anterior path dorsal to the origin of the pterygoideus. A second nerve divides lateral to the pseudotemporalis with one branch passing laterally to glandular tissue along the upper lip and the second swinging dorsally, superficial to the facial vein, to enter the ventral surface of the adductor mandibulae externus superficialis. Two other nerves also course dorsally after exiting from the foramen. Both pass deep to the facial vein, but one enters the medial face of the adductor mandibulae externus medialis (deep division) and the other enters the medial face of the adductor mandibulae externus superficialis. The fifth nerve leaving this foramen passes laterally.

Through the mandibular foramen exit six branches of the trigeminal nerve. The largest branch is the mandibular division (V_3) that passes posteriorly and then turns ventrally following a route that carries it between the adductor mandibulae externus profundus and the adductor mandibulae posterior. Eventually it enters a foramen in the mandible located at the anterior end of the mandibular fossa. A second branch of the trigeminal courses posteriorly, then swings dorsally, bifurcates, and enters the medial face of the adductor mandibulae externus profundus and medioposterior face of the adductor mandibulae externus medialis (superficial division). A third nerve passes posteriorly deep to the mandibular division. It sends

one branch between medial and lateral divisions of the adductor mandibulae posterior, another between the pars minimus and the lateral division of adductor mandibulae posterior, and several branches into the medial surface of the adductor mandibulae externus profundus. The remaining three nerves of the trigeminal that exit through the mandibular foramen pass ventrally—one disappears between the pterygoideus and the levator pterygoidei, one enters the lateral face of the pseudotemporalis, and the last runs laterally into the glandular tissue along the upper lip.

Facial Nerve (VII). Two divisions of the facial nerve exit through the mandibular foramen. The larger is the hyomandibular nerve that passes posteriorly over the columella, under the quadrate, and enters the depressor mandibulae. A slender communication arising from the base of the hyomandibular travels posteriorly and merges with craniocervical trunk. The second division of the facial nerve is the palatine nerve. It courses ventrally along the underside of the braincase, is joined by the cranial sympathetic nerve, and then enters the posterior Vidian canal in the ventral aspect of the basisphenoid bone.

Craniocervical Trunk. The glossopharyngeal (IX), vagus (X), and hypoglossal (XII) cranial nerves combine to form a single large nerve or plexus, the craniocervical trunk (Auen and Lagebartel, 1977). In addition, a slender communication runs between the base of the hyomandibular and this trunk. Finally, a spinal nerve (presumably the ventral ramus of the first spinal nerve) emerges from between the rectus capitus anterior pars dorsalis and longissimus dorsi (ventral head) cervical muscles to join with the craniocervical trunk. The trunk sweeps around the side of the body at about the angle of the jaws and supplies various members of the hypobranchial musculature.

Lateral Jaw Musculature

M. cervicomandibularis (cm)
Figs. 1, 4c

The epimysium of the spinalis-semispinalis complex near the dorsal midline serves as the surface of origin. This origin extends along a line even with neural spines 3 to 8 in the nape of the neck and

tachments with certainty. As a result, some of the peripheral distributions of the nerves were lost before they could be traced with confidence. The blood vessels proved impractical to follow for the same reasons. Consequently, only those pathways and distributions of nerves and blood vessels that could later be confirmed are included in the descriptions. No bilateral asymmetry in jaw musculature was detected. Muscle and ligament terminology follows Haas (1973), Kardong (1973, 1974), and Pregill (1977); interpretation of cranial nerves relies upon Auen and Langebartel (1977); and cephalic gland nomenclature is based on Taub (1966). One departure in nomenclature concerns the muscle running between the neck and dorsal end of the quadrate, which is often referred to as *M. retractor quadrati* especially in descriptions of venomous snakes (e.g. Dullemeijer, 1956). Others employ this same term for a quite different muscle (e.g. Kochva, 1962). To avoid confusion herein, the term *M. cervicoquadratus* is used instead.

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Through the mandibular foramen exit six branches of the trigeminal nerve. The largest branch is the mandibular division (V_3) that passes posteriorly and then turns ventrally following a route that carries it between the adductor mandibulae externus profundus and the adductor mandibulae posterior. Eventually it enters a foramen in the mandible located at the anterior end of the mandibular fossa. A second branch of the trigeminal courses posteriorly, then swings dorsally, bifurcates, and enters the medial face of the adductor mandibulae externus profundus and medioposterior face of the adductor mandibulae externus medialis (superficial division). A third nerve passes posteriorly deep to the mandibular division. It sends

one branch between medial and lateral divisions of the adductor mandibulae posterior, another between the pars minimus and the lateral division of adductor mandibulae posterior, and several branches into the medial surface of the adductor mandibulae externus profundus. The remaining three nerves of the trigeminal that exit through the mandibular foramen pass ventrally—one disappears between the pterygoideus and the levator pterygoidei, one enters the lateral face of the pseudotemporalis, and the last runs laterally into the glandular tissue along the upper lip.

Facial Nerve (VII). Two divisions of the facial nerve exit through the mandibular foramen. The larger is the hyomandibular nerve that passes posteriorly over the columella, under the quadrate, and enters the depressor mandibulae. A slender communication arising from the base of the hyomandibular travels posteriorly and merges with craniocervical trunk. The second division of the facial nerve is the palatine nerve. It courses ventrally along the underside of the braincase, is joined by the cranial sympathetic nerve, and then enters the posterior Vidian canal in the ventral aspect of the basisphenoid bone.

Craniocervical Trunk. The glossopharyngeal (IX), vagus (X), and hypoglossal (XII) cranial nerves combine to form a single large nerve or plexus, the craniocervical trunk (Auen and Lagebartel, 1977). In addition, a slender communication runs between the base of the hyomandibular and this trunk. Finally, a spinal nerve (presumably the ventral ramus of the first spinal nerve) emerges from between the rectus capitus anterior pars dorsalis and longissimus dorsi (ventral head) cervical muscles to join with the craniocervical trunk. The trunk sweeps around the side of the body at about the angle of the jaws and supplies various members of the hypobranchial musculature.

Lateral Jaw Musculature

M. cervicomandibularis (cm)
Figs. 1, 4c

The epimysium of the spinalis-semispinalis complex near the dorsal midline serves as the surface of origin. This origin extends along a line even with neural spines 3 to 8 in the nape of the neck and

partially overlaps the anterior origin of the neuromandibularis. This broad muscle travels ventrally, passing over the deep cervico-quadratus, and narrows abruptly to insert on the lateral epicondyle of the quadrate and on the adjacent part of quadrato-maxillary (dermal) ligament, which passes posteriorly to its own attachment on the dorsolateral retroarticular process.

M. depressor mandibulae (dm)
(M. occipito-quadrato-mandibularis)
Figs. 1, 4 a–c

There are two parts of this muscle, superficial and deep, divided by the cervicoquadratus that passes between these two parts en route to its own insertion. Branches of cranial nerve VII also pass through the belly of the deep division, then along the medial side of the superficial division.

The superficial division has an origin that runs from the parieto-supratemporal ligament next to the adductor mandibulae externus medialis, across the supratemporal to the anterodorsal corner of the quadrate, and extends down along the surface epimysium of adductor mandibulae externus profundus near its own origin. It inserts directly on the lateral rim of the mandibular retroarticular process, overlapping the attachment site of the quadrato-maxillary ligament.

The deep division arises from the posterior tip of the supratemporal and the posterior, dorsomedial edge of the quadrate. It is a parallel muscle that inserts on the dorsomedial surface of the retroarticular process.

M. cervicoquadratus (cq)
### Figs. 1, 4 a–c

This is a long, tapering muscle that takes origin in the dermis of the lateral integument posterior to the belly of the neuromandibularis over the intercostal muscles. It gradually narrows as it courses forward, slipping under the more superficial cervicomandibularis, becoming a cord-like tendon that passes between the superficial and the deep divisions of the depressor mandibulae to insert laterally on the proximal end of the quadrate just below its posterior corner.

Figure 1.   Lateral view of the skull and ventral view of the quadrate and lower jaw showing sites of muscle attachments.

Figure 2.   Ventral view of head. The bones of the left palato-maxillary arch have been removed to expose deep structures. On the right, the M. pterygoideus (pg) has been cut and partially reflected and the mandible rotated outward to better expose some of the underlying structures.

Abbreviations:

am	M. adductor mandibulae externus medialis
ap	M. adductor mandibulae externus profundus
apo	M. adductor mandibulae posterior
as	M. adductor mandibulae externus superficialis
br	transverse ridge on basisphenoid
c	columella
cm	M. cervicomandibularis
cp	choanal process of palatine
cq	M. cervicoquadratus
ct	craniocervical nerve trunk (IX, X, XII)
dm	M. depressor mandibulae
gg	M. genioglossus
gt	M. geniotrachealis
Hd	Harderian gland
ima	M. intermandibularis anterior
ipa	M. intermandibularis posterior, pars anterior
ipp	M. intermandibular posterior, pars posterior
lfp	ligamentum fronto-prefrontale
lim	ligamentum intramaxillare
lmp	ligmentum maxillo-postorbitale
loi	ligamentum orbitale inferioris
lp	M. levator pterygoidei
lqm	ligamentum quadrato-maxillare
nm	M. neuromandibularis
pg	M. pterygoideus
pga	M. pterygoideus accessorius
pp	M. protractor pterygoidei
pq	M. protractor quadrati
pst	M. pseudotemporalis
rcd	M. rectus capitus anterior, pars dorsalis
rcv	M. rectus capitus anterior, pars ventralis
rp	M. retractor pterygoidei
rv	M. retractor vomeris
V_2	Trigeminal nerve, maxillary division
V_3	Trigeminal nerve, mandibular division
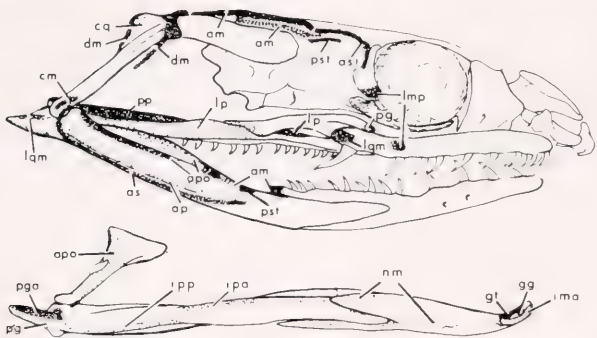
M. adductor mandibulae externus superficialis (as)
Figs, 1, 3 c–d, 4 a–c

A temporal crest, prominent posteriorly, becomes lower as it passes forward along the dorsolateral side of the skull. Anteriorly it curves outward to terminate on the postorbital process of the parietal. The superficialis originates directly from the anterior half of this temporal crest and from the base of the postorbital bone. It passes posteriorly and downward, partially overlying the adductor mandi-

Figure 3. Lateral view of head showing progressively more structures (A–D) in place.

Abbreviations:

am	M. adductor mandibulae externus medialis, deep (d) and superficial (s) divisions
ap	M. adductor mandibulae externus profundus
apo	M. adductor mandibulae posterior, lateral division (1), medial division (m), pars minimus (mi)
as	M. adductor mandibulae externus superficialis
c	columella
ct	craniocervical nerve trunk (IX, X, XII)
ec	ectopterygoid
f	frontal
Hd	Harderian gland
if	infralabial nerve foramen (posterior)
ilc	M. iliocostalis
ld	M. longissimus dorsi
lp	M. levator pterygoidei
mf	mental foramen
mx	maxilla
n	nasal
pf	prefrontal
pg	M. pterygoideus
pga	M. pterygoideus accessorius
po	postorbital
pp	M. protractor pterygoidei
pq	M. protractor quadrati
pst	M. pseudotemporalis
q	quadrate
rcv	M. rectus capitus anterior, pars ventralis
ssp	M. spinalis-semispinalis
st	supratemporal
tc	temporal crest
V_2	Trigeminal nerve, maxillary division
V_3	Trigeminal nerve, mandibular division
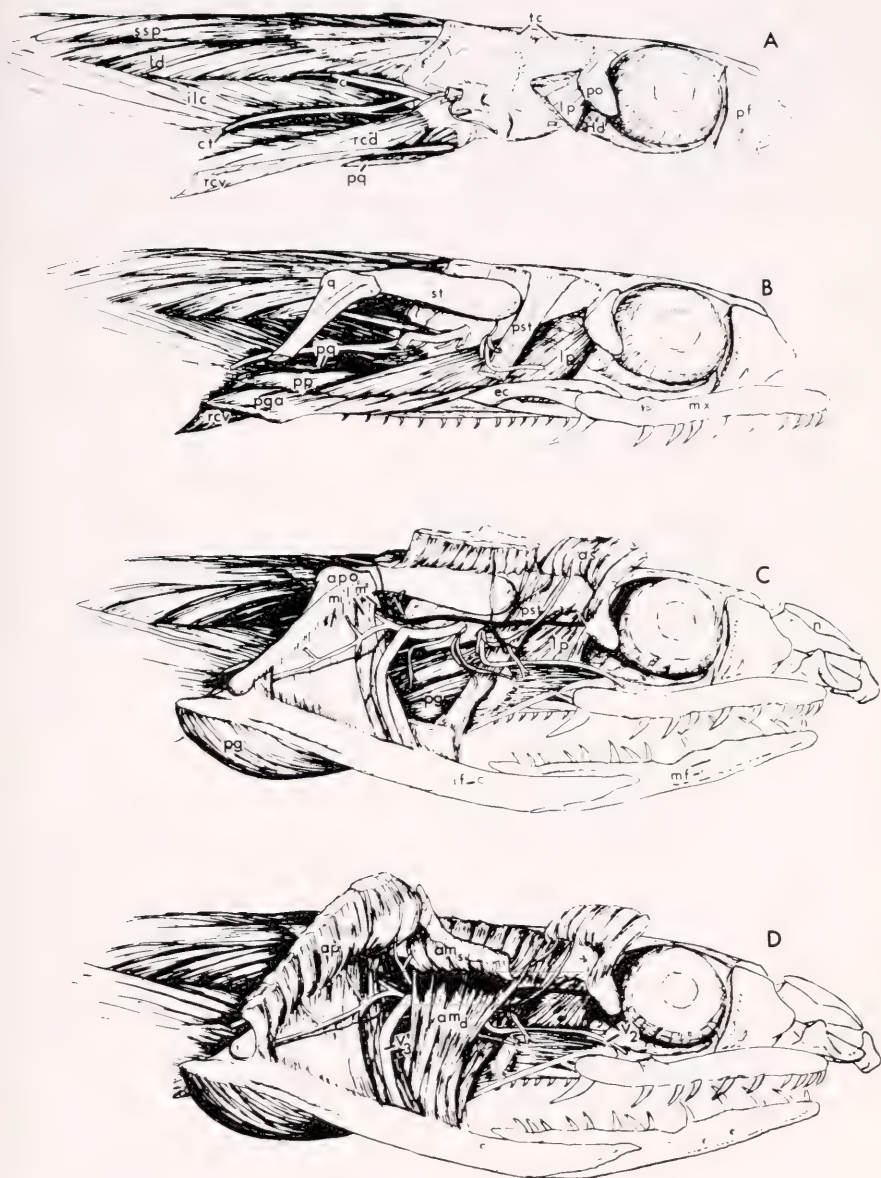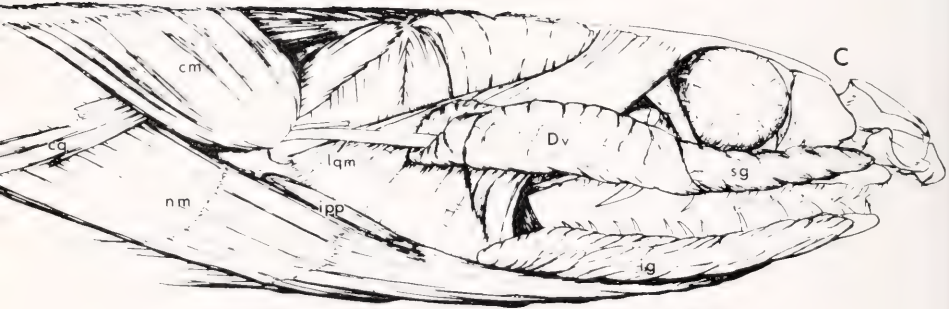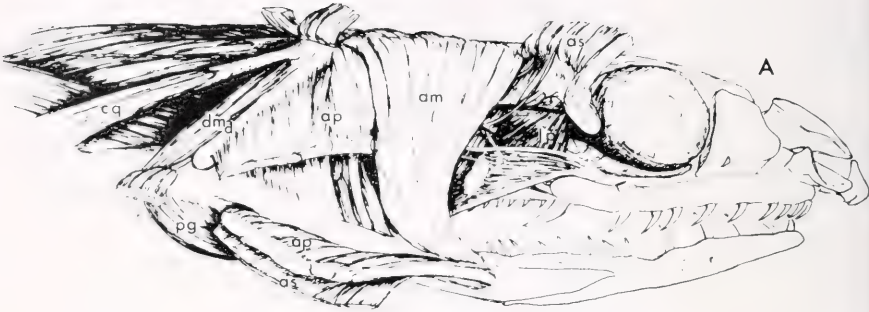
bulae externus medialis. Its anterior fibers arch around the corner of the mouth without forming any attachments to the buccal membrane and pass to the mandible, where they directly insert on the compound bone just posterior to the end of the dentary tooth row and lateral to the anterior insertion of the adductor mandibulae externus profundus. The remaining fibers of this flat muscle terminate superficial to the profundus in a broad aponeurosis that spreads across the surface epimysium of the profundus and can be followed to an insertion extending in a narrow line from the lateral epicondyle of the quadrate along the mandible, ventral to the insertion of the profundus, and forward to a point not quite reaching the directly inserting anterior fibers described above.

M. adductor mandibulae externus profundus (ap)
Figs. 1, 3 c–d, 4 a–c

This is a large, triangular block of muscle divisible into two muscle wedges that separate cleanly along a vertical cleft between them. The anterior wedge takes origin from the lateral, anterodorsal corner of the quadrate. The origin of the posterior wedge also begins on this corner of the quadrate beneath the attachment of the anterior wedge. However, the origin of the posterior wedge extends

Figure 4.   Lateral view of skull showing progressively (A–C) more structures in place.

Abbreviations:

am	M. adductor mandibulae externus medialis
ap	M. adductor mandibulae externus profundus
as	M. adductor mandibulae externus superficialis
cm	M. cervicomandibularis
cq	M. cervicoquadratus
dm	M. depressor mandibulae, deep division (d), superficial division (s)
Dv	Duvernoy's gland
Hg	Harderian gland
ig	infralabial gland
ipp	M. intermandibularis posterior, pars posterior
lmp	ligmentum maxillo-postorbitale
lp	M. levator pterygoidei
lqm	ligamentum quadrato-maxillare
nm	M. neuromandibularis
pg	M. pterygoideus
sg	supralabial gland

distally along the anterolateral edge of the quadrate reaching the lateral epicondyle. Both parts form a large, thick muscle that inserts directly on the lateral side of the compound bone in a low depression from below the quadrato-mandibular articulation forward to the posterior infralabial nerve foramen.

M. adductor mandibulae externus medialis (am)
Figs. 1, 3 c–d, 4 a–c

This muscle takes origin from the parieto-supratemporal ligament and the posterior half of the temporal crest, filling a depression and area adjacent to the crest. As the muscle passes ventrally its fibers gather into two divisions—superficial and deep. Dorsally a few fibers intermingle between both but as they pass downward they become more discrete. The deep division takes origin along the posterior temporal crest only. This division descends as a wide, thin sheet that inserts directly to the compound bone medial to the adductor mandibulae posterior. This insertion then extends forward and upward to the dorsal edge of the compound bone reaching a point posterior to the end of the dentary tooth row. The superficial division contains most of the fibers of this muscle and originates from both the posterior temporal crest and the parieto-supratemporal ligament. It narrows and gives rise to a short tendon that inserts on the dorsal, posterior end of the dentary.

M. adductor mandibulae posterior (apo)
Figs. 1, 3 c–d

This muscle, composed of parallel fibers, is triangular in shape and concealed beneath the adductor mandibulae externus profundus. It passes to both sides of the prearticular crest and so is divided naturally into two major parts—lateral and medial. In addition, a distinctive broad, flat muscle sheet forms the most lateral division, here referred to as the pars minimus.

The pars minimus takes origin at the base of the proximal end of the quadrate and then extends along its entire anterior, lateral edge to a point above the lateral condyle. It inserts along the dorsal edge of the surangular crest forward to a point just posterior to the adjacent mandibular nerve. The lateral division of the muscle takes origin along the anteromedial length of the quadrate. Its parallel fibers pass ventrally and forward to insert directly on the floor of the mandibular fossa and lateral side of the prearticular crest.

The medial division of this muscle takes origin along the medial side of the quadrate but more posterior in position than the lateral division. A few central fibers arise from a small, short, common tendon, but most are parallel and all collectively form a sheet that passes in an anteroventral direction eventually inserting directly on the dorsal edge of the prearticular crest and along a low depression on its medial face. The anterior part of this insertion passes lateral to the posterior insertion of the deep division of adductor mandibulae externus medialis.

M. pseudotemporalis (pst)
Figs. 1, 3 b–d

This muscle arises beneath the anterior part of the adductor mandibulae externus medialis and the posterior part of the adductor mandibulae externus superficialis along the mid-temporal crest. It is a ribbon-like muscle of parallel fibers that courses ventrally, passing deep to the maxillary division of the trigeminal (V) nerve, the facial carotid artery, and jugular vein. It attaches directly to the compound bone medial and slightly anterior to the front of the deep division of the adductor mandibulae externus medialis.

M. pterygoideus (pg)
Figs. 1, 2, 3 c–d, 4 a–b, 5 a–b

The pterygoideus takes origin from the lateral maxillary process of the ectopterygoid, primarily by a prominent tendon. The tendon remains superficial and passes ventrally reaching the middle of the muscle. Most muscle fibers arise along the length of this prominent tendon although a few directly arise from a small area on the ectopterygoid immediately medial to the origin of this tendon. The fibers sweep backward forming, on approach to the insertion, the swollen belly of the muscle that projects below the compound bone. The fibers curve upward to insert on the ventral surface of the mandibular retroarticular process. Specifically, this insertion includes the ventroposterior surface of the retroarticular process and extends a short distance forward along the ventrolateral edge of the process to a point even with the articular notch.

There are two further noteworthy anatomical features of this muscle. First, along its anterolateral surface the epimysium is drawn up into a loose fascial connection that joins it with the anterior edge

of the nearby adductor mandibulae externus medialis. Second, fibers composing the anterodorsal part of the muscle form a separate fascicle. Though anatomically an integral part of the pterygoideus, these fibers insert, via a wide aponeurosis, on the ventrolateral edge of the retroarticular process. Most fibers of this slip arise directly from the prominent ventral tendon near its anterior end, but a few arise directly from the lateral maxillary process of the ectopterygoid medial to this tendon.

M. pterygoideus accessorius (pga)
Figs. 1, 2, 3b

This muscle arises directly from the ventral surface of the pterygoid and base of the ectopterygoid. Specifically, this origin includes the ventral surface of the lateral projection of the pterygoid, its lateroventral groove, and lateroposterior base of the ectopterygoid.

The muscle passes backward to insert on the inner side of the retroarticular process along its medial curvature, parallel with but medial to the insertion of the pterygoideus.

M. protractor quadrati (pq)
Figs. 2, 3 a–b

This muscle arises from a tendon, shared with its contralateral partner, that originates from the midventral basioccipital. It is a flat muscle, passing horizontally in a posterolateral direction over the dorsal surface of the protractor pterygoidei. A few fibers insert on the medial epicondyle of the quadrate, but most insert directly to the dorsomedial side of the mandibular retroarticular process, dorsal to the origin of the pterygoideus accessorius.

M. protractor pterygoidei (pp)
Figs. 1, 2, 3b

This muscle takes origin from the basisphenoid, specifically from a mid-transverse ridge, and forward parasagittally along the basisphenoid to a point just past the anterior Vidian foramen. It passes posteriorly, becoming fusiform in shape, and inserts across the posterodorsal end of the pterygoid with an especially firm attachment to the caudal tip of the bone.

M. levator pterygoidei (lp)
Figs. 1, 2, 3 a–d, 4a

A low depression in the posterior, ventral face of the postorbital process of the parietal serves as the surface from which this muscle takes origin. It passes ventrally, widening along an anteroposterior axis to form a long insertion on the pterygoid. This insertion begins posteriorly on the dorsolateral side of the pterygoid, runs forward to the ectopterygoid-pterygoid articulation, across the base of the ectopterygoid, and ends on the adjacent outer side of the pterygoid short of the pterygo-palatine articulation. The insertion thus lies along the shaft of this bone occupying the dorsolateral fossa.

M. retractor pterygoidei (rp)
Fig. 2

This muscle arises directly from the anterior slope of the transverse ridge on the basisphenoid, adjacent to the origin of the protractor pterygoidei. It passes forward to insert directly on the anterodorsal surface of the pterygoid and posterodorsal surface of the palatine, and by a broad aponeurosis to the posterior edge of the choanal process of the palatine.

M. retractor vomeris (rv)
Fig. 2

This muscle arises from the sphenoid, lateral to the anterior end of the origin of the protractor pterygoidei. It passes forward as a spindle-like muscle bounded laterally by the retractor pterygoidei. Anteriorly, its fibers converge into a slender cord-like tendon that accounts for half the total muscle length. This tendon inserts on posterodorsal corner of the vomer.

Throat Musculature

M. neuromandibularis (nm)
Figs. 1, 4c, 5 a–b, 6b

Beginning in the neck, this broad, flat muscle sweeps downward and forward around the side of the body, passing under the cervico-quadratus and over the axial musculature, to insert at several sites
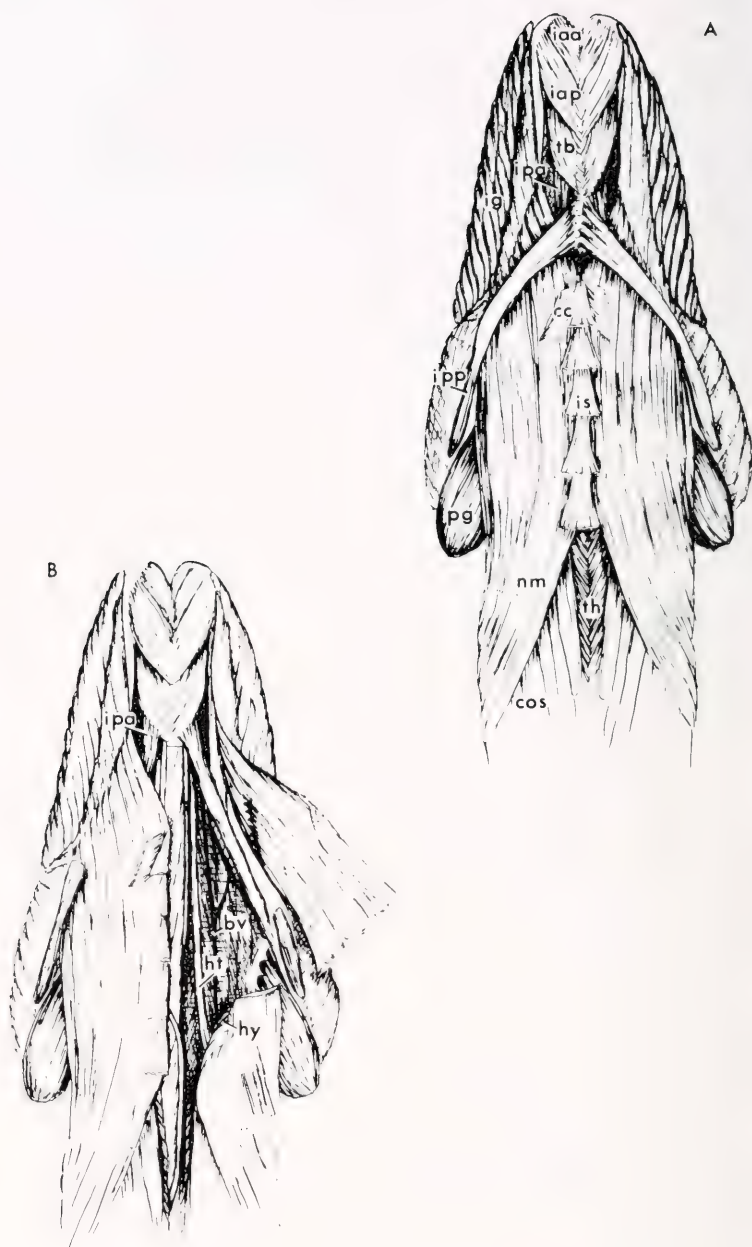
along the mandible via aponeuroses. It has been variously treated by other authors, some dividing it into several parts (Langebartel, 1968; Kardong, 1973; Haas, 1973) while others include it as part of a composite muscle (Albright and Nelson, 1959; Cundall, 1974). For descriptive purposes, it is here treated as a single unit. It originates from the epimysium of the spinalis-semispinalis muscles adjacent to neural spines 6–11. The anterior part of this origin lies under the posterior part of the cervicomandibularis. As it passes into the throat, it is crossed by two inscriptions. A separate muscle, the costomandibularis arises by three separate slips from the ventrolateral tips and costal cartilages of ribs 2–4. From here the costomandibularis passes forward to join and most fibers terminate on the medial face of neuromandibularis along the posterior inscription. Farther anteriorly, the neuromandibularis is joined by a few additional fibers originating from the lingual process and anterior end of the ceratobranchial of the hyoid; these fibers contribute to the medial border of the muscle.

Insertion on the mandible is by a broad aponeurosis, but along three specific sites. One site of insertion, via an aponeurosis, is along the ventral edge of the angular and posteroventral edge of the splenial. A second insertion, also via an aponeurosis, begins along the posterolateral edge of the dentary where it articulates with the com-

Figure 5.   Ventral view of throat musculature. At bottom (B), a section of each intermandibularis posterior, pars posterior (ipp) has been removed. The left neuromandibularis (nm) has been cut and reflected to expose the underlying structures, including a prominent blood vessel (bv).

Abbreviations:

cc	M. constrictor colli
cos	M. costomandibularis
ht	M. hyotrachealis
hy	hyoid
iaa	M. intermandibularis anterior, pars anterior
iag	M. intermandibularis anterior, pars glandularis
iap	M. intermandibularis anterior, pars posterior
ig	infralabial gland
is	M. interscutali
ipa	M. intermandibularis posterior, pars anterior
ipp	M. intermandibularis posterior, pars posterior
nm	M. neuromandibularis
tb	M. transversus branchialis
th	M. transversus hyoideus

pound bone. This insertion extends forward along the lateral face of the dentary, passing below the anterior mental foramen and terminates behind the intermandibularis anterior. Thirdly, the epimysium along the superior face of the neuromandibularis forms an aponeurosis that passes dorsal to the origin of intermandibularis posterior, pars anterior to insert adjacent to it on the mandible. This forms a sleeve through which intermandibularis posterior, pars anterior passes from its origin forward toward its insertion (5b, 6b).

M. intermandibularis posterior (ipa, ipp)
Figs. 1, 4c, 5 a–b, 6b

The intermandibularis posterior, pars posterior takes origin beneath the insertions of the adductores mandibulae profundus and superficialis along the ventral surface of the compound bone. It is a strap-like muscle that passes forward superficial to the neuromandibularis to join its contralateral partner in inserting in the dermis at the central midline, just posterior to the origin of transversus branchialis.

The origin of intermandibularis posterior, pars anterior is also along the ventral edge of the mandible, but anterior to the insertion of the pars posterior. Forming into a strap-like muscle, it passes through a sleeve formed by the insertion of the neuromandibularis and then runs medial to the mandibular ramus. It inserts in the posteroventral epimysium of the transversus branchialis.

M. intermandibularis anterior (iaa, iap, iag)
Figs, 1, 5 a–b, 6 a–b

The muscle originates from the anteroventral tip of the dentary as the bone narrows and bends inward. This is lateral to the origins of the genioglossus and geniotrachealis. Though not anatomically separate, two regions of this muscle can be recognized—an anterior region (pars anterior), whose fibers pass inward to insert on the interramal pad, and a posterior region (pars posterior), that also passes inward to insert in dermis with its contralateral partner on a midventral raphé.

Anterior fibers of the intermandibularis anterior, pars glandularis (=constrictor of Langebartel, 1968) are fan-shaped and attach to the lateral edge of the interramal pad. The narrow posterior part of the muscle wraps around the ventral aspect of the lateral sublingual gland and attaches along the posteroventral surface of this gland.

M. transversus branchialis (tb)
Figs. 5 a–b, 6 a–b

This muscle originates from two heads, glandular and mucosal (pars glandularis and pars mucosalis respectively, of Albright and Nelson, 1959). The glandular head arises on the posterior end of the lateral sublingual gland. It passes as a ribbon-like band, arching posteriorly around the more medial genioglossus and geniotrachealis, then ventromedially to form the anterior part of the muscle. It is joined by fibers of the mucosal head arising from the dermis of the buccal epithelium midway between mandible and trachea to form the middle and posterior parts of the muscle. It inserts in the dermis of the chin integument at the ventral midline, between insertions of intermandibulares anterior and posterior.
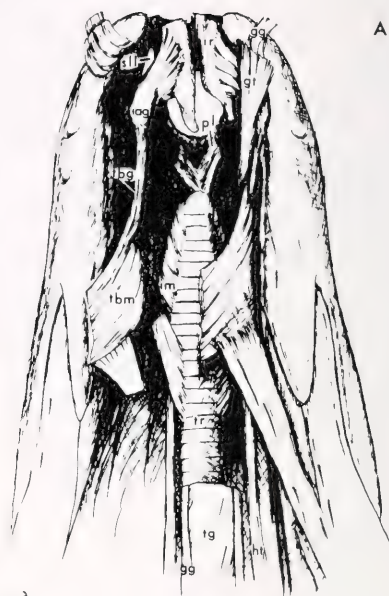
M. genioglossus (gg)
Figs. 1, 6 a–b

Posteriorly this paired muscle is entwined around the tongue. Anteriorly, it originates from two heads. The medial head arises from the posterior tip of the interramal pad, then passes caudally around the lateral face of the medial sublingual gland.

The lateral head receives a few fibers from the dorsal surface of the intermandibularis anterior, but most arise from the anterior tip of the dentary along its inward inflection ventral to the geniotrachealis and dorsal to the intermandibularis anterior. It slants inward as a narrow cord-like muscle to join with the medial head near the middle of the medial sublingual gland. Just posterior to this gland, the muscle passes to the tongue sheath along which it runs caudally. About half way along the tongue, right and left genioglossus muscles change sides. The right muscle passes across the ventral surface to the left side and, at the same point, the left muscle passes across the dorsal surface to the right side. They stay in these reversed positions until reaching their posterior insertions on the hyoglossus, at the point of termination of the tongue sheath.

M. geniotrachealis (gt)
Figs. 1, 5b, 6 a–b

This muscle inserts along the side of the trachea beginning just posterior to the intrinsic laryngeal musculature (Kardong, 1972) spanning 9 cartilaginous rings. It passes forward as a ribbon-like

muscle to its origin along the medial curve of the anterior dentary dorsal to and expanding across a wider area of origin than the genioglossus.

M. hyotrachealis (ht)
Figs. 5b, 6 a–b

This slender, ribbon-like muscle inserts along the side of the trachea dorsal to the anterior origin of geniotrachealis. This insertion begins immediately posterior to the intrinsic largyngeal muscles (*M. dilatator laryngis*) and spans three cartilaginous rings. The muscle

Figure 6.   Ventral view of deep throat musculature. At bottom (B), the left neuromandibularis (nm) and right transversus branchialis (tbm) are reflected. The middorsal surface of the neuromandibularis develops a short attachment to the nearby mandible that forms a sheath-like (sh) channel for the origin of the intermandibularis posterior, pars anterior (ipa). The label for the hyoid (hy) here lies on the lingual process. The intermandibularis anterior (iaa and iap) has been sectioned along its midventral insertion and pulled slightly to one side. At top (A), most of the muscles and infralabial gland have been removed to reveal the course of the transversus branchialis (tbm and tbg), intermandibularis anterior, pars glandularis (iag), and geniotrachialis (gt). The anterior part of the tongue (tg) has been removed to expose the trachea (tr) and a few muscle attachments to it.

Abbreviations:

gg	M. genioglossus
gt	M. geniotrachealis
gt	M. hyotrachealis
hy	hyoid
iaa	M. intermandibularis anterior, pars anterior
iag	M. intermandibularis anterior, pars glandularis
iap	M. intermandibularis anterior, pars posterior
ig	infralabial gland
im	intrinsic musculature of larynx
ipa	M. intermandibularis posterior, pars anterior
ir	inter-ramal pad
nm	M. neuromandibularis
pl	M. protractor laryngeus
sh	sleeve formed by neuromandibularis about origin of intermandibularis posterior, pars anterior
sll	sublingual gland, lateral
slm	sublingual gland, medial
tbg	M. transversus branchialis, glandular head
tbm	M. transversus branchialis, mucosal head
tg	tonguc
tr	trachea

passes posteriorly along the floor of the buccal cavity coursing next to the trachea and reaches its origin on about the middle of the hyoid cornu, which lies, at this point, on the dorsal face of the neuromandibularis.

M. protractor laryngeus (pl)
Fig. 6 a–b

This short, flat muscle takes origin from the posterior tip of the interramal pad and adjacent lateral head of genioglossus. It passes medially, running in the dermis of the buccal integument. Its anterior fibers meet their contralateral partners at the midline posterior to the orifice of the tongue sheath. The posterior fibers insert on the anterior tip of the glottis.

DISCUSSION

Jaw musculature of *Alsophis cantherigerus brooksi* conforms closely to the descriptions of several other colubrids (Albright and Nelson, 1959; Varkey, 1973; Haas, 1973; Cundall, 1974). The internal divisions of the adductor mandibulae externus medialis, adductor mandibulae externus profundus, adductor mandibulae posterior, and depressor mandibulae that were noted are often not included in these earlier papers. This probably does not indicate species difference, but rather differences in investigator emphasis in selecting subtle internal detail of muscle to include in the descriptions. There does, however, seem to be an actual anatomical difference in protractor quadrati. As suggested by the name, this muscle inserts on the quadrate in *Opheodrys* (Cundall, 1974), but here in *A. c. brooksi, Elaphe* (Albright and Nelson, 1959), and *Nerodia* (Varkey, 1973) it inserts on the retroarticular process of the mandible. As in most other colubrids, a definitive *M. levator anguli oris* is absent, but a weakly developed *M. constrictor colli* is present.

In regard to lateral jaw musculature, the subspecies of *Alsophis cantherigerus* are a uniform morphological group (*sensu* Bock, 1963). As in *A. c. brooksi,* the adductor mandibulae externus superficialis arises from the anterior temporal crest and inserts as a broad aponeurosis on the lateral side of the mandible. A slip of fibers

persists at the anterior edge of the muscle, continues around the corner of the mouth, and inserts directly to the mandible. The only exception is found in *A. c. adspersus* where this muscle inserts not on the mandible but to the epimysium of the adductor mandibulae externus profundus. However, this condition occurs only on the right side, the left being like other subspecies, and thus likely represents an individual, rather than a subspecific difference.

In all subspecies, the triangular adductor mandibulae externus profundus consists of anterior and posterior wedges of muscle separated by a vertical cleft that is often tendinous and forms a site of origin for some fibers. Similarly in all, the adductor mandibulae externus medialis is separable into superficial and deep divisions, each with different sites of insertion. The adductor mandibulae posterior always possesses three parts—two major parts, lateral and medial, that pass to the respective sides of the prearticular crest and a third part, the pars minimus. In all, the protractor quadrati arises from a tendon shared with its partner and inserts along the medial retroarticular process. The general attachments of the depressor mandibulae are similar in all subspecies, and the muscle is divisible into superficial and deep portions divided by the insertion of the cervicoquadratus. However, the deeper part tends to split lengthwise in *fuscicauda, pepei,* and *ruttyi* into two parallel divisions, one arising from the posterior corner of the quadrate, the other from here and from the posterior end of the supratemporal. Both, however join to insert directly on the retroarticular process.

In none of the subspecies examined did the lateral jaw musculature differ fundamentally as to specific bones involved in the attachment sites. The observation that the only differences are in the nature of internal muscle anatomy again emphasizes the uniform nature of these island subspecies.

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